The neurochemical correlate of consciousness: exploring neurotransmitter systems underlying conscious vision
van Loon, A.M.

Citation for published version (APA):
van Loon, A. M. (2014). The neurochemical correlate of consciousness: exploring neurotransmitter systems underlying conscious vision

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
Chapter 7. The role of recognition in shaping neural category representations in lateral occipital complex

Our visual system efficiently transforms sensory input into distinguishable object representations. The lateral occipital complex (LOC) is the brain area that it crucially involved in this process. Previous research using fMRI demonstrated that category information such as the animate / inanimate distinction could be decoded using representational dissimilarity matrices (RDM) (Kriegeskorte, et al., 2008). We investigated with RDM whether behavioral recognition was required to shape the spatial patterns of fMRI activation into distinguishable categories in the LOC. We used Mooney images depicting two categories - animate (animals) and inanimate (vehicles). The Mooney images were presented in two phases: before and after the presentation of a greyscale photo version of the same images, which ensured recognition for the second presentation of the Mooney images. Our results demonstrate that recognition was not required for the animate / inanimate categorization in the LOC, since this categorization was already apparent during the first Mooney phase. Recognition did however increase the animate / inanimate categorization responses in the LOC for the second Mooney phase. Basic-level categorization (e.g. fish vs. cat) was only apparent for the greyscale images. We speculate whether low-level images statistics between the two categories may explain some of our results. The findings suggest that animate / inanimate category selective responses in the LOC can arise based on the physical properties of the images independent of recognition whereas perceptual or object basic-level categorization responses in the LOC do require recognition.

Introduction

Recognizing and categorizing objects is one of the most important abilities of the human visual system. Using multi-voxel pattern analysis (MVPA) it is possible to decode category-specific information of objects based on their neural representations (Haxby, et al., 2001; Kriegeskorte, et al., 2008). Interestingly, object category information can also be decoded for unattended stimuli (Peelen, Fei-Fei, & Kastner, 2009), invisible stimuli (Fahrenfort, et al., 2012) and even in anesthetized monkeys (Ku, et al., 2011). During anesthesia and when stimuli are made invisible by masking, forward or bottom-up activation of visual pathways and higher level areas is still intact whereas feedback or top-down activity is reduced (Lamme, et al., 1998; van Loon, et al., 2012). This suggests that purely bottom-up feedforward activation could already induce category-selective responses (Serre, Oliva, & Poggio, 2007). However, top-down facilitation has been shown to be important for object recognition (e.g. basic-level identification) (Bar, et al., 2006; Bar, et al., 2001), as object recognition altered the neural activity (Grill-Spector, Kourtzi, & Kanwisher, 2001) and neural spatial patterns in the lateral occipital complex (Grill-Spector, et al., 2001; Hsiez, et al., 2010).

Hence, these results suggest that neural category representations might be shaped by bottom-up input, whereas object recognition or identification does require top-down information. In order to elucidate this we investigated the effect of recognition on shaping neural category representations in the lateral occipital complex (LOC). The LOC is a functionally defined set of regions in the lateral occipital and inferior temporal cortex (IT) that responds more strongly to images of intact than scrambled objects (Malach et al., 1995). It has been suggested to be crucially involved in object recognition (Malach et al., 1995; Grill-Spector, 2003). A previous study demonstrated that neural responses in IT are particularly strongly distinguishing between animate and inanimate categories (Kriegeskorte, et al., 2008). We therefore studied the role of recognition in the formation of neural representations of animals (animate images) and vehicles (inanimate images). Of each category we presented three basic-level categories: cat, fish, bird and airplane, bicycle, boat. Next, we manipulated object recognition by converting the images in two-tone Mooney images (Mooney, 1957; Moore & Cavanagh, 1998). Mooney images are hard to recognize when never seen before, yet are easily recognized after a greyscale version of it has been shown. They therefore give the opportunity to isolate the perceived identity or category of the object from its bottom-up input by comparing the response before and after recognition. We presented each ambiguous Mooney image twice: before and after presenting unambiguous a greyscale photo version of the same image, which induced a substantial difference in recognition of the Mooney images between the first and second presentation. We used representation dissimilarity matrices (RDM) to assess the animate / inanimate category and basic-level category responses in the LOC, and the effect of recognition. An RDM is a simple method to visualize the differences between the neural representations of categories based on their multi-voxel pattern of activation (Kriegeskorte, et al., 2008).

