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The Representation of Valence by Visual Category in the Orbitofrontal Cortex and Amygdala

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ABSTRACT

Emotion is critical for survival in all animals. Even in modern humans, processing emotion holds significant adaptive value. In neuroscientific investigations of emotion, both the amygdala, part of the evolutionarily primitive limbic system, and the orbitofrontal cortex, part of the evolutionarily newer cortical system, have been highly implicated in the representation of valence, a major emotional component. Although the strict divide between the limbic system and the cortical system in brain function has been rejected, the underlying notions of theories of brain evolution lead to the hypothesis that the amygdala is advantageous in processing evolutionarily older adaptive value whereas the orbitofrontal cortex is advantageous in processing evolutionarily newer adaptive value. In this study, this hypothesis is tested using a functional magnetic resonance imaging dataset in which human participants made valence judgments on natural items and scenes (i.e., evolutionarily old with greater immediate adaptive value) and man-made items and scenes (i.e., evolutionarily new with lesser immediate adaptive value). The results show that the amygdala represents valence of natural but not man-made scenes, consistent with the hypothesis. The orbitofrontal cortex, in contrast, represents valence of both natural and man-made scenes, partially consistent with the hypothesis. The findings illustrate how visual categories defined by adaptive value shape the neural representation of valence in the contrasting limbic and cortical systems.

Introduction

While the human race today by and large does not face extreme threats to survival, emotion historically has held notable adaptive value, meaning evolutionary advantage, as a significant component in survival. A prime example of emotion's place in survival is the fight-or-flight response, an automatic and immediate activation of fear that is undoubtedly and intuitively critical for survival. Previous studies on the fight-or-flight response have demonstrated the presence in the central nervous system, namely the hypothalamus and brainstem, of specialized neurons that can control both the neural cardiovascular response in addition to the endocrine adrenal catecholamine response of the sympathetic nervous system (Jansen et al., 1995). On a molecular level, the fight-or-flight response, which exists in not only humans but also other mammals, releases epinephrine to engage cardiac muscle cells to increase heart rate and cardiac output (Fuller et al., 2010). As further evidence for the relationship between emotion and survival, algorithms that trained populations of virtual robots demonstrated that behaviors to maximize the chances of survival -- that is, emotion -- spontaneously formed as innate strategies regardless of the neural architecture (Pacella et al., 2017). Additionally, simply the fact that a set of emotions most advantageous for survival including fear and disgust has convergently evolved across human socio-cultural boundaries serves to demonstrate emotion's fundamental relation to survival (Pacella et al., 2017).

As emotion is a somewhat ambiguous and subjective phenomenon, the more objective and empirical concept of valence, defined as the component of emotion representing the subjective association of goodness or badness with a stimulus, has been employed in scientific studies (*Valence*, n.d.). Valence forms one axis of the emotional plane, the other axis being arousal, the magnitude or intensity of the emotional response. Additionally, valence is measured on a positive-to-negative spectrum in which positive represents attractiveness and negative unattractiveness.

Studies of valence at the behavioral level have illustrated that actions of avoidance -- arm extension, for example -- were quicker in response to negative valence stimuli than to positive valence stimuli while actions of approach -- arm flexion, for example -- were quicker in response to positive valence stimuli than to negative valence stimuli (Alexopoulos & Ric, 2007). This finding suggests the validity of the connection critical for survival between valence-inducing stimuli and reactionary behavior; that is, avoiding stimuli of negative valence and approaching those of positive valence.

In the brain, valence is represented in fine patterns of activation that can be discovered through only multivariate analysis and not univariate analysis (Jin et al., 2015). However, there exist competing theories explaining the neural representation of valence. One such theory is the distinct regions model, in which distinct brain systems underlie the processing of positive and negative valence separately, while another is the "affective workspace" model, in which the same brain regions represent both positive and negative valence through varying patterns of activation (Lindquist et al., 2016). Even so, studies concerning both theories, albeit proposing differing methods of valence processing, suggest that the orbitofrontal cortex and amygdala are the predominant anatomical brain regions involved in the neural representation of valence (Čeko et al., 2022; Kirk, 2008; Lindquist et al., 2016).

