The Nature of the Animacy Organization in Human Ventral Temporal Cortex

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Abstract:

The principles underlying the animacy organization of the ventral temporal cortex (VTC) remain hotly debated, with recent evidence pointing to an animacy continuum rather than a dichotomy. What drives this continuum? According to the visual categorization hypothesis, the continuum reflects the degree to which animals contain animate-diagnostic features. By contrast, the agency hypothesis posits that the continuum reflects the degree to which animals are perceived as social agents. Here, we tested both hypotheses with a stimulus set in which visual categorizability and agency were dissociated based on representations in convolutional neural networks and behavioral experiments. Using fMRI, we found that visual categorizability and agency explained independent components of the animacy continuum in VTC. Modeled together, they fully explained the animacy continuum. Further analyses revealed that the clusters explained by visual categorizability were localized posterior to the clusters explained by agency. These results provide evidence for multiple animacy continua in VTC that follow different organizational principles.

Keywords: object categorization; category selectivity; fMRI; ventral stream; animacy

Introduction

Decades of human neuroimaging and monkey electrophysiology studies have provided convincing evidence that object representations in the ventral temporal cortex (VTC) show a categorical organization. Most prominent in this organization is the division between animate and inanimate objects (Grill-Spector & Weiner, 2014). The principles underlying this animacy organization remain hotly debated.

One possibility is that the animacy organization reflects evolutionary pressures to rapidly detect the presence of animals (e.g., as potential mates or predators). This *visual categorization* demand may then have resulted in the grouping of visual feature representations that are diagnostic of animals to support fast read-out by downstream decision-related brain regions (Grill-Spector & Weiner, 2014).

However, recent research has shown that the animacy organization in the ventral stream is a continuum rather than a dichotomy: lower animals like insects and reptiles are lower on this continuum than mammals and humans (Sha et al., 2015). This evidence was interpreted as reflecting the graded psychological property of *agency* rather than visual categorization demands.

Here, combining convolutional neural networks (CNNs), behavioral experiments, and fMRI, we show that visual categorization demands and agency each explain independent components of the animacy organization in VTC. Modeled together, they fully explained the animacy continuum in VTC. Finally, the two organizing principles were localized in different parts of VTC, with visual categorization (i.e., the presence of animate-diagnostic features) driving the organization in posterior VTC and agency driving the organization in anterior VTC.

Methods

Stimuli

To create a stimulus set in which visual categorizability and agency are dissociated, we selected 12 animals from a total of 40 animals. Visual categorizability was quantified in two ways, using CNNs and human behavior. Agency was measured using a rating experiment in which participants indicated the degree to which an animal can think and feel (Fig. 1A). For a detailed description of the materials and methods, see Thorat, Proklova, & Peelen (2019).

The first measure of visual categorizability was based on the features extracted from the final layer (FC8) of a pre-trained CNN (VGG-16; Simonyan & Zisserman, 2014). This layer contains rich feature sets that can be used to accurately categorize objects as animate or inanimate by a support vector machine (SVM) classifier. This same classifier was then deployed on the 40 candidate objects (4 exemplars each) of our experiment to quantify their categorizability. This resulted, for each object, in a representational distance from the decision boundary of the animate-inanimate classifier (Fig. 1B). Because this measure was based on a feedforward transformation of the images, we label this measure *image categorizability*.

The second measure of visual categorizability was based on reaction times in an oddball detection task (Mohan & Arun, 2012; Fig. 1C). Participants were instructed to detect whether an oddball image appears to the left or the right of fixation. Reaction times in this task are an index of visual similarity (Proklova, Kaiser, & Peelen, 2016), with relatively slow responses to oddball objects that are visually relatively similar to the surrounding objects (e.g., a dog surrounded by cats). These similarity values were then used as features in an SVM trained to classify animate vs inanimate objects. Testing this classifier on the images of the fMRI experiment resulted, for each object, in a representational distance from the decision boundary of the animate-inanimate classifier (Fig. 1C). Because this measure was based on human perception, we label this measure *perceptual categorizability*.

The final set of 12 animals for the fMRI experiment were chosen from the set of 40 images such that the correlation between image categorizability and agency was minimized (Kendall's $\tau = 0.06$).

fMRI experiment

Participants Seventeen healthy adults (6 females; age range: 20-32, median: 25) were scanned at the Center for Mind/Brain Sciences of the University of Trento. All participants gave informed consent. All procedures were approved by the ethics committee of the University of Trento.