As a post-hoc analysis, we wanted to assess whether the animate / inanimate distinction was potentially driven by low-level physical properties of the images. We used a biologically realistic model (Scholte, Ghebreab, Waldorp, Smeulders, &
Lamme, 2009) to compute a set of low-level image statistics for each Mooney image. This model simulates the pooled responses from two types of low-level contrast-sensitive cells in the LGN. Previous work has shown that this model predicts category similarity in evoked EEG responses (Groen, Ghebreab, Lamme, & Scholte, 2012), in particular the distinction between man-made and natural scenes (Groen, Ghebreab, Prins, Lamme, & Scholte, 2013).

**Methods**

**Participants**

Twenty participants (11 males, $M = 23.25$ years of age, $SD = 1.07$ years) participated in the study. We obtained written informed consent from each participant before experimentation. Participants had normal or corrected-to-normal vision. The experiment was approved by the Medical Ethical Committee of the Academic Medical Center of Amsterdam. Five participants were excluded due to head motion (> 1mm) and technical failures. All analyses are based on the remaining fifteen participants (7 males, $M = 23.24$ years of age, $SD = 1.20$ years).

**Stimuli**

The stimuli consisted of photo images containing either an animal or a vehicle. We used 24 images in total, divided over two sessions. Each set consisted of two main categories (animate / inanimate) containing three basic-level categories: bird, cat, fish (animate), and airplane, bicycle, boat (inanimate). Each basic-level category had two exemplars. All images were cropped to 300 x 300 pixels and converted to both greyscale images and two-tone Mooney images (Mooney, 1957; Moore & Cavanagh, 1998) using GIMP (v 2.8, www.gimp.org): images were thresholded, all light colors were translated to white, all dark colors were translated to black. As a result we had for each photo a Mooney version, for which it is difficult to identify what is depicted on the image at the first presentation, and the greyscale version, for which it is easy to identify the object. Selection of the final images was based on a separate experiment in which we tested whether the Mooney images were not recognized at first presentation but were recognized after the experimental procedure.

**Ketamine**

This experiment was part of a larger study investigating the effect of a subanesthetic dose of S-Ketamine, which is a non-competitive N-methyl-D-aspartate (NMDA) receptor antagonist, on visual awareness (see Chapter 5 and 6). However, we did not observe any effect of ketamine on our neural results in LOC, therefore we averaged the data from the placebo and ketamine condition. Behaviorally we only observed in the fMRI categorization task that ketamine slightly reduced categorization performance in the Mooney II condition as compared to placebo ($t_{(14)} = 2.145, p = .050$) (see Chapter 6).

**Experimental Procedure**

To assess whether the Mooney images were difficult to identify at first presentation, we presented each Mooney image once for 180 ms on the center of a computer screen. After each presentation, participants were instructed to write down what was depicted on the image (referred to as Mooney identification task).
**Figure 7.1. Experimental design**

(A) Run design of the fMRI categorization task. (B) Lateral occipital complex (LOC). (C) Example Representational Dissimilarity Matrix (RDM). The images on top of the RDM depict the stimuli from one of the two sessions. The basic-level categories are (from left to right): birds, cats and fish (animate) and airplanes, bicycles and boats (inanimate), two each. Shown is a theoretical RDM that would be obtained if animate / inanimate categories would be strongly distinguished, and basic-level categories more weakly distinguished in the neural patterns of activation, where blue indicates stimuli being similar and red dissimilar.

