Can Category-selective Cortex Predict Categorization Behavior?

Timothee Maniquet[1], Huangxu Fang[1], N. Apurva Ratan Murty[2], and Hans Op de Beeck[1,2]

Abstract

■ One of the distinctive features of the human visual system is the presence in occipito-temporal cortex (OTC) of regions that show preferential activation to specific categories of visual objects. To understand how this selectivity relates to categorization behavior, studies have employed a distance-to-bound (DTB) approach, where multivariate brain activity is used to estimate a decision boundary, from which behavioral performance can be predicted. Using this approach, correlations have been found between activity in OTC, and behavioral performance when carrying out certain categorization tasks. However, it remains unclear what determines where in OTC this correlations can be found and with which categorization tasks they can be found. Here, we bridged this gap by relating category-selective regions of OTC, to behavioral performance while participants categorized images as belonging or not to their preferred categories. We adopted a more basic approach and considered simple, univariate activity, rather than relying on decoding to build our DTB. Our results show that activation in regions selective to faces (fusiform face area and occipital face area), bodies (extrastriate body area), and scenes (parahippocampal place area) is sufficient to predict behavioral performance while categorizing images as being faces, bodies, or scenes, respectively. These results are largely consistent across RT and motor movements and generalize to animacy classification. Overall, our data add to evidence that category-selective regions in OTC can serve to guide categorization behavior and underline the validity of the DTB approach to address this relationship. ■

INTRODUCTION

A hallmark of human visual cortex is the presence of regions in occipito-temporal cortex (OTC) that shows preferential activation to images of certain categories (Bracci & Op de Beeck, 2023), for instance faces in the fusiform face area (FFA) and occipital face area (OFA; Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996), bodies in the extrastriate body area (EBA; Downing, Jiang, Shuman, & Kanwisher, 2001), and scenes in the parahippocampal place area (PPA; Epstein & Kanwisher, 1998). Across these regions, a superordinate selectivity to animate and inanimate objects exists, whereby regions more medial in OTC, including PPA, tend to preferentially respond to images of inanimate objects, whereas regions more lateral, including FFA, tend to preferentially respond to images of animate objects (Kiani, Esteky, Mirpour, & Tanaka, 2007). This animacy gradient has been described as the progressive preference for living and nonliving objects (Thorat, Proklova, & Peelen, 2019; Sha, et al., 2015; Caramazza & Shelton, 1998). However, the surface it covers encloses the smaller regions of OTC, and an alternative explanation is that it reflects selectivity to face- and body-like stimuli (Leys, Chen, von Leupoldt, Ritchie, & Op de Beeck, 2025; Proklova & Goodale, 2022; Ritchie et al., 2021).

To understand whether the pattern of response in these regions serves behavior, research has linked it to categorization behavior by estimating a decision criterion directly from brain activity, through a distance-to-bound (DTB) approach (Ritchie & Carlson, 2016). Making use of this approach, negative correlations were found between the DTB extracted from a classifier trained on animacy-selective regions, and RT in classifying stimuli as animate or inanimate (Ritchie & Op de Beeck, 2019; Grootswagers, Cichy, & Carlson, 2018; Grootswagers, Ritchie, Wardle, Heathcote, & Carlson, 2017; Ritchie, Tovar, & Carlson, 2015; Carlson, Ritchie, Kriegeskorte, Durvasula, & Ma, 2014). Specifically, the animals that are furthest from the neurally derived decision boundary, often mammals, are categorized the fastest in behavior. Despite the frequent limitation of only finding this correlation in animate stimuli, these studies provide evidence that the organization of stimulus-evoked activity in visual cortex could be linearly decoded downstream in the brain to guide categorization behavior.

These results have been replicated for other categories, including superordinate (e.g., manmade vs. natural in Karapetian et al. [2023] and Singer, Karapetian, Hebart, and Cichy [2025]) and basic categories (e.g., faces vs.

[1]KU Leuven Humanities and Social Sciences Group, [2]Georgia Tech School of Psychology

bodies in Grootswagers et al., 2018). These correlations seem to be found regardless of the task performed during brain recording, even when brain data are recorded while doing a task orthogonal to the categories decoded (Singer et al., 2025; Karapetian et al., 2023; Grootswagers et al., 2018; Ritchie et al., 2015; Carlson et al., 2014). However, not all categories that can be decoded from brain data show correlations with RT or accuracy. Some classifiers hence perform above chance on brain data, but their distances do not correlate with human categorization performance (e.g., human vs. animal in Grootswagers et al. [2018]; living vs. nonliving in Contini, Goddard, and Wardle [2021]), suggesting that the pattern of stimulus-evoked activity in visual cortex cannot always serve as a direct readout for downstream areas to guide behavior.

What determines which categories can be linked to brain activity and, in turn, which regions of OTC can be linked to behavioral performance? Answering this question could help understand the behavioral relevance of category selectivity in OTC. A first obvious starting point in this investigation are the categorical distinctions that define the best-known category-selective regions: faces (vs. nonfaces), bodies, and scenes. Strikingly, these distinctions have not been tested yet with the DTB approach.

Here, we asked whether distances to a one-dimensional bound extracted from univariate activity in FFA, OFA, EBA, and PPA can relate to the categorization behavior of their preferred categories. Although previous fMRI DTB studies looked for correlations DTB extracted from populations of voxels, the presence of univariate selectivity provides the opportunity to investigate whether the overall univariate activity would already be sufficient to predict behavioral performance in a categorization task.

We correlated this univariate DTB with RTs and motor movements in categorizing stimuli as belonging to the preferred category of each ROI or not (e.g., "Is this a face? Yes/no" to correlate with FFA). We found that all our ROIs correlated significantly with behavioral performance in categorizing images from nonpreferred categories. In addition, FFA and OFA also correlated with performance for images of faces.

Finally, we extended our approach to an animacy classification task, using the same univariate activity that we correlated with the motor movements of participants classifying stimuli as animate or inanimate. Surprisingly, we found that we could largely replicate the patterns of correlations observed with our basic category tasks. This is consistent with an account of animacy as progressive selectivity to human faces and bodies (Leys et al., 2025; Proklova & Goodale, 2022; Ritchie et al., 2021).

METHODS

Stimulus Set

Across all experiments, we used a stimulus set of 185 color images introduced by Ratan Murty, Bashivan, Abate, DiCarlo, and Kanwisher (2021). These images include exemplars from one of four categories: faces (25 images), bodies (50 images), objects (60 images), and scenes (50 images; see Figure 1A). Each exemplar was left on its original color background, and most of the pictures were taken from the THINGS data set (see Ratan Murty et al., 2021, for more information).

Participants

Four sets of participants are included in our data. First, the fMRI data set we used was collected on an independent set of participants, outside of the scope of this project by Ratan Murty and colleagues (2021). Then, three different sets of participants were recruited to collect data for each of the three behavioral experiments we conducted in the scope of this project. We chose sample sizes of ±80 participants, in the upper range of previous DTB studies (example sample sizes: 30 participants in Ritchie et al. [2015], 50 participants in Grootswagers et al. [2018] and Carlson et al. [2014], 100 participants in Contini et al. [2021]).

fMRI Data

All fMRI data used in this project come from the work of Ratan Murty and colleagues (see Ratan Murty et al. [2021] for full details). In short, data were collected from four participants (two females) using a 3 T MRI scanner, over the scope of five scanning sessions during which a localizer was performed, as well as a passive fixation task.