There is strong reason to believe that the amygdala and orbitofrontal cortex (OFC) are functionally distinct in processing and representing emotion and valence, thus serving as a motivation to conduct a study comparing the valence representation in these two regions of interest. Firstly, there is a difference in the evolutionary developmental history of these two regions that serves as a basis for their proposed differences in valence representation. The amygdala is part of an evolutionarily primitive limbic brain structure, highly involved in the primal sense of fear, while the orbitofrontal cortex is part of the evolutionarily newer neocortex, associated with higher-level cognitive functions (Mineka & Ohman, 2002). One caveat is that there exists not a clear-cut distribution of emotional function to primitive circuits and cognitive function to cortical circuits, but rather an interconnection of emotional and cognitive processing in the primitive and cortical regions (LeDoux, 2000). Nevertheless, the respective evolutionary pasts and the current observed functional differences of the amygdala and the OFC lead to a hypothesized difference in the two regions in their neural representations of emotion. For example, the OFC is considered to be more directly related to the emotion of anger while the amygdala is considered to be more related to the emotion of fear (Machado et al., 2009). At the temporal level, the encoding of valence in the amygdala is known to start earlier and last for a longer period of time compared to that in the OFC (Jin et al., 2015). In addition, the OFC has been shown to have a more prominent role in processing positive valence than does the amygdala (Omigie et al., 2015).

To study such distinctions of valence encoding in the orbitofrontal cortex and the amygdala, vision is an appropriate sensory modality. Previous studies have shown that in the perception of affective visual stimuli, there is a heightened sensitivity to magnocellular cells, associated with coarser features like motion and depth, than to parvocellular cells, associated with finer features like texture and color, through an inhibition of the pathways of the latter by those of the former. This development may be attributed to the quicker processing speed of magnocellular pathways that are more favorable in quickly reacting to potential threats from the environment (Bocanegra & Zeelenberg, 2009). Additionally, fear-related visual stimuli were identified more quickly in a matrix of distracting background objects than were visual stimuli that were not fear-related, further supporting the connection between emotion, especially those negative like fear, visual perception, and survival (Öhman et al., 2001).

Another important established observation about the neural representation of vision is its categorical nature. There appears to be a distinction in the neural representation of animate versus inanimate visual stimuli, particularly in the inferior temporal region (Kriegeskorte et al., 2008). Also, a fusiform face area, a brain region that is activated significantly more during the task of facial recognition than other brain areas, has been identified in addition to a parahippocampal place area for place recognition (Haxby et al., 2001; Epstein & Kanwisher, 1998). Furthermore, the fusiform face area was found also to be particularly activated in response to food stimuli, suggesting that it may have general expertise in the recognition of certain stimuli (Jain et al., 2023).

While there is currently abundant research on valence neural representation and the categorical representation of vision independently, there still remain outstanding unanswered questions regarding the more niche interest of the combination of those two topics: valence categorization and whether the valence of stimuli of different visual categories are represented differently in the brain based on their evolutionary adaptive value for survival. Because of the evolutionary distinction between the amygdala and orbitofrontal cortex discussed previously, it is reasonable to hypothesize that the amygdala is more tightly related to the valence of images of evolutionarily older items and scenes (with higher adaptive value for immediate survival) and the orbitofrontal cortex to the valence of images of evolutionarily newer items and scene (with lower adaptive value for immediate survival). This hypothesis is tested using a public functional magnetic resonance imaging (fMRI) dataset in which human participants made valence judgments on natural and man-made items and scenes. Images of natural items and scenes arguably have high adaptive value from an evolutionary perspective. This is because a seemingly safe area or a friendly animal that may associate with positive valence -- or a seemingly dangerous area or a threatening creature that may associate with negative valence -- are more directly related to survival. In contrast, images of man-made items and scenes arguably have low adaptive value from an evolutionary perspective. For example, while objects like cars and scenes like buildings could have associations with either positive or negative valence today, those valence associations would not have held significant relation to survival at a time when these evolutionarily newer man-made creations did not exist. Considering the temporal difference in the visual processing of natural versus man-made images in just the first 100 milliseconds of perception, it is reasonable to assume that these two visual categories have differences in their representation of valence as well (Lowe et al., 2018).