A Viewsonic LCD screen was used with a refresh rate of 60 Hz (40 x 26° of visual angle) and stimuli were presented with Presentation (Neurobehavioral Systems, Albany, CA, USA). After this task, an anesthesiologist administered the drug (placebo or a subanesthetic dose of S-Ketamine) intravenously. Fifteen minutes after drug administration participants were led to the MRI-scanner in which they participated in the fMRI categorization task (described below). This was followed by a resting state scan of 10 minutes. After the fMRI scanning participants performed three behavioral tasks that are beyond the scope of this study (see Chapter 5). After this, drug-administration was ended. To assess whether the Mooney images were indeed recognizable after the fMRI categorization task, participants again performed the Mooney identification task at the end of the session.

In a separate session, one week prior to the to start of the experiment, participants performed region of interest (ROI) localizer tasks in the scanner and were informed about the procedure of the experiment.

**fMRI Categorization Task**
This task consisted of three different fMRI recognition phases: 1) Mooney I: presentation of the Mooney images. 2) Greyscale: presentation of the easily identifiable greyscale photographic versions of the same images and 3) Mooney II:
presentation of the same Mooney images as in the Mooney I phase. To ensure that the Mooney images were recognizable in the third phase (Mooney II), we presented both the greyscale and the corresponding Mooney image simultaneously side by side after the Greyscale phase (Paired). Each pair was presented for 4 sec, and was presented twice. Participants were instructed to memorize the association between the two images (see Figure 7.1A for overview).

Every phase (Mooney I, Greyscale, and Mooney II) consisted of three runs. The twelve stimuli (either the Mooney images or the greyscale images) were presented for 180 ms and participants indicated within 1500 ms whether the stimulus depicted an animate or inanimate category by means of a button press. Response buttons were counterbalanced across participants and sessions. In each run the stimuli were presented four times (48 presentations in total) and were interleaved with null events. Each run started with 10 sec. fixation en ended with 12 sec. fixation. The trial order was optimized for single-trial BOLD estimation using optsec2, a sequencing program (NMR center, Massachusetts General Hospital, Boston, MA). The stimuli were back-projected on a 61 x 36 cm LCD screen using Presentation (Neurobehavioral Systems, Albany, CA, USA) and viewed through a mirror attached to the head coil. Eye tracking data (EyeLink 1000, SR Research, Canada) were recorded to ensure fixation in each run.

**fMRI Acquisition**

Scanning was done on a 3T Philips Achieva TX MRI scanner with a 32-elements head coil. At the beginning of each session a high-resolution 3DT1-weighted anatomical image (TR 8.175 ms, TE 3.74 ms, FOV, 240 x 220 x 188, 1 mm³ voxel size, 2 averages) was recorded for every participant.

During the fMRI categorization task and LOC mapper, BOLD-MRI was recorded using Echo Planar Imaging (EPI) (TR 2000 ms, TE 27.63 ms, FA 76.1, 37 slices with ascending acquisition, voxel size 3 mm³, slice gap 0.3 mm, FOV 240 x 121 x 240).

**fMRI Analysis**

Anatomical scans were automatically segmented using the Freesurfer package (http://surfer.nmr.mgh.harvard.edu/) (Dale, et al., 1999). BOLD-MRI data was registered to the subject specific T1 scan using boundary based registration (Greve & Fischl, 2009). The subject specific T1 scan was registered to the MNI brain using FMRIB’s Nonlinear Image Registration Tool (FNIRT). For the functional imaging data we used FEAT version 5, part of FSL (Oxford Centre for Functional MRI of the Brain (FMRIB) Software Library; www.fmrib.ox.ac.uk/fsl (Smith, et al., 2004)). Preprocessing steps consisted of motion correction, brain extraction, slice-time correction, alignment, and high-pass filtering (cutoff 100 s). For each subject and each run a general linear model (GLM) was fitted to the data, where every image (4 presentations) was convolved with a standard HRF and taken as a regression variable. The data was further analyzed in Matlab (The MathWorks, Natick, MA, USA). For every participant, we created per region of interest (ROI) a vector containing the t-value per voxel for each stimulus. That vector comprised the spatial pattern of activity evoked by that stimulus. For each run of every recognition phase (Mooney I, Greyscale, Mooney II) we created a representational dissimilarity matrix
(RDM) (Kriegeskorte, et al., 2008). An RDM is a symmetric square matrix and a simple method to visualize the differences between activation patterns of stimuli. Each cell of the matrix represents a 1-r (Pearson correlation) of the activity patterns of two stimuli. The RDM of each run in every recognition phase were averaged to get one RDM per phase. Since every participant performed two sessions (one placebo and one ketamine session) we also averaged the RDM of these two conditions.