Main Experiment Procedure The stimuli consisted of colored images (4 exemplars each) of 12 animals, humans, and 3 inanimate objects (cars, plants, and chairs). There were a total of 64 images (16 x 4). The main experiment consisted of eight runs. Each run consisted of 80 trials that were composed of 64 object trials and 16 fixation-only trials. In object trials, a single stimulus was presented for 300ms, followed by a 3700ms fixation period. In each run, each of the 64 images appeared exactly once. Trial order was randomized. Participants were instructed to press a button whenever they detected a one-back object repetition.

Animacy Localizer Procedure In addition to the main experiment, participants completed one run of a functional localizer experiment. During the localizer, participants viewed grey-scale images of 36 animate and 36 inanimate stimuli in a block design. Participants were asked to detect one-back image repetitions, which happened twice during every non-fixation block.

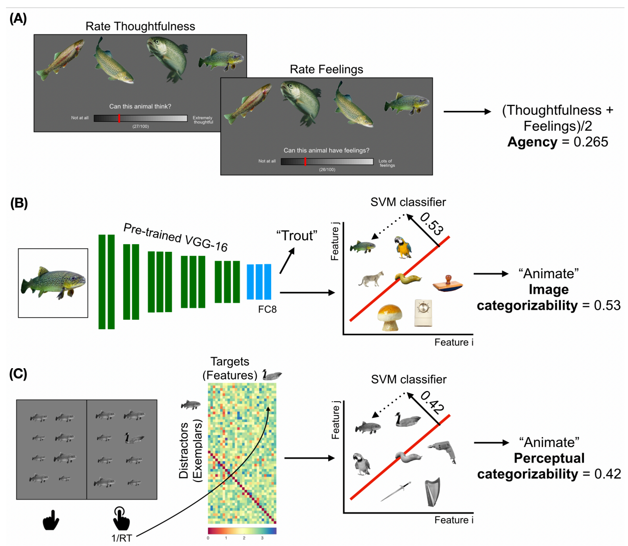

Figure 1. Obtaining the models to describe animacy in the ventral temporal cortex. (A) Participants were asked to rate 40 animals on thoughtfulness and feelings. The average of these ratings was taken as a measure of agency. (B) A schematic of VGG-16. Linear classifiers are trained on layer FC8 of the CNN to classify the activation patterns in response to animate and inanimate images. The distance from the decision boundary, towards the animate direction, is the image categorizability of an object. (C) A trial in the oddball detection task. The inverse of the pairwise reaction times are arranged as shown. Either the distractors or the targets are assigned as features of a representational space on which a linear classifier is trained to distinguish between animate and inanimate exemplars. These classifiers are then used to categorize the set of images relevant to subsequent analysis; the distance from the decision boundary, towards the animate direction, is a measure of the perceptual categorizability of an object.

Results

An SVM classifier was trained on activity patterns in VTC (Fig 2A) to distinguish between blocks of animate and inanimate objects in the animacy localizer, and tested on the 16 individual objects in the main experiment. The distances from the decision boundary, towards the animate direction, were taken as the animacy scores. There was systematic and meaningful variation in the animacy scores for the objects in the main experiment (Fig. 2B). Among the animals, humans were the most animate whereas reptiles and insects were the least animate, replicating previous findings of an animacy continuum (Sha et al., 2015).

What are the contributions of visual categorizability and agency to the animacy continuum in VTC? To address this question, we correlated the visual categorizability scores (Fig. 2B) and the agency ratings (Fig. 2B) with the VTC animacy scores (Fig. 2B). VTC animacy scores significantly correlated with all three measures (Fig. 2C). A combined model of image categorizability and perceptual categorizability ("visual categorizability"') also positively correlated with VTC animacy (Fig. 2C). Importantly, the correlation between VTC animacy and agency remained positive in all individual participants after regressing out both image categorizability and perceptual categorizability (Fig. 2D). Similarly, the correlation between VTC animacy and visual categorizability remained significantly positive after regressing out agency (Fig. 2D).

Finally, to test whether a combined model including visual categorizability and agency fully explained the animacy continuum, we performed leave-one-out regression on VTC animacy with all three factors as independent measures. The resultant combined model captures more variance of VTC animacy than any of the three factors alone. Furthermore, the correlation between the combined model and VTC animacy is at VTC animacy noise ceiling (Fig. 2D).

Whole-brain searchlight analysis Results of a whole-brain searchlight analysis (Fig. 3) showed that both visual categorizability and agency explained unique variance in clusters of VTC. Moreover, there was a consistent anatomical mapping of the two factors: the independent visual categorizability contribution was located posterior to the independent agency contribution in both hemispheres.