FFA, OFA, EBA, and PPA were localized during the first session using a dynamic localizer, consisting of short videos containing five types of stimuli (faces, bodies, scenes, objects, and scrambled objects).

A passive fixation task was repeated over the next four sessions, where each stimulus was repeated at least 20 times across participants. Participants were only instructed to maintain fixation on a fixation cross at the center of each image. Trials consisted of a 300-msec presentation of the stimulus, followed by a variable ISI of 3700–11,700 msec. Images were displayed to span 8 dva in size. Univariate activity was then extracted using beta maps from a general linear model applied on the preprocessed data (see Figure 1B for a bar plot visualization of the univariate activity per ROI).

Basic Category RT Experiment

Task

For the basic category RT experiment, we collected data from 78 participants (69 females, mean age = 19.05 *SD* = 2.25, range = 17–31, all of them right-handed). All participants provided informed consent before participation. The experiment was done on-site at the Faculty of Psychology of KU Leuven and was approved by the ethics committee of KU Leuven.

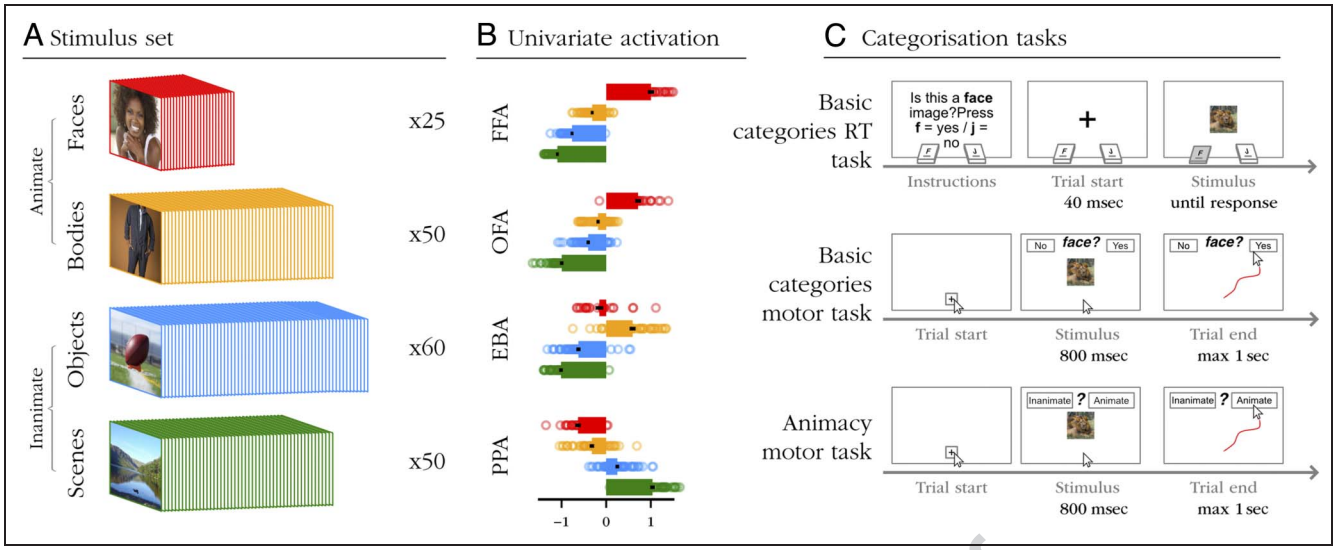

Figure 1. Stimulus set, fMRI data, and behavioral tasks. (A) Stimulus set included in the fMRI and all three behavioral experiments. One hundred eighty-five images in total, including faces (25 images), bodies (50 images), objects (60 images), and scenes (50 images). Animate images were those of faces and bodies (75 images in total), whereas inanimate images were those of objects and scenes (110 images in total). (B) Standardized univariate activity per ROI, across categories. Bars indicate average activity for each category of images; error bars indicate *SEM*. Dots show average activity for individual images. For details on both images and brain data, see Ratan Murty and colleagues (2021). (C) Categorization tasks used in this experiment. In both basic categories tasks (RT and motor tasks), participants had to classify images as belonging or not to faces, bodies, or scenes. In the animacy task, participants had to indicate whether images were of animate objects or not. For the three behavioral experiments, we additionally created a smaller, 22-image stimulus set for training. All were freely accessible on the Kaggle data set website (kaggle.com). The following images were included: three images of faces, six images of bodies, six images of scenes, and seven images of objects.

Participants performed a keyboard-based categorization task, where they were asked to categorize as quickly and accurately as possible whether a presented image belonged to a certain category or not (see Figure 1C). After a short training, they were presented with 18 blocks of the task. During each block, one categorization task was performed, from one of the three following categories: faces, bodies, and scenes (*Is this a face?* yes/no, *Is this a body?* yes/no, etc.). To remove potential motor activity confounds, the keys associated with the *yes* and *no* answers (keys *F* and *J*) were alternated across blocks. This combination of three tasks and two key mappings yielded the six blocks. All 185 images of the stimulus set were presented in each of the blocks, in random order. The code to run this experiment is publicly available on GitHub.

Preprocessing

To ensure good data quality, we first excluded participants whose average accuracy was below 0.7 (five participants excluded). We then ensured all trials had reasonable RT values and were in the range of the 0.5th to the 99.5th percentiles (from 0.17 to 1.93 sec, 2376 trials excluded). Finally, given the long nature of the task, we calculated average accuracies per participant and per block as well as removed blocks with average accuracies below 0.6 (30 blocks removed). After preprocessing, 73 participants were left, for 235,164 trials.

Basic Category Motor Movement Experiment

Task

After collecting keyboard-based RT data on the basic categories task, we replicated the paradigm with mouse tracking to collect time-resolved motor data (see Figure 1C). Instead of responding to images by pressing a key on a keyboard, participants here responded by moving their mouse cursor toward a *yes* or a *no* button, positioned at the top-left and top-right of the display.

We designed our mouse-tracking experiment broadly following the procedure described by Koenig-Robert, Quek, Grootswagers, and Varlet (2024). To ensure a comparable movement trajectory, each trial started when participants pressed a small *start* button at the bottom center of the display. At that point, images appeared on screen for 800 msec. Instructions required to move as quickly as possible toward the correct answer. To ensure fast movement onsets, trial durations were capped to 1 sec, at which point the task would move on to the starting box of the next trial.

The full experiment consisted in four blocks, one for each of the four categories in the stimulus set: faces, bodies, objects, and scenes (*Is this a face?* yes/no, *Is this a body?* yes/no, etc.). The order of the blocks was randomized. Within each block, all 185 images were presented once, in random order. Button positions were switched halfway through the block after a short break to avoid potential motor activity confounds.

Data were collected from 81 participants (59 females, mean age = 19.78 *SD* = 4.82, range = 17–56, 76 right-

handed). The experiment was conducted online and was approved by the ethics committee of KU Leuven. Participants signed a digital consent form before starting the task. The code for this experiment is available on GitLab.

Preprocessing

We took the following steps to preprocess the mouse trajectory data: Trials were aligned by flipping the x coordinates when necessary so that all trials could be analyzed assuming the *No* button was on the left and the *Yes* button was on the right of the display. All x and y data points were scaled and standardized according to individual screen sizes to bring all trials into a common space, spanning from -1 to 1 for the x axis (with the starting box roughly at 0, the *No* box roughly at -1, and the *Yes* box roughly at 1) and from 0 to 1 for the y axis.