Methods

Public fMRI Dataset

This study utilized a public fMRI dataset called BOLD5000. The fine details of the BOLD5000 study may be found at the following link: https://www.nature.com/articles/s41597-019-0052-3.

To provide a handful of key points concerning the BOLD5000 dataset, it contains blood-oxygen-level-dependent (BOLD) response data pertaining to roughly 5000 different visual stimuli from four participants.

The demographics and the number of sessions each subject underwent are the following: 27-year-old male with 15 functional sessions, 26-year-old female with 15 functional sessions, 24-year-old female with 15 functional sessions, and 25-year-old female with 9 functional sessions. All subjects also underwent one additional structural session each. Each functional session contained 9 or 10 runs, and each run contained 37 images.

For each run in the MRI scanner, participants viewed an image for 1 second, after which they viewed a fixation cross for 9 seconds before proceeding to the next image, following this procedure for all 37 images. Within the 9-second fixation cross period, participants were asked to indicate the valence (positive, neutral, negative) of the image they had just previously viewed by pressing one of three buttons on an MRI-compatible glove.

Pre-processed data from Release 2.0 of the public repository for this dataset (https://bold5000-dataset.github.io/website/) is used for this study. For this study, the GLMbetas-TYPED-FITHRF-GLMDENOISE-RR files were used, which represents the map of the response amplitude to each of the over 5000 images for each subject, quantified from the General Linear Model fit of the BOLD response.

Stimuli Organization

For the purposes of the current study, only data associated with the ImageNet and Scene UNderstanding (SUN) databases were considered. The Common Objects in Context (COCO) database was excluded because the metadata for image categorization could not be accessed.

The data from the ImageNet and SUN databases' images were split into two categories -- nature and man-made -- to examine the role of adaptive value in valence representation, as discussed in the introduction. The image label lists for the two image databases found in the BOLD5000_Stimuli folder were used to determine which images belonged in the nature and man-made categories, respectively. In the ImageNet database, the images with labels containing a number less than or equal to 02655020 were found to be of animals (and hence nature) and those with labels containing a number greater than 02655020 to be of man-made objects. In the SUN database, the scene images were hand-selected appropriately for the nature and man-made categories. The natural and man-made images in both the ImageNet and SUN databases were each given distinct categorical labels. Using these categorical labels, the natural images from the ImageNet and SUN databases were grouped into one broader class of natural images, and likewise for the man-made images.

fMRI Data Preparation

To prepare the fMRI data for analysis, the original high-resolution T1 map (t1W_MPRAGE) is normalized to the standardized MNI space using SPM12 (REF), hence resulting in y_t1W_MPRAGE. Using the normalization parameters, the GLM beta maps in the individual brain space (GLMbetas-TYPED-FITHRF-GLM-DENOISE-RR) were also normalized to the standardized MNI space.

Regions of Interest

The region of interest (ROI) masks for the medial orbitofrontal cortex (mOFC) and amygdala (AMYG) were obtained using WFU_pickatlas (REF) (Fig. 1). In the IBASPM 71 of HUMAN ATLAS of WFU_pickatlas, the "medial front-orbital gyrus left" and "medial front-orbital gyrus right" regions were selected for the mOFC mask. In the IBASPM 116 of HUMAN ATLAS of WFU_pickatlas, the "Amygdala_L" and "Amygdala_R" regions were selected for the AMYG mask. The mOFC and AMYG were chosen for their notable involvement in valence representation, as demonstrated by numerous previous studies, and for their relative difference in age in the scope of the historical development of the human brain. Additionally, the lingual gyrus (LG), defined by "lingual gyrus left" and "lingual gyrus right" in IBASPM 71, was chosen as a control ROI, as it is a part of the primary visual cortex but not directly associated with valence representation. The ROI masks were resliced to the normalized brain space for ROI analysis. It should be noted that the medial OFC was chosen instead of the entire OFC in order to best balance the number of voxels in each ROI. In the final normalized space, the mOFC had 1167 voxels, the AMYG had 468 voxels, and the LG had 2308 voxels.