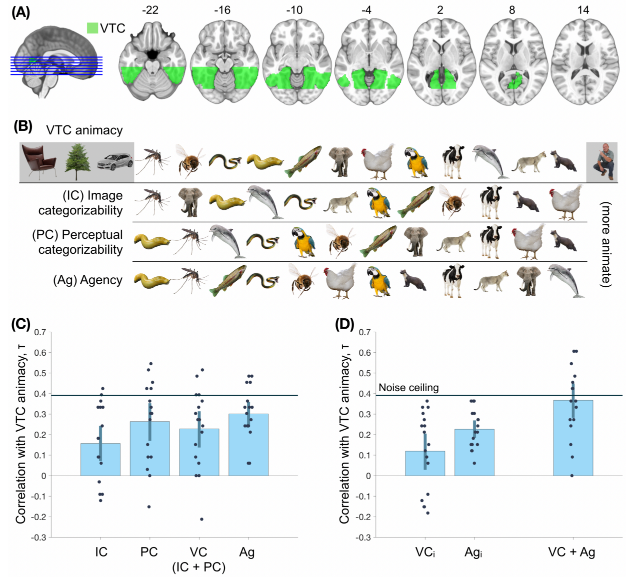

Figure 2: Assessing the nature of the animacy continuum in VTC. (A) The VTC region-of-interest. (B) The order of objects on the VTC animacy continuum, image categorizability (IC), perceptual categorizability (PC), and agency (Ag). (C) The within-participant correlations between VTC animacy and IC, PC, visual categorizability (VC, a combination of IC and PC), and Ag are shown. All four models correlated positively with VTC animacy ($p < 0.001$). (D) The left panel shows the correlations between VTC animacy and VC and AG after regressing out the other measure from VTC animacy. Both correlations are positive ($p < 0.005$), providing evidence for independent contributions of both agency and visual categorizability. The right panel shows the correlation between VTC animacy and a combination of agency and visual categorizability. The combined model does not differ significantly from the VTC animacy noise ceiling. This suggests that visual categorizability and agency are sufficient to explain the animacy organisation in VTC. Error bars indicate 95% confidence intervals for the mean correlations.

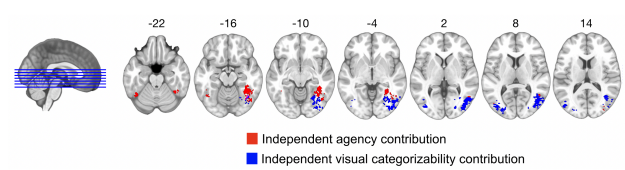

Figure 3. Searchlight analysis testing for the independent contributions of agency and visual categorizability to the animacy continuum. The analysis followed the approach performed within the VTC ROI (Figure 2D). Results are corrected for multiple comparisons.

Discussion

The present study was designed to distinguish between two possible organizing principles underlying the animacy continuum in human VTC, reflecting the degree to which an animal is visually animate (visual categorizability) and the degree to which an animal is perceived to have thoughts and feelings (agency). We found that both dimensions independently explained part of the animacy continuum in VTC; together, they fully explained the animacy continuum. Whole-brain searchlight analysis revealed distinct clusters in which visual categorizability and agency explained the animacy continuum, with the agency-based organization located anterior to the visual categorizability-based organization.

The independent contribution of visual categorizability observed here shows that the animacy continuum in VTC is at least partly explained by the degree to which the visual features of an animal are typical of the animate category. These findings are in line with recent work showing that these features can elicit a VTC animacy organization in the absence of object recognition (Long, Yu, & Konkle, 2018). Our results show that (part of) the animacy *continuum* is similarly explained by visual features: animals that were more easily classified as animate by a CNN (based on visual features) were also more easily classified as animate in VTC. These findings support accounts that link the animacy organization in VTC to visual categorization demands (Grill-Spector & Weiner, 2014).

The current results additionally show that (part of) the animacy continuum reflects the perceived agency of the animals: animals that were perceived as being relatively more capable of having thoughts and feelings were more easily classified as animate in VTC. This correlation persisted after regressing out the influence of animate-diagnostic visual features. The agency organization may reflect the specialized perceptual analysis of facial and bodily signals that allow for inferring internal states, or the perceptual predictions that follow from this analysis. Future research will need to test whether agency is computed within the visual system based on visual features or whether it reflects feedback from downstream regions, for example brain regions involved in social cognition.

The unique contributions of agency and visual categorizability were observed in different parts of VTC, with the agency cluster located anterior to the visual categorizability cluster. This posterior-anterior organization mirrors the well-known hierarchical organization of visual cortex. A similar posterior-anterior difference was observed in our previous study dissociating shape and category representations in VTC, with object shape represented posterior to object category (Proklova et al., 2016). The finding of two anatomically distinct clusters suggests that there are multiple animacy continua in VTC, with the posterior cluster representing visual features that are diagnostic of animacy and a more anterior cluster that reflects perceived agency.

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