Given the challenging nature of the task (in particular due to the capping of trial duration to 1 sec), and to try and capture with maximum sensitivity the motor movement dynamics associated with each image, we adopted exclusion criteria as light as possible. First, we excluded participants who had completed (i.e., managed to click on a response button) less than 200 out of the possible 555 total trials of the task (four participants excluded).

We then excluded outlier trials where the trajectory significantly differed from normal. For that, we looked at trajectories that did not move far enough vertically (end point less than 0.05 away from the starting box), trajectories too short (that generated less than 10 coordinate points, compared with an average of 33), and trajectories that ended below the starting box (18,275 trials excluded). After preprocessing, 77 participants were left, for 41,665 trials.

Animacy Motor Movement Experiment

Task

We adapted the motor movement paradigm we created for basic categories to turn it into an animacy classification task (see Figure 1C). Methodological details for this task were largely in line with those of the basic category motor movement experiment, with the exception that the animacy task was this time repeated 3 times across blocks (the same division was adopted within blocks to switch response buttons). Instructions required participants to classify images as animate if they portrayed living things and as *inanimate* if they portrayed nonliving things. As per this distinction, participants effectively had to separate images of scenes and objects from images of bodies and faces. No image in the stimulus set portrayed living beings/objects that could have been ambiguous to place on the animacy continuum (e.g., insects, amphibians, human-like robots), or for which there would be a dissociation between animacy and living (e.g., plants).

Data were collected from 84 participants (82 females, mean age = 18.26, SD = 1.04, range = 17–24, 77 right-handed). The experiment was conducted online and was approved by the ethics committee of KU Leuven. Participants signed a digital consent form before starting the task. Code for this experiment is available on GitLab.

Preprocessing

Preprocessing for the animacy motor movement data followed the same steps exposed in. After preprocessing, 75 participants remained, 16,546 trials were excluded for 30,074 trials left.

RESULTS

Univariate Activity from Category-selective Cortex Correlates with RT in Categorizing Basic Categories

In our RT behavioral experiment, participants were instructed to categorize images as belonging, or not, to one of three basic categories: faces, bodies, and scenes. Here, we tried to understand whether activation in patches of cortex selective to these categories could guide categorization behavior. To this end, we adopted a DTB approach, whereby brain activity is used to estimate a decision boundary from which behavioral performance can be predicted, in line with previous work (e.g., Grootswagers et al., 2017; Ritchie et al., 2015; Carlson et al., 2014). DTB studies typically estimate this decision boundary from the multidimensional space of brain activity (for instance, using voxel space with fMRI, fitting a classifier algorithm to decode image category from brain data, and using the resulting decision values as a proxy for the distance of each image to the decision bound).

In contrast with these previous studies, we consider simple univariate activity (i.e., averaged across voxels, rather than using multivariate voxel patterns) as a proxy for the distance of each image to the categorical decision bounds. In doing so, we test the hypothesis that overall activation in the ROIs we investigate, rather than the complex patterns of voxel activity, can map onto behavioral categorization performance. This simple univariate approach would fail with regions that lack strong stimulus-specific preferences, but category-selective ROIs are obvious examples of regions that do have such preferences, by definition.

We averaged univariate activity from FFA, OFA, EBA, and PPA, per image, across participants and hemispheres. We averaged RTs per image from accurate trials only from participants in the basic category RT experiment (n = 73, see). We did so separately per task (one task per target category: faces, bodies, and scenes), showing differences in RT distributions (see Figure 2A), as expected given the differences in target/nontarget image numbers (e.g., faster RTs in the face task, as compared with the scene task, because of fewer faces than scenes; see Figure 1).

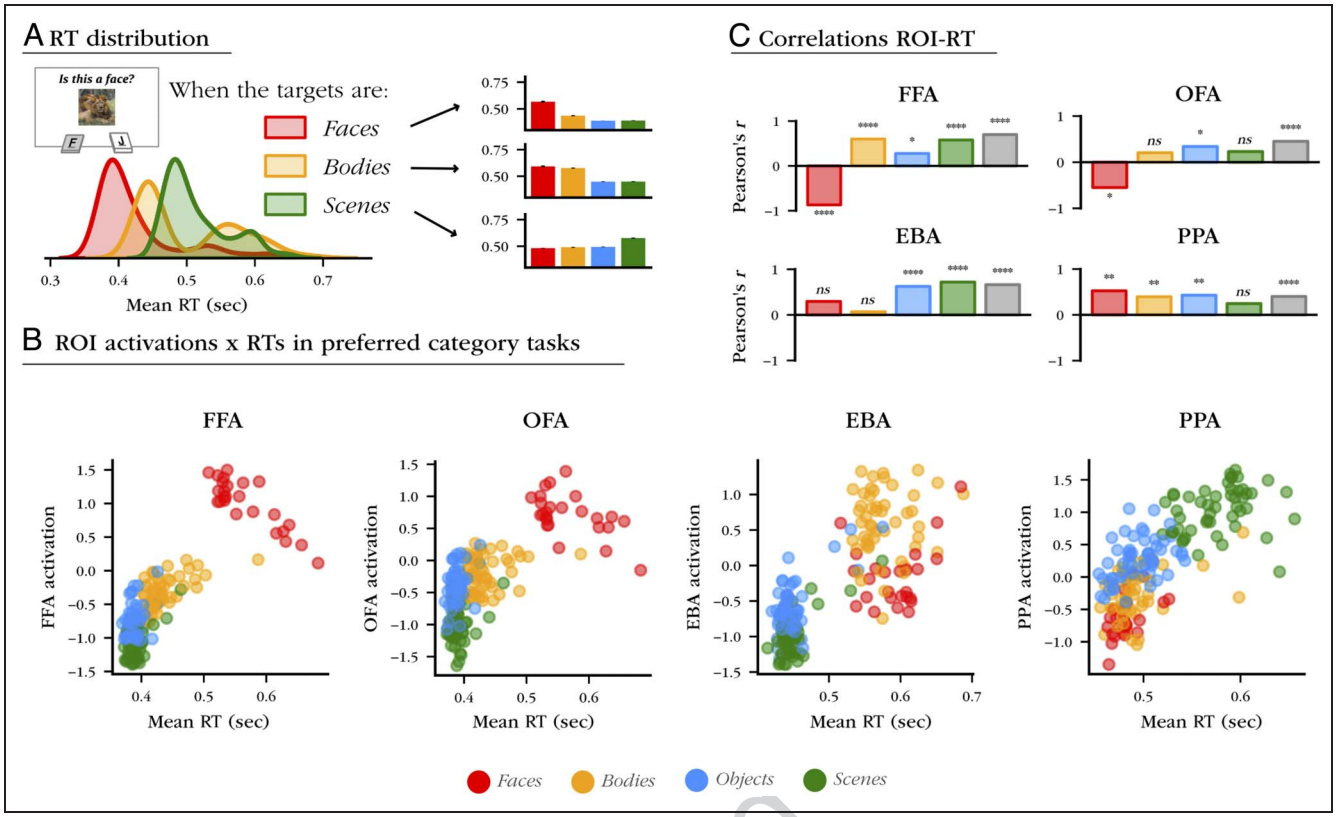

Figure 2. Results from the basic category RT experiment correlate with ROI univariate activity. (A) Distribution of RTs in each of the three tasks, using only correct trials. For each task, participants had to indicate whether the image belonged to the target category or not, using keys on a keyboard. (B) Correlations between average RTs per image and average univariate activity per image. Each plot shows data from the task where the preferred category of the ROI was the target (FFA activation is shown against RTs in categorizing faces, EBA activation against RTs in categorizing bodies, etc.). (C) Correlation scores from the data in B. For each ROI, we correlated the RTs and univariate activity per image. Results are split between categories. Gray bars indicate the correlation between univariate activity and RTs for stimuli from all nonpreferred categories pooled together (e.g., all images of bodies, objects, and scenes for FFA and OFA).