**Region of Interest**

The lateral occipital complex (LOC) was mapped using the region in the central occipito-temporal cortex that responded more strongly to intact vs. scrambled objects (Malach, et al., 1995), see Figure 7.1B). Stimuli were presented for 300 ms and consisted of 20 intact and 20 scrambled objects that were presented in separate blocks (16 in total). Participants were asked to push a button when two consecutive images were identical to ensure attention. Participants performed two of these runs.

For this mapper, BOLD-MRI was recorded using Echo Planar Imaging (EPI) (TR 2000 ms, TE 27.63 ms, FA 76.1°, 37 slices with ascending acquisition, voxel size 3 mm\(^3\), slice gap 0.3 mm, FOV 240 x 121 x 240).

The same fMRI acquisition parameters and preprocessing steps as described for the fMRI categorization task, were used for the LOC mapper. We combined the two runs for each subject using a fixed effects analysis (Beckmann, et al., 2003).

**Low-level Image Statistics**

We calculated two low-level image statistics for each Mooney image, namely contrast energy (CE) and spatial coherence (SC). These statistics are derived by means of weighted averaging of simulated output of early contrast-sensitive cells; the model that implements this computation is described in detail in (Groen, et al., 2013; Scholte, et al., 2009). In natural scenes, CE and SC typically correlate highly with parameters of a Weibull function fitted to the distribution of contrast values of the image (Scholte, et al., 2009). CE is a biologically realistic approximation of the distribution mean, whereas SC is an approximation of its shape. These two statistics thus capture information about the overall presence of edges in an image (CE) and higher-order correlations between them (SC). As a result, images with high CE/SC values often contain strong figure-ground segregation (e.g. because of the presence of a coherent object with sharp edges), whereas images with low values are often cluttered or textured. We transformed the CE and SC values for each image into z-scores.

**Independent Mooney Image Set**

We used ImageNet (Deng, et al., 2009) to make a random selection of 100 images for each object basic-level category to create an independent Mooney image set. Initial search using the keyword of the object’s basic-level category (“bird”, “cat”, “fish”, “airplane”, “bicycle”, “boat”) led to between 1000-2000 images per basic-level category. Next, we excluded images if the image contained any added material (such as text or lines), was converted (for example monochrome or sepia filtered), or reshaped by a lens (panorama or fish eye), or when the quality or resolution was low. This selection resulted in 500-1000 images per basic-level category of which we randomly selected 100 images. These images were then resized to 300 x 300 pixels,
and converted to Mooney images. For the resulting 600 Mooney images we calculated the CE and SC values, which we then transformed into z-scores.

**Statistical Analysis**

Behavioral performance and reaction times were compared using a repeated measures ANOVA with as factors recognition phase (Mooney I, Greyscale, Mooney II) and category (animate, inanimate). Only correct trials were included in the reaction time analyses. To compute the effect of categorization (animate vs. inanimate) on neural representations, we subtracted the within dissimilarity (animate / animate and inanimate / inanimate) from the between similarity (animate / inanimate). The effect of basic-level categorization was calculated by subtracting the dissimilarity within a basic-level (for example cat / cat) from the dissimilarities between basic-levels (cat / (bird, fish, airplane, bicycle, boat)). See Figure 7.1C for an illustration. These category-responses (between – within) were tested using one-sample t-tests, a repeated measures ANOVA with recognition phase (Mooney I, Greyscale, Mooney II) as factor, and paired t-tests. To test whether animate and inanimate images differed in their low-level image statistics we performed an independent t-test. Statistical analyses were performed using SPSS 17.0 (IBM, Armonk, USA) and Matlab (The MathWorks, Natick, MA, USA).