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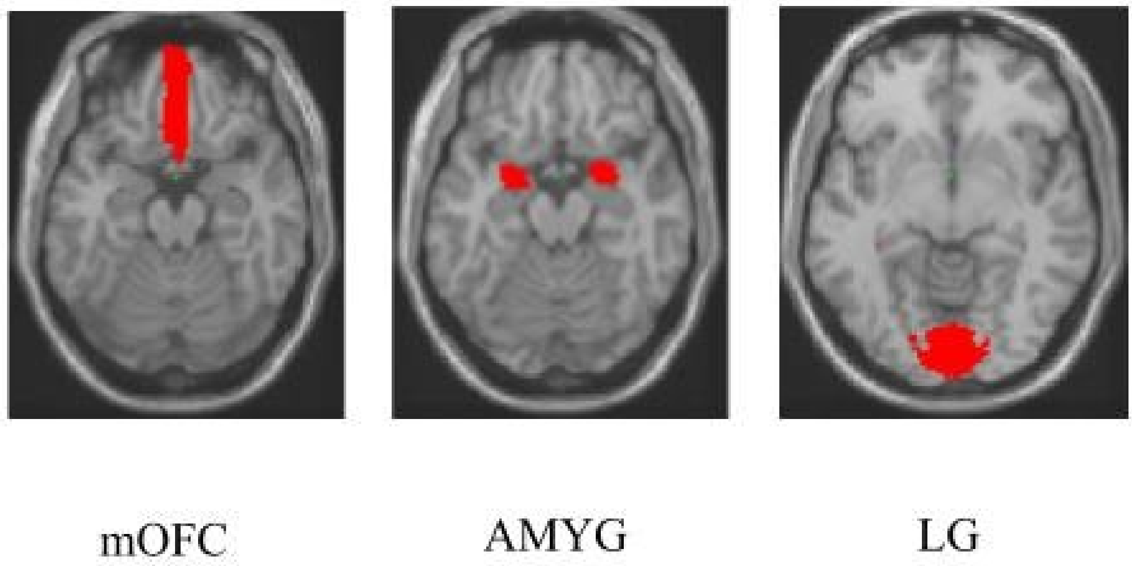

Figure 1. The medial orbitofrontal cortex (mOFC), the amygdala (AMYG), and the lingual gyrus (LG) selected as regions of interest.

Classification Analysis

As the objective of the study was to determine the interaction between adaptive value and valence representation, it would be appropriate to analyze the classification accuracies of the support vector machine (SVM) with 2-fold cross validation classifying the valence of nature images and the valence of man-made images (see Haynes & Rees, 2006). The MATLAB interface of the SVM function from LIBSVM (https://www.csie.ntu.edu.tw/~cjlin/libsvm/), an open library for machine learning methods, was used for greater efficiency of speed in running the analyses.

Instead of combining the data from all subjects into one dataset for a population analysis, each subject was analyzed separately. For each subject, arrays of masked beta maps associated with nature or man-made images were generated. In the original BOLD5000 study, in response to each of the images, participants reported their valence using 1 for "like," 2 for "neutral," and 3 for "dislike." In the current study, a linear binary SVM classifier classified the positive (1) versus non-positive (neutral and negative valence were combined to 3 because there were far too few instances of negative valences) responses separately for nature and man-made images. For example, to examine the valence representation of nature images in subject CSI1's mOFC, the fMRI volumes in the beta map volume array corresponding to the nature category labels would be found using the category label array. Each of these volumes would then be labeled as 1 or 3 based on their corresponding valence response, and SVM would be run using this information. Additionally, a further control analysis was conducted in the form of a categorical SVM classification -- that is, natural versus man-made stimuli -- in each of the ROI's using the same methods as for the valence response SVM analysis (Fig. 2).