We correlated average brain activity with average RT image-wise, for each ROI with the RTs to the categorization task of its preferred category (FFA and OFA: face categorization task, EBA: body categorization task, PPA: scene categorization task; see Figure 2B). Pearson correlation coefficients were computed, and the statistical significance of the resulting correlations was assessed via a two-tailed t test ($df = n - 2$). All p values were corrected for multiple comparisons (false discovery rate [FDR] correction, five comparisons: four categories + all nonpreferred images; Benjamini & Hochberg, 1995).

We expected activations from each ROI to be negatively correlated with RTs to stimuli from its preferred category, as would be predicted from a DTB approach. We found such a negative correlation for both of our face-selective regions (FFA: $r = -.87$, $p < .001$, FDR-corrected; OFA: $r = .55$, $p = .01$, FDR-corrected), but found a null correlation for EBA ($r = .07$, $p = .63$, FDR-corrected), and a nonsignificant positive correlation for PPA ($r = .24$, $p = .09$, FDR-corrected; see Figure 2C).

Then, we expected activations to positively correlate with RTs to stimuli from nonpreferred categories, as indicative of longer RTs to images closer to the boundary defined by univariate brain activity. We found this significant positive correlation for all our ROIs (FFA: $r = .7$; OFA: $r = .45$; EBA: $r = .67$; PPA: $r = .4$; all $p < .0001$, FDR-corrected). Overall, these results indicate that univariate activity from category-selective patches of cortex can be linked to RTs from categorization tasks.

RT Correlations with Univariate Activity from Category-selective Regions Replicate in Motor Movements

We next replicated our analyses, using time-resolved behavioral data in place of RTs, considering RTs alone do not capture the entire decision process behind categorization. We adopted a more sophisticated approach to ensure the pattern of results would not differ significantly if we were able to look at image decisions before decisions were actually made.

To this end, we designed a mouse-tracking experiment, where participants categorized images as belonging, or not, to the same basic categories as before (faces, bodies, scenes), but this time responded by clicking a button on the screen rather than a key on their keyboard. In doing so, we were able to analyze the trajectory of their

mouse cursor and take that motor movement as a proxy for the different steps taken in making a categorization decision.

We focused on the horizontal (x) position of the mouse cursor across time, as it reflects the proximity of participants to making either a yes or no decision at every time point during a trial. We extracted horizontal position at each time point, separately for each category task (see Figure 3A), and averaged it over participants. In doing so, we obtained one time-resolved average horizontal trajectory per image and per task (see Figure 3B). With the *yes* response button aligned to the value 1 on the x axis and the *no* response button aligned to the value -1, we expected average mouse trajectories to drift toward positive values in the case of target images and toward negative values in the case of nontarget images. This is indeed what was observed, with movements drifting away from the central position after roughly 400 msec, with a bias early on toward negative values, as expected from the larger number of nontarget images (see Figure 3B).

From the horizontal position of each image across time, we replicated the correlation analysis shown in Figure 2B–C, this time calculating one correlation value per time point (1000 values in total, for trials of 1 sec). We correlated activations from each ROI to horizontal positions obtained from its preferred category task. We obtained Pearson correlation coefficients and computed their statistical significance via a two-tailed t test, with p values FDR-corrected for multiple comparisons, effectively replicating the approach described in at every time point.

As per our DTB approach, we again predicted that motor movements would show correlations with ROI activity. First, for preferred images, we expected that participants would move faster toward the *yes* button (i.e., horizontal positions would get close to 1.0 earlier). Following this expectation, we predicted positive correlations between horizontal positions and ROI activity, homologous to the negative correlations we expected previously with RT. Second, for nonpreferred images, we expected faster movements toward the *no* button (i.e., horizontal