**Results**

**Behavioral Results: Mooney identification task**

To assess whether the Mooney images were not recognized initially but recognized following the fMRI categorization task, participants had to identify what was depicted on the Mooney stimuli before and after the fMRI categorization task (see Figure 7.2A).

An answer was regarded as correct if the participant had written down the correct category (animal / vehicle). We observed a significant interaction effect between category and time of assessment ($F_{(1,14)} = 24.39$, $p < .001$). Participants more accurately categorized what was depicted on the Mooney images after they had performed the fMRI categorization task compared to before (main effect of time ($F_{(1,14)} = 147.02$, $p < .001$). Moreover, there was a main effect of category ($F_{(1,14)} = 6.65$, $p = .022$), participants more accurately categorized inanimate images compared to animate images. This main effect was driven by the difference between animate and inanimate before scanning as assessed with paired t-tests (before: $t_{(1,14)} = 3.90$, $p = .002$, after scanning: $t_{(1,14)} = 1.32$, $p = .207$).

**Behavioral results: fMRI categorization task**

Behavioral performance and reaction times (RT) were compared using a repeated measures ANOVA with as two factors recognition phase (Mooney I, Greyscale, Mooney II) and category (animate, inanimate) (see Figure 7.2B). We observed interaction effects between recognition phase and category both for percentage correct: $F_{(2,28)} = 5.95$, $p = .007$ and RT: $F_{(2,28)} = 8.21$, $p = .002$. Categorization between animate and inanimate objects was better and faster after participants had prior experience with the greyscale image (Mooney II) and for the greyscale images themselves as compared to before recognition (Mooney I); main effect of recognition phase (percentage correct: $F_{(2,28)} = 58.46$, $p < .001$ and RT: $F_{(2,28)} = 53.44$, ...
Interestingly, category also influenced performance: participants were better and faster for the inanimate images compared to the animate images (main effects; percentage correct: $F_{(1,14)} = 6.49, p < .023$ and RT: $F_{(2,28)} = 12.74, p = .003$).

**Figure 7.2 Mooney identification task and fMRI categorization task**

(A) Results for the Mooney identification task. Participants categorized more Mooney images correctly after the fMRI categorization task than before. (B) Results of the fMRI categorization task. Categorization between animate and inanimate objects was better (left panel) and faster (right panel) than in the Mooney I phase after participants had prior experience with the greyscale image (Mooney II) and for the greyscale images themselves (Greyscale). Error bars indicate SEs.

**fMRI Results: Animate / inanimate categorization in LOC**

Next, we tested the effect of recognition on animate / inanimate categorization using RDM’s of the activity evoked by these images in the LOC (see Figure 7.3A). Previous studies have demonstrated that spatial patterns in object-related areas are more similar within categories than between categories (Haxby, et al., 2001; Kriegeskorte, et al., 2008). Therefore, to assess the category response, we subtracted the mean dissimilarity for within categories from the mean dissimilarity for between categories (see Methods and Figure 7.1C).

Categorization (between – within) was present in all recognition phases in that dissimilarity was higher between categories than within categories (difference >
0) as assessed with one-sample t-tests (Mooney I: $t_{(1,14)} = 4.19, p = .001$, Greyscale: $t_{(1,14)} = 3.48, p = .004$ and Mooney II: $t_{(1,14)} = 5.14, p < .001$, see Figure 7.3B). However, the category effect seemed specifically driven by the animate pictures (all $t_{(1,14)} > 3.21, ps < .006$) in that the animate images were represented as less dissimilar than the inanimate images (all $t_{(1,14)} < 1.35, ps > .197$), which were equally dissimilar as the between categories (Figure 7.3C).