Furthermore, in addition to the observed classification accuracy discussed immediately above, a set of null distribution classification accuracies were obtained to test the statistical significance of the observed classification accuracy (see Fig. 3 and 4). For this non-parametric statistical analysis, 1000 rounds of the same 2-fold cross validation SVM as above were run for each ROI of each subject but with randomized 1 and 3 valence response labels in order to obtain the set of 1000 null distribution classification accuracies. The significance of the observed classification accuracy was then measured through the calculation of the *p*-value; that is, the proportion of null distribution classification accuracies greater than or equal to the observed classification accuracy.

It is also important to note that both the number of instances of 1 and 3 valence responses for nature and man-made stimuli and the number of instances of nature and man-made stimuli themselves were all equalized in order for a valid comparison of classification accuracies. In other words, by taking the lowest number of instances found in any one of the Nature 1, Nature 3, Man-made 1, and Man-made 3 subdatasets and extracting that number of instances from each subdataset, the number of each valence response in each category would be the same. However, this would inevitably mean that less than the total number of instances in three of the four subdatasets would be chosen for analysis. In order to account for this, different random instances of the subdatasets were implemented in the analysis through 20 rounds of the regular SVM that were run to obtain 20 different observed classification accuracies in addition to 20 rounds of the null distribution SVM of 50 randomized label permutations each. The mean of the 20 observed classification accuracies was used was the overall observed classification accuracy, and the 50 null distribution classification accuracies from each of the 20 different rounds were combined for a total of 1000 null distribution classification accuracies. An analogous approach was implemented for the categorical SVM as well but with only 100 null distribution classification accuracies due to the large size of the dataset.

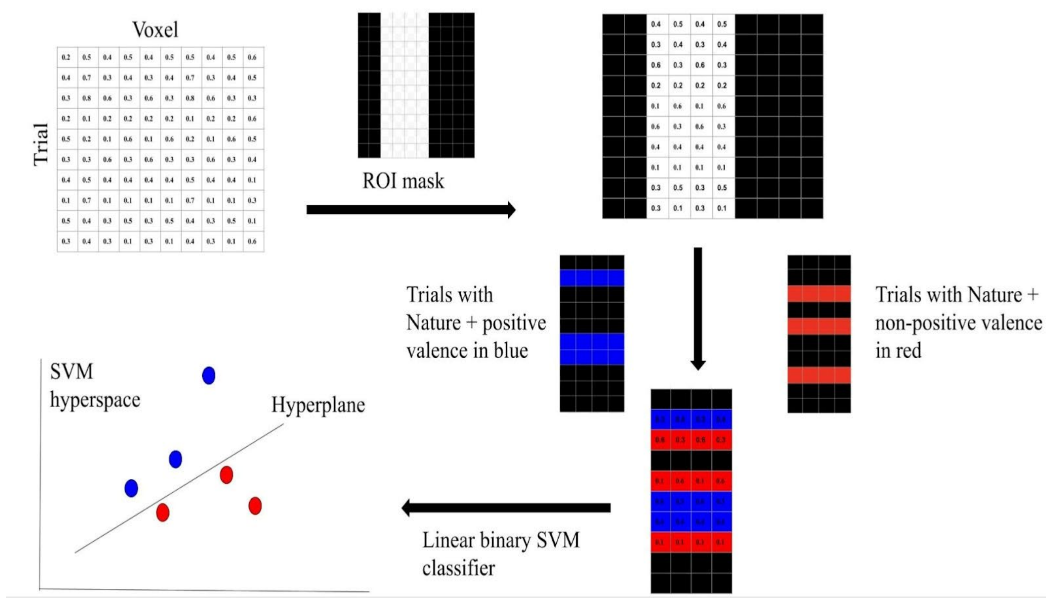

Figure 2. This figure illustrates the process through which the data was prepared for SVM analysis by looking at an example of SVM classification for "natural" stimuli. At the top left is the initial dataset with beta values from each voxel, represented by columns, and each trial, represented by rows. In the top right, a ROI mask is placed over the initial dataset to extract only the beta values from the voxels of interest. In the bottom right, a further sifting extracts only the trials of the nature category and positive valence and of the nature category and non-positive valence separately, as represented in blue and red, respectively. With the beta values of the two classes of valence from the nature category labeled, a linear binary SVM classifier is run, as illustrated in the bottom left.