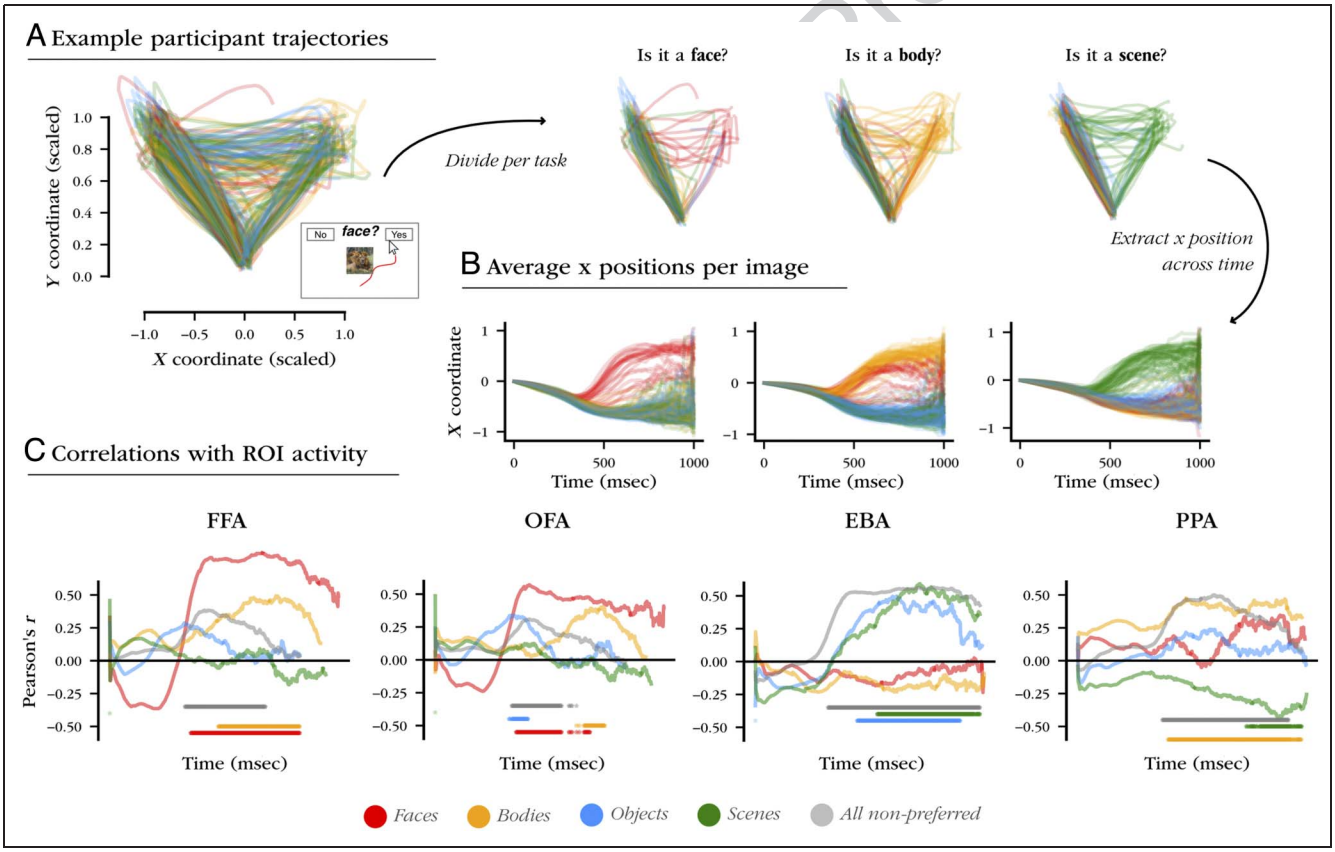

Figure 3. Results from the basic category motor task largely replicate those from the RT task. (A) All trajectories (one per trial) from one example participant. Trajectories are flipped when necessary so that the *yes* button is always on the right (close to $x = 1.0$). The left side plot shows all trajectories from one experimental session, that is, pooled across tasks. Dividing trials based on the target category, we get the plots on the right side (e.g., all trials from that example participant for when the target was a face under the *Is this a face?* title). (B) Average horizontal (x) position per image and per task, across time. Average data from all participants are shown here. The y axis represents the horizontal position, with more positive values closer to the *yes* button. The x axis represents time (with trials capped at 1 sec). (C) Correlations between average x position per image and average ROI activation per image, across time. As in Figure 2B, each ROI is shown against data from trials where its preferred category was the target. Dots below the graphs indicate time points where the correlation is significantly different from zero ($p < .05$, FDR-corrected). Correlations are divided across images from each category (one line per category). The gray line shows correlations for all stimuli from nonpreferred categories pooled together.

positions closer to −1.0). As a result, we predicted a positive correlation between horizontal positions and ROI activity, homologous to the positive correlations we expected previously with RT.

We first looked for positive correlations between ROI activations and horizontal position for preferred category images (see Figure 3C). First, both our face-selective ROIs showed strong correlations with face images. FFA had its peak correlation ($r = .82$) at 659 msec, with values significantly larger than 0 ($p < .05$, FDR-corrected) from 350 msec onward. OFA had its peak correlation ($r = .57$) at 407 msec, with values significantly larger than 0 ($p < .05$, FDR-corrected) from 350 msec onward. Second, we did not find a significant correlation between EBA activation and the horizontal position of body images. Third, and contrary to predictions, we found negative correlations between PPA activation and horizontal positions of scene images, with peak value (−0.44) at 870 msec (significantly below 0 from 731 msec onward, $p < .05$, FDR-corrected).

We then looked for positive correlations between ROI activations and horizontal position for nonpreferred category images, with the same assumption that higher activation would associate to images closer to the boundary, and hence to images further away from the *no* response button. We were able to find such a correlation for all our ROIs (peak values: 0.41 for FFA, 0.31 for OFA, 0.776 for EBA, and 0.594 for PPA).

Strikingly, when looking at results from the basic category motor task, we found that they largely replicate results from the basic category RT task. In place of finding temporal dissociations in the time-resolved signal which would bring nuance to the previous section, we found almost the same patterns of correlation with our four ROIs. (1) First, where we found a negative correlation between univariate activity in FFA and OFA and RT to face images, we found a corresponding positive correlation with horizontal positions for face images (Figure 3C FFA and OFA, red lines). (2) Second, where we found a positive correlation between univariate activity for all our ROIs and RT to nonpreferred images, we found a corresponding positive correlation with horizontal positions for nonpreferred images (Figure 3C all four plots, gray lines). (3) Third, where we did not find the expected negative correlations between univariate activity in EBA and RT to body images, we also did not find the corresponding positive correlation with horizontal position for body images (Figure 3C EBA, yellow line). The only exception to this pattern of replication is in the unexpected negative correlation that was found late on between univariate activity in PPA and horizontal position for scene images (we come back to this in section).

This conjunction across our ROIs of the correlations found with simple RTs and with motor movements consolidates our results and suggests that motor movements can reliably capture the relationship between categorization performance and brain activation.

Univariate Activity in Category-selective Regions Correlates with Animacy Categorization Behavior

We finally extended our approach to the categorization of animacy. Several previous publications have already found correlations between RTs in categorizing objects as animate or inanimate, and multivariate activity in OTC (Ritchie & Op de Beeck, 2019; Ritchie et al., 2015; Carlson et al., 2014). On the other hand, it has been suggested that the animacy continuum observed in OTC is driven by the progressive selectivity to face-like and body-like features (Leys et al., 2025; Proklova & Goodale, 2022; Ritchie et al., 2021). We hence wondered if we could extend our correlations to an animacy categorization task. Therefore, we asked whether univariate activity in patches of cortex with selectivity for basic categories (e.g., faces and bodies) could also be linearly readout by the brain to guide behavior in categorizing the superordinate categories of animate and inanimate.

Considering the results presented above (see), we chose to use a motor movement task to investigate animacy, as it is able to reproduce results found with simple RTs and provides an extra time-resolved sensitivity. We therefore designed a task where participants classified images as animate or inanimate, and used the mouse cursor movements to create average x positions across time per image, which we then correlated to brain activations (see Figure 4A–B).

Just like previously, we expected to find correlations in line with a DTB interpretation. Here, we have to consider what we observed in the basic category task (taking the motor movement version as the comparison). In that task, we found all expected correlations in FFA and OFA, so for these ROIs, the predictions in the animacy categorization are straightforward. Instead, for EBA and PPA, we only found the predicted (positive) correlation for nonpreferred categories, again resulting in straightforward predictions here for those images. However, EBA showed no correlation and PPA an opposite correlation for the preferred category, which should result in similarly nonstraightforward predictions in animacy categorization—at least if our assumption is correct that category-selective ROIs can predict animacy categorization RTs the same way they can predict face, body, and scene categorization RTs.

The straightforward predictions are that activations from regions selective to animate categories (faces, bodies, i.e., FFA, OFA, and EBA) should positively correlate with horizontal positions (stimuli eliciting more activity in those regions closer to the *animate* button). Conversely, we expected activations regions selective to inanimate categories (scenes, i.e., PPA) to correlate negatively with horizontal positions. This is because trajectories from the animacy categorization task were aligned so that the *inanimate* button would be on the left, as a result of which more inanimate images are expected to fall closer to −1 and animate images closer to 1.