Therefore, we ran a repeated measures ANOVA including image category (animate, inanimate) and recognition phase (Mooney I, Greyscale, Mooney II) as within-factors. The interaction effect was not significant ($F_{(2,28)} = 2.13, p > .137$), but we did observe a main effect for image category ($F_{(1,14)} = 28.76, p < .001$) and recognition phase ($F_{(2,28)} = 5.12, p = .013$). Next, we assessed the effect of recognition phase on categorization separately for animate and inanimate images using paired t-tests. For the animate images the categorization effect increased with the prior experience of the greyscale images (Mooney II) as compared to not having the experience (Mooney I) ($t_{(1,14)} = 2.48, p = .027$). Surprisingly, categorization in Mooney II was also higher compared to greyscale images ($t_{(1,14)} = 3.28, p = .006$; see Figure 7.3C). No differences between recognition phases were observed for the inanimate images (all $t_{(1,14)} < .65, ps > .524$). Thus, recognition increased the categorization for the animate Mooney images.

A  Representational Dissimilarity Matrices

![RepsMatrices](image)

**Figure 7.3. RDM's and mean animate / inanimate categorization**

(A) RDM per recognition phase (left to right: Mooney I, Mooney II and Greyscale). The color-coding represents the amount of dissimilarity in the LOC-activation patterns, where blue indicates stimuli being similar and red dissimilar. (B) Animate / inanimate categorization: mean dissimilarity for between categories (animate / inanimate) minus within categories (animate / animate and inanimate / inanimate). In all recognition phases mean dissimilarity was higher between categories than within. (C) Categorization separately for animate and inanimate categories. Categorization effect seemed driven specifically by the animate images Prior experience with the greyscale images (Mooney II) did increase the categorization effect as compared to before (Mooney I) but only for animate images not for the inanimate images. Error bars indicate SEs.
fMRI Results: Basic-level categorization in LOC

Next, we wanted to assess whether basic-level categorization (e.g. a cat) depend on recognition. Since we presented two exemplars of each basic-level category we could subtract the within basic-level dissimilarity (cat1 with cat2) from the between basic-level categorization (cat vs. bird, fish, airplane, boat, bicycle) (Figure 7.4A). Basic-level categorization (between – within) was only present for the greyscale images: neural representations were more dissimilar between basic-level categories than within basic-level category as assessed with one-sample t-tests ($t_{(1,14)} = 4.09, p = .001$, see Figure 7.4A). Again, the effect was specific for the animate images ($t_{(1,14)} = 5.36, p < .001$) (Figure 7.4B). Therefore, we ran a repeated measures ANOVA including image category (animate, inanimate) and recognition phase (Mooney I, Greyscale, Mooney II) as within-subject factors. The interaction effect ($F_{(2,28)} = 7.17, p < .003$), as well as the main effect for image category ($F_{(1,14)} = 14.70, p < .002$) were significant. Basic-level categorization of the animate images was significantly higher for the greyscale images than for the Mooney I ($t_{(1,14)} = 3.15, p = .007$) and Mooney II ($t_{(1,14)} = 2.99, p = .010$) phases, as assessed with paired t-tests (Figure 7.4B). This could imply that the neural object representations of the animate greyscale images were more fine-grained since basic-level categorization only occurred for these images.

Figure 7.4. Basic-level categorization

(A) Basic-level categorization only occurred in the Greyscale phase, in that for example the neural representation of a cat image was more similar to that of the other cat image than to the images of other basic-level categories. (B) Basic-level categorization separately for animate and inanimate categories. Basic-level categorization was only present for the Greyscale phase and the categorization seemed driven specifically by the animate images. Error bars indicate SEs.

In sum, these results suggest that recognition shaped the neural representations in LOC. Having prior experience with the greyscale images increased the animate / inanimate categorization for the Mooney images. However, basic-level categorization was only apparent for the greyscale images. Moreover, these effects seem specifically driven by the animate images and were not present for the inanimate images.
**Low-level image statistics**

Recognition thus influenced both behavioral performance and the neural representations in LOC. However, even in the Mooney I phase, before recognition, participants already performed around 85% correct in discriminating between animate and inanimate images and we also observed animate / inanimate categorization effects in the RDM for this phase. We hypothesized that this might be explained by a difference in the physical properties of the animate and inanimate Mooney images: for example, animate images may on average have stronger edges or a different amount of clutter compared to inanimate images. This possible difference could induce a difference in the bottom-up input that they provide to the visual system and thereby induce the animate / inanimate categorization.