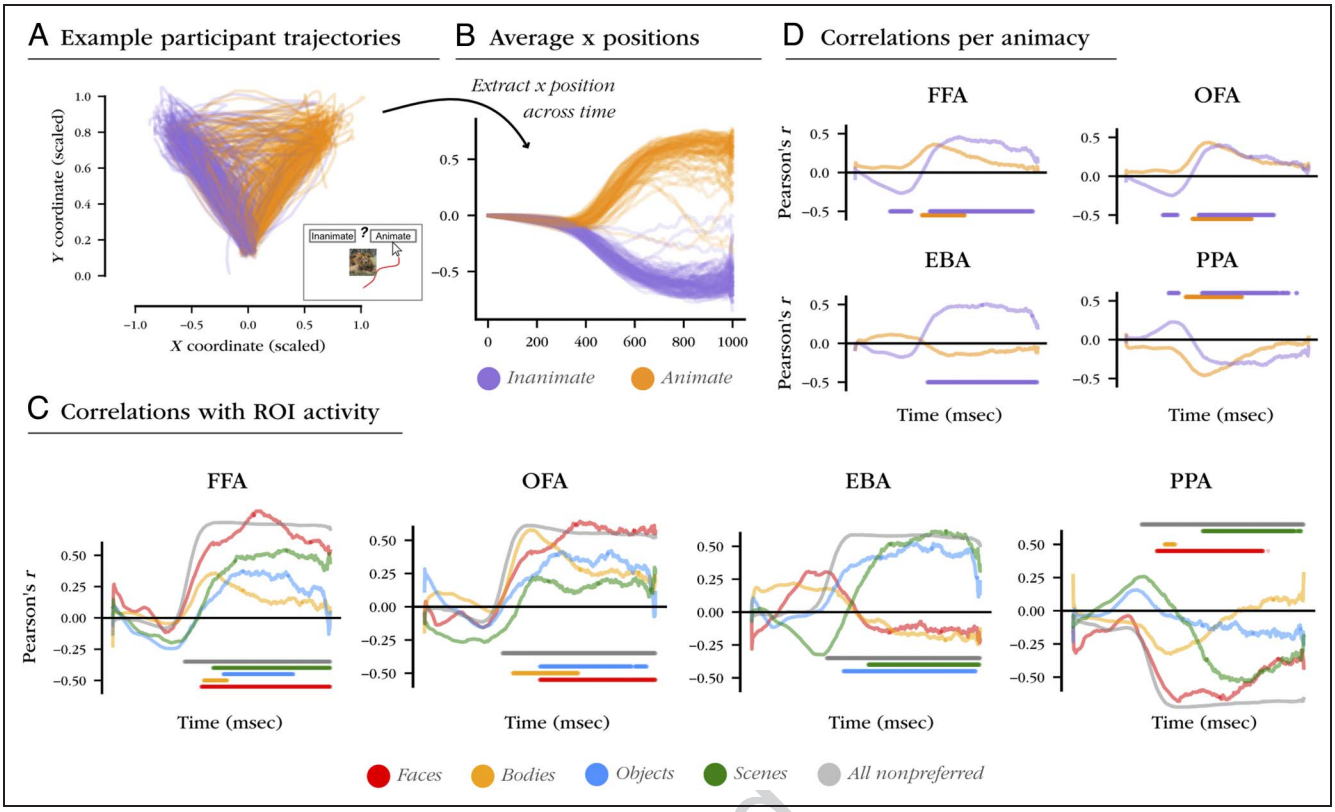

Figure 4. Conjunction of animacy motor task and basic category motor task results. (A) All trajectories (one trajectory per trial) for one example participant. Trajectories were flipped when needed to align the *animate* response button to the right side of the screen, close to $x = 1$. (B) Average horizontal position per image, for all participants. Positions more positive are closer to the *animate* button. (C) Correlations between ROI univariate activity and average horizontal position per image across time. As in Figure 3B, correlations are divided per categories, with the gray line representing images from all the nonpreferred categories. Dots below or above the plots indicate time points where correlations are significantly different from zero ($p < .05$, FDR-corrected). (D) Correlations between ROI univariate activity and image horizontal position across time, pooled between images of animate objects (faces and bodies) and inanimate objects (objects and scenes).

Results matched these straightforward predictions for the face-selective regions. FFA and OFA showed strong, positive correlations with face images (FFA: peak correlation $r = .85$ at 674 msec, significantly above 0 from 406 msec onward; OFA: peak correlation $r = .64$ at 673 msec, significantly above 0 from 499 msec onward; significance threshold for both $p < .05$, FDR-corrected), as well as with all nonpreferred images (FFA: peak correlation $r = .76$ at 504 msec, significantly above 0 from 329 msec onward; OFA: peak correlation $r = .61$ at 457 msec, significantly above zero from 337 msec onward; see Figure 4B; significance threshold for both $p < .05$, FDR-corrected). These basic category results are reflected at the superordinate level: when aggregating bodies and faces together as animate categories, we found significant positive correlations of FFA and OFA activations with both animate and inanimate images (see Figure 4C).

We did not find a positive correlation between EBA activity and body images in the animacy categorization task, in line with the absence of a correlation for preferred images in the basic category task. Conversely, we found a positive correlation between EBA activity and nonpreferred images (peak correlation $r = .59$ at 466 msec, correlation significantly above 0 from 328 msec onward; significance threshold $p < .05$, FDR-corrected). This also translated into no correlation with animate images, and a significantly positive correlation with inanimate images.

Lastly, we found a significant, negative correlation between PPA activation and horizontal position for scene images in the animacy categorization task (peak correlation: $r = -.54$ at 750 msec, significantly below 0 from 561 msec onward; significance threshold $p < .05$, FDR-corrected). This correlation, in line with our expectations, contradicts what was found in the basic category RT task and the basic category motor task. We also found a significant negative correlation between PPA activation and horizontal position for nonpreferred images (peak correlation $r = -.73$ at 461 msec, significantly below 0 from 296 msec onward; significance threshold $p < .05$, FDR-corrected). This in turn translated into a significant negative correlation with both animate and inanimate images when pooled at the superordinate level.

To sum up, when looking at results from the animacy motor task, we again found correlations with univariate ROI activity that replicate those from the basic category motor task. Namely, we found that (1) the straightforward prediction is true for OFA and FFA for face images; (2) the straightforward prediction is true for all ROIs for

nonpreferred images, and (3) the straightforward prediction is not verified for EBA univariate activity and horizontal position for body images. The only major divergence from patterns of results in is that of PPA, for which the straightforward prediction was found to be true for scene images.

In summary, overall, the brain–behavior correlations in the animacy motor task show a close correspondence to brain–behavior correspondences in the basic category motor tasks.

Category Membership Ratings Correlate with Behavior More than Univariate Activity

To try and explain what is driving these results, we analyzed category membership ratings collected by Ratan Murty and colleagues (2021). Those ratings were collected by asking participants to align images on the screen based on how face-, body-, or scene-like they were. These category likeness ratings were collected online on 115 participants, with a procedure that allowed for a measure of reliability, so that only the more reliable participants were kept in the final analyses (n = 106 for faces, n = 115 for bodies, n = 60 for scenes).

We first asked whether the rated category membership of an image is predictive of categorization performance for that image. We used RTs from the basic category keyboard-based experiment (see) as a benchmark of categorization performance for our images and correlated it with category membership ratings.

In line with the DTB approach used before, we expected that higher ratings on a target category would negatively correlate with RTs in categorizing it. For instance, if a face was rated as highly face-like, then we predicted that it would be associated with a faster RT. In that same example, conversely, if a nonface stimulus (e.g., a scene image) was rated as highly face-like, then we predicted that it would be associated with a slower RT.

We found this prediction to be true of all categorization tasks for ratings of nontarget images (see Figure 5A). This means that for all tasks, the ratings of nontarget images on their membership to the target category is correlated with RT in categorizing them as nontargets. For target images, only ratings of face-likeness and scene-likeness correlated with RTs in categorizing faces and scenes, respectively, whereas no correlation was found for bodies.

We then applied this approach to ROIs, and we correlated brain activations with category membership ratings. We expected positive correlations: If brain and behavior aligned, then face likeness, for instance, should positively correlate with activations in FFA. We looked for these positive correlations in preferred categories (faces for OFA and FFA, bodies for EBA, and scenes for PPA) and in nonpreferred categories pooled together. Among preferred categories, only face-selective regions were found to

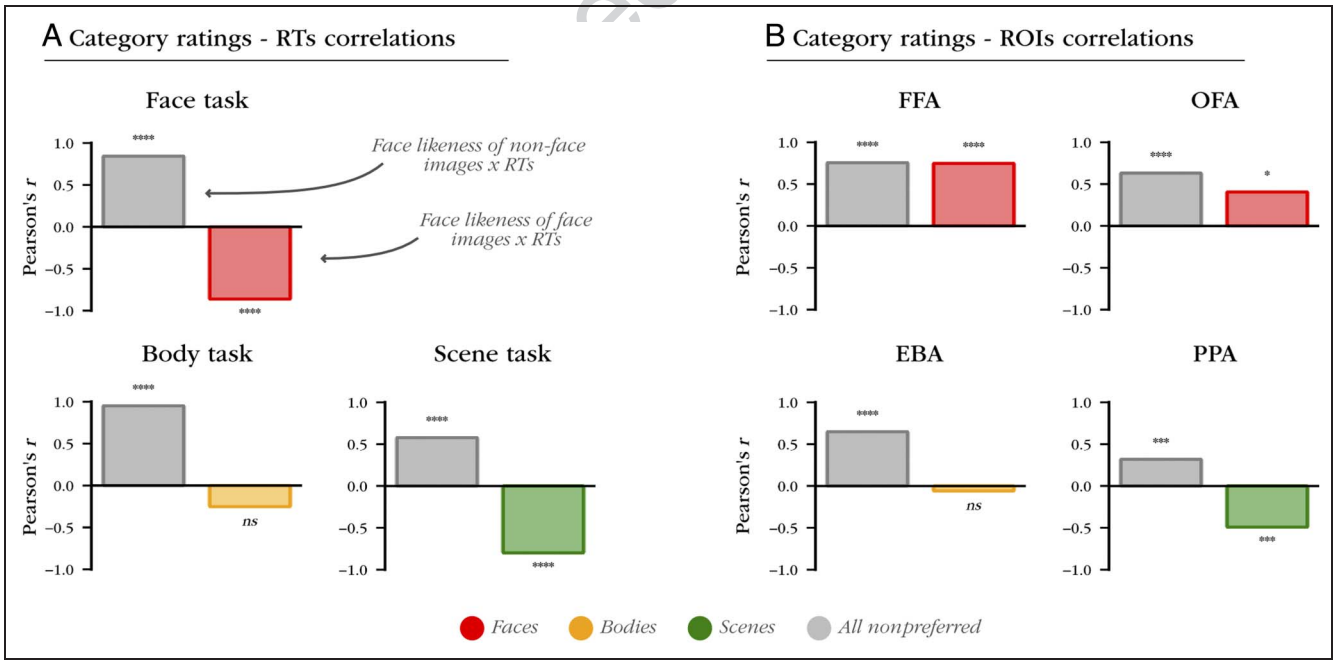

Figure 5. Category membership ratings explain most correlations. (A) Correlations between category membership ratings and average RTs in the basic category RT task. For each task, RTs are correlated with ratings from the target category during that task (e.g., RTs from the task *Is this a face? yes/no* are correlated with ratings on face likeness). Color bars indicate correlations between ratings for the target categories and RTs to images from the target categories. Gray bars indicate correlations between ratings for the target categories and RTs to images from all nontarget images. (B) Correlations between ROI univariate activity and category membership ratings. Just like in A, ratings for the likeness to the preferred category of each ROI is correlated with activations from that ROI (e.g., ratings of face likeness are correlated with activations from FFA). Gray bars indicate correlations with the category likeness of stimuli from nonpreferred categories.

correlate positively with face likeness ratings for faces, with EBA not correlating significantly with body likeness ratings for bodies and PPA correlating significantly negatively with scene likeness for scenes. Note that these unexpected correlations of EBA and PPA are in line with results from previous section (see the previous Results sections).

Overall, these results show that category membership ratings relate differently to behavior and ROI activation. On the one hand, categorization RTs for faces and scenes seem to be linearly correlated with face likeness and scene likeness ratings, respectively. This indicates that, for these two categories, how much participants judge images as target-like directly maps onto the speed of their perceptual decision. This does not apply for bodies, for which body likeness judgments seem orthogonal to perceptual decision speed.

On the other hand, face-selective regions show a similar pattern to face-selective categorization tasks, whereby face likeness ratings directly map onto ROI activations for FFA and OFA. This is not true of EBA, which shows a nonsignificant correlation to body-likeness for body stimuli, and of PPA, which shows a negative correlation to scene-likeness for scene stimuli.

Taken together, results on preferred category images paint a different picture across ROIs. First, they point to FFA and OFA as particularly suitable for a direct readout by other parts of the brain for guiding categorization behavior, which is probably mediated by a pattern of univariate activations very close to the pattern of face likeness ratings of images. EBA, on the other hand, appears to respond to body images in a pattern orthogonal to body likeness ratings and, therefore, orthogonal to body categorization behavior. Finally, PPA appears to respond to scene images in a manner opposite to that of behavior, with weaker responses to stimuli that would be rated high on scene likeness, and, therefore, would be faster to classify as scenes.

DISCUSSION

In this work, we asked whether univariate activity in FFA, OFA, EBA, and PPA can drive categorization behavior. We build on previous DTB studies with four main innovations:

- We used and compared category-selective ROIs (instead of OTC and/or early visual cortex more broadly; Ritchie & Op de Beeck 2019; Grootswagers et al., 2018; Carlson et al., 2014) or a single of those regions (Singer et al., 2025);
- Our stimulus set was directly designed to elicit activations in these regions (Ratan Murty et al., 2021) and was used in both a basic and a superordinate categorization task;
- We calculated a one-dimensional DTB through univariate activity directly;
- We combine two behavioral metrics: RTs and time-resolved mouse-tracking-based motor movements, allowing us to measure categorization behavior over time.

DTB Predictions Are Partially But Consistently Found across Experiments for Category-selective ROIs

Across our three behavioral experiments, we made two types of hypotheses: about the relationship between ROI activation and preferred images and about the relationship between ROI activation and nonpreferred images. For preferred images, we expected activation amplitudes to predict easier categorization. For instance, if FFA had a high response amplitude to a certain image of a face, then we expected this image to be easily categorized as a face. For nonpreferred images, we expected activation amplitudes to predict harder categorization. In the same example, an image of a scene that elicited a high FFA activation was expected to be harder to categorize as a nonface.

In the first experiment, regarding preferred images, we found a negative correlation between RTs and univariate activation only for FFA and OFA, with EBA and PPA not correlating with body and scene stimuli, respectively. Conversely, regarding nonpreferred images, we found significant, positive correlations between all ROI activations and RTs in categorizing stimuli from nonpreferred categories.

The second experiment replicated results from the first experiment, using horizontal position from a motor movement task instead of RTs. The only exception was PPA, with a late, significant negative correlation with performance (when a positive one would have been expected, had preferred images effects been found).