*Figure 7.5. Low-level image statistics*

The animate and inanimate Mooney image used in this study differed in their contrast energy (solid lines represent mean and standard deviation (SD)). A random sample based on 600 images (dotted lines represent mean and SD), showed very similar pattern.

In order to assess this possibility, we calculated for each Mooney image the contrast energy (CE) and spatial coherence (SC) statistics (see Methods). As can be seen in Figure 7.5 (solid line), animate and inanimate Mooney images indeed differ in their physical low-level image statistics, more specifically in their contrast energy ($t_{(2,22)} = 2.16, p = .041$) not in spatial coherence ($t_{(2,22)} = 0.74, p = .465$). This difference in contrast energy between the animate and inanimate images might explain the category-selective responses in the neural representations of the Mooney I phase. To ascertain that the images used in this sample were a representative sample for each basic-level category, we randomly selected 100 images for each basic-level category and created an independent Mooney image set (see Methods). As can be seen in Figure 7.5 (dotted lines), our sample seemed representative since the location of the mean and standard deviation in the low-level image statistics space appeared very similar.
Discussion

We investigated the effect of recognition on the neural representations of object categories in LOC. Independent of recognition, we observed that neural responses differed between the animate / inanimate categories in that within category representations were more similar as between category representations. This suggests that categorical differences in neural activity patterns do not require recognition. However, recognition did increase the animate / inanimate categorization of the Mooney images. Only for the greyscale images we observed basic-level categorization, i.e. larger similarity for within basic-level representations (e.g. cat1 vs. cat 2) than for between basic level category representations (e.g. cat vs. fish). The effects were mainly driven by the animate images and not by the inanimate images. Moreover, low-level images statics might have given rise to the observed animate / inanimate category differences during the first Mooney presentations since the animate and inanimate images differed in their contrast energy.

Taken together, our results seem in line with the suggestion that categorization can occur in a purely feedforward manner (Serre, et al., 2007), especially for animate / inanimate discrimination (Thorpe, Fize, & Marlot, 1996) and naturalness (Greene & Oliva, 2009). Additionally, theories of visual processing propose that a global impression of the scene precedes (Hochstein & Ahissar, 2002) or accompanies (Rousselet, Joubert, & Fabre-Thorpe, 2005; Wolfe, Võ, Evans, & Greene, 2011) detailed feature extraction (“coarse-to-fine” processing) (Hegdé, 2008). Categorizing animate and inanimate images could therefore occur on the basis of a global percept often described as visual gist (Oliva & Torralba, 2006; Torralba & Oliva, 2003). Interestingly, our low-level image statistics have been associated with visual gist (Groen, et al., 2013). Therefore, decoding category information independent of attention (Peelen, et al., 2009) or awareness (Fahrenfort, et al., 2012, Ku, et al. 2011) might even be explained by a difference in low-level image statistics or physical properties of the stimuli and thus by a difference in visual input that they provide to the visual system. This visual input reflects more the physical similarities “these images both contain higher contrast energy” instead of reflecting the object or categorical similarity between images, “these images are both animals”. The latter might require recognition of the image. Indeed, we did observe increased object category responses for the Mooney images after the prior experience with the greyscale images. This could imply that when prior knowledge about the object becomes available, this information is used to adjust neural representations towards their perceptual rather than physical properties, giving rise to category representations that are less tied to physical similarities of the images.

Interestingly, in line with this suggestion, other studies have shown that representations in LOC reflect both physical and perceptual similarities. For example, when presenting artificial stimuli it was found that neural representations in different parts of LOC reflect either the physical similarity or the perceptual similarity of these stimuli (Haushofer, Livingstone, & Kanwisher, 2008). Related to that, objects that were rated as having a very similar shape induced very similar response patterns, whereas objects rated as having very different shapes evoked more different response patterns (Op de Beeck, Torfs, & Wagemans, 2008). Moreover,
LOC contains information that distinguishes between natural scene categories and these representations overlap with the natural scene categorization by humans (Walther, Caddigan, Fei-Fei, & Beck, 2009). Interestingly, the low-level image statistics that we used to assess physical similarity were shown to be predictive for both neural and perceptual similarity in naturalistic image categories (Groen, et al., 2012). Further research could elucidate the role of recognition and low-level image statistics in shaping neural object category representations, for example by matching different object categories on physical similarity, or the other way around by presenting objects with the same object identity but with different physical properties.