Finding effects for nonpreferred images across these two experiments and across all ROIs shows that univariate activity can be sufficient to correlate with categorization performance. It also corroborates the long-standing observation that patches of category-selective cortex, despite showing a preference for a given category, also respond in a meaningful way to stimuli from other categories (Haxby et al., 2001).

The correlations we found with preferred images in FFA and OFA are largely in line with literature connecting the face network to face-recognition behavior (see, e.g., Pitcher, Walsh, Yovel, & Duchaine, 2007). In addition, results from category membership ratings show that FFA especially, but also OFA, largely agree with human participants in judging which images are more or less face-like (see Figure 5B).

Not finding a correlation between preferred images and PPA aligns with a recent report showing no correlation between PPA and RT in categorizing scene images (Singer et al., 2025). In addition, category membership ratings (see Figure 5B) seem to address the unexpected negative

correlation of PPA in our second experiment (see Figure 3C): Although in line with participant judgement, they are actually inverse to PPA response (see Figure 5). This could be explained by the rectilinearity of images: Although PPA tunes more strongly to rectilinear image contents (for man-made and interior scenes, see Figure [suppfig:preferred_images_ppa]; Nasr, Echavarria, & Tootell, 2014; Kravitz, Peng, & Baker, 2011), participants judged natural scenes more scene-like and categorized them faster than man-made scenes (see RTs for scene images in RT scene categorization task in Figure [suppfig:fastest_images_scene] as well as larger area under the curve for scene images in motor scene categorization task in Figure [suppfig:auc_images_scene]).

Lastly, we did not measure correlations between EBA and nonpreferred images, which seems to indicate that its activity did not map directly onto body classification behavior for body images, despite reports that EBA is linked to body recognition performance (Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009). This might be because our stimuli lack variability in the body features that EBA is specifically tuned (see the Limitations of This Study section). Regardless, EBA correlated with performance for other categories of images, showing that it does tune to image features that are relevant to categorization behavior.

Animacy Behavior Is Recapitulated in Basic Category Behavior

In our third experiment, we asked whether univariate activity amplitude in our ROIs would also correlate with behavior in classifying images as animate or inanimate. We were motivated by research suggesting that the animacy continuum in OTC is the result of progressive selectivity to human face- and body-likeness, rather than a taxonomy-like continuum (Leys et al., 2025; Proklova & Goodale, 2022; Ritchie et al., 2021). If true, this account would predict that animacy categorization behavior would be largely similar to face and body categorization behavior.

Interestingly, we largely replicated what we found in the basic categorization task experiments (see Figure 4) regarding our Hypotheses a and b, with the one exception of PPA, which was found to be in line with hypothesis a, in contradiction with results found in our first two experiments.

Overall, our results are in line with accounts of animacy selectivity as the combination of selectivities to various basic categories (Leys et al., 2025; Proklova & Goodale, 2022; Ritchie et al., 2021). In addition, this account would predict similar correlation trajectories across basic and animacy categorizations, which is in line with what we found (e.g., first significant correlation with nonpreferred stimuli, average across all 4 ROIs: 328 msec for basic categorization tasks, vs. 327 msec for animacy categorization task; Figures 3C vs. 4C).

Interpretation of Our Results in Light of Previous DTB Studies

Several studies until now have found correlations with behavioral performance only for animate objects. We did not replicate this effect (see). We found correlations with inanimate stimuli both in the animacy (see Figure 4D) and basic categorization tasks (see FFA and OFA with scene and objects in 2, for instance). Overall, the animacy status of our stimuli did not seem to drive whether they would correlate with ROI activation.

This animacy asymmetry has previously been explained by the absence of a real inanimate dimension in the brain (Carlson et al., 2014) or the use of a *A - not A* strategy (Grootswagers et al., 2018). The present correlations for inanimate stimuli during animacy categorization, and the binary choice nature of our tasks, suggest a different interpretation. The absence of correlation for a set of stimuli cannot exclude that a different set of stimuli within the same category, or a different behavioral task with the same stimuli (Contini et al., 2021), would yield a correlation.

Task behavior at the time of brain recording could also influence our results (Ritchie, Wardle, Vaziri-Pashkam, Kravitz, & Baker, 2025). For instance, EBA could have not correlated with the categorization of body stimuli because participants did not need to attend to body-like features while being scanned. If this is true, the fact that some brain–behavior correlations are found in the absence of any task demand suggests that activation in certain regions of OTC automatically aligns with behaviorally relevant dimensions of stimuli. FFA provides a good example of such a region, as its activation directly maps onto face categorization behavior, by showing sensitivity to the same features that participants judge as face-like (see).

Limitations of This Study

Our study has some limitations. First, we used a limited number of stimuli, potentially not allowing us to sample across a large variety of category features (e.g., the lack of effect with body stimuli could be due to too little variability in body image features).

Second, a disadvantage of our DTB approach is that we apply binary category labels onto our stimulus set. Although the continuous nature of ROI activation and behavioral metrics (RT and mouse position) allow us to tap into the continuous nature of category selectivity, we measured correlations across images grouped together on the basis of a binary category label. These labels are a useful approximation, as confirmed by the correlations we describe in this project. However, using categories as binary rather than dimensional constructs is limiting (Op de Beeck, 2025; Contier, Baker, & Hebart, 2024). This might have consequences for our results. For instance, the correlation between RT and activation from PPA in response to images of scenes (see Figure 2B) might be positive in the absence of the lowest activation outlier

(see Figure [suppfig:preferred_images_ppa]), which contains bodies. Without the forced categorization of this image as a scene, behavior and brain might have been positively correlated, as is well captured in the ratings—ROI correlations, which shows that PPA is inversely correlated to how scene-like images are, while this metric is strongly correlated with RTs.

Finally, we did not set out to explore the downstream readout that could be operated from OTC activation. Such a readout could potentially extract more information to drive behavior than we suggested (Birman & Gardner, 2019). For instance, we report that ROI activity could be linearly readout, but we cannot exclude a nonlinear mapping with downstream areas. In addition, we cannot arbitrate whether a single decoder or several decoders would be best fitted to extract meaningful information from this readout.

Conclusions

Using a DTB approach, we showed that activity in category-selective patches of cortex are relevant to categorization behavior, as evidenced by correlations with categorization performance. Although not all ROIs correlate with images from their preferred category, we found a consistent relationship with nonpreferred images, across tasks (basic and superordinate categorizations) and across behavioral metrics (RT and motor movements). Taken together, these results highlight the mechanisms through which category-selective activity in visual cortex can guide categorization behavior.

Corresponding author: Timothee Maniquet, KU Leuven Humanities and Social Sciences Group, Leuven, Belgium, e-mail: timotheemaniquet@gmail.com.

Data Availability Statement

Data and code to reproduce the analyses presented in this article are available at this URL: https://github.com/TimManiquet/cortical_selectivity. Supplemental Material can be accessed on this article's homepage: https://doi.org/10.1162/JOCN.a.2629.

Author Contributions

Timothee Maniquet: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Software; Visualization; Writing—Original draft; Writing—Review & editing. Huangxu Fang: Data curation; Formal analysis; Investigation. N. Apurva Ratan Murty: Data curation; Resources; Writing—Review & editing. Hans Op de Beeck: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Validation; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this paper report its proportions of citations by gender category to be: M/M = .633; W/M = .233; M/W = .1; W/W = .033.

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