Additionally, we observed basic-level categorization only for the greyscale images. Interestingly, object representations in LOC can be decoded both at the level of object category as well as object identity (Cichy, Chen, & Haynes, 2011). Basic-level object recognition (Bar, et al., 2006) and becoming aware of an object does require top-down processing (Ahissar & Hochstein, 2004; Dehaene, et al., 2006; Hochstein & Ahissar, 2002; Lamme, 2006). More specifically, the functional connectivity between the LOC and dorsolateral prefrontal cortex increases when the object depicted in a Mooney image is identified (Imamoglu, et al., 2012). Furthermore, it seems that initially, low spatial frequency components are processed all the way to orbito-frontal cortex, which then sends information to object related areas to facilitate object recognition (Bar, et al., 2006). Thus, more fine-grained object basic-level categorization could require recognition-related top-down processing.

However, disambiguation of the Mooney images only induced an increase in the animate / inanimate categorization and resulted not into the more fine-grained basic-level categorization as observed for the greyscale images. A possible explanation might be that when prior knowledge about the image becomes available, this information is used to adjust neural representations towards the task at hand (animate / inanimate categorization) rather than object identification based on its basic-level. Indeed, improvement in the sensitivity of LOC for object form seemed task-dependent (MacEvoy, 2013) and task demands determine how concept meaning is processed (Taylor, Devereux, Acres, Randall, & Tyler, 2012). More general, cortical representations of object category are continuously modulated by experience (Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006). Further research should investigate the influence of task-demand on object category representations.

Our results were mainly driven by the animate images. Animals are considered to be a special category that are processed very rapidly (Thorpe, et al., 1996). This is further supported by a study showing that auditory presentation of animal names elicit greater activity than nonliving stimuli in the lateral fusiform area, even in blind patients (Mahon, Anzellotti, Schwarzbach, Zampini, & Caramazza, 2009). Therefore it could be that in comparing animals with vehicles we look at rather different neural systems. In our data, we observe that animate images are represented as more similar whereas inanimate images are represented as more dissimilar from each other (see Figure 7.3A, where there animate section of the RDM is more blue than the inanimate section which is more red). The animals thus form a more homogenous group (which could be the reason why they drive the category distinction between animals and non-animals, Figure 7.3C). Indeed, animals have
many shared features with other animals (Tyler, et al., 2013), whereas nonliving things have more distinctive features (Randall, Moss, Rodd, Greer, & Tyler, 2004; Taylor, Salamoura, Randall, Moss, & Tyler, 2008), which may in turn be reflected in a difference in feature statistics such as co-occurrence or distinctiveness of features between animate and inanimate categories. Further research using object categories that are better matched on shape and feature statistics is necessary (Cichy, et al., 2011; Clarke & Tyler, 2014; Haushofer, et al., 2008; Op de Beeck, et al., 2008).

We should also consider a possible role for visual attention. For example, with an unrecognizable Mooney image, attention is presumably uniformly distributed. In a recognizable image, such as the greyscale image or Mooney image after it has been disambiguated, spatial attention could be spatially directed at important parts of the image. Attention has been reported to sharpen the selectivity of responses in LOC (Murray and Wojciulik, 2004). The Mooney images used in the current study were natural images, containing multiple objects that were converted to a black and white contrast. Previous research has indicated that spatial pattern of fMRI responses about standard object categories is enhanced by attention when multiple objects are present simultaneously (Reddy and Kanwisher, 2007). Moreover, contrast invariance in LOC depends on attention (Murray and He, 2006). Further studies parametrically manipulating the state of attention will be required to assess how attention and recognition shape neural object representations.

In sum, our results suggest that when images are unrecognizable, categorization can still occur based on the bottom-up physical dissimilarities between these images. With recognition, perceptual basic-level object categorization arises, using top-down and experience dependent processing.