Results

SVM Classification of Valence in mOFC and AMYG

Through the valence classification SVM of the two regions of interest -- the medial orbitofrontal cortex and the amygdala -- the present study sought to determine a difference, if any, in how these two regions represent the valence of natural versus man-made images, as their respective evolutionary histories might suggest. For subjects CSI1, CSI2 and CSI3, the medial OFC reliably distinguished the valence of both natural and man-made images (p-values from the non-parametric test ranging between 0.008 and 0.034). In contrast, the amygdala reliably distinguished the valence of natural images only (p-values ranging between 0.015 and 0.048) and not of man-made images (p-values ranging between 0.132 and 0.170) (Table 1). Such findings illustrate a distinction between the valence representation of these two visual categories in the ROIs, supporting the initial hypothesis to an extent.

It should also be noted that subject CSI4 showed no significant classification of valence in the two ROIs. It is unclear what caused this outlying pattern, although it is worth noting that subject CSI4 completed only nine sessions instead of fifteen like the other subjects did due to discomfort in the MRI machine, according to the original study. Such a discomfort may have led to irregularities or disturbances in the data or valence response collection process. However, the other three subjects showed the exact same pattern of SVM classification results in mOFC and amygdala.

SVM Classification of Valence in a Control Region (LG)

The control analysis with the lingual gyrus was conducted to confirm that the phenomenon of the neural representation of valence did not occur in just any brain region, and that the medial OFC and amygdala are indeed regions special in their involvement in valence representation. For all four subjects, including subject CSI4, the lingual gyrus consistently failed to distinguish the valence of both natural and man-made images, thus demonstrating that valence representation is present not in a random brain area but selectively in the medial OFC and amygdala.

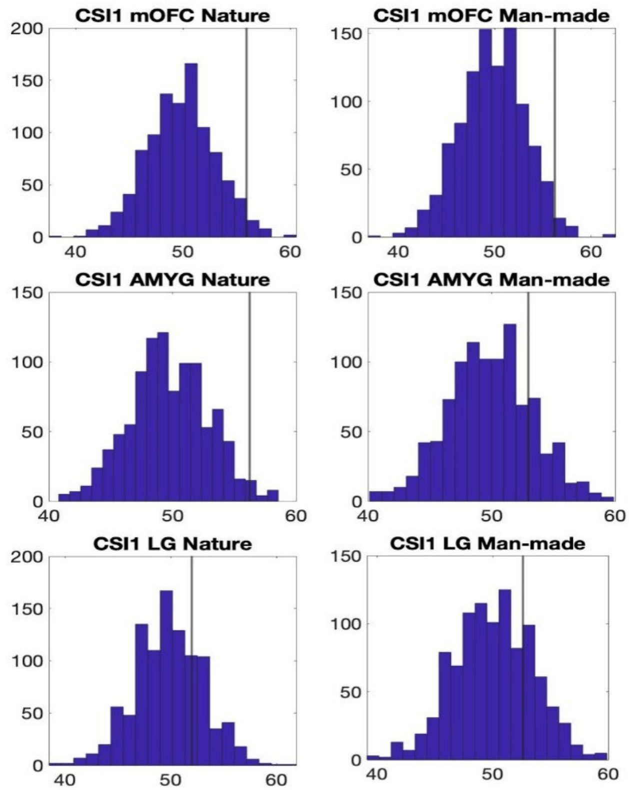

Figure 3. Histograms of the null distributions and observed classification accuracies of the SVM classifying positive versus negative valence (indicated by vertical lines) for the three ROIs separately for nature and man-made images for subject CSI1.

Table 1. Classification accuracies and *p*-values for valence SVM

Participant	ROI	Nature CAs and *p*-values	Man-Made CAs and *p*-values
CSI1	mOFC	CA = 55.9211% $p = 0.026$	CA = 56.2500% $p = 0.018$
	AMYG	CA = 56.2500% $p = 0.015$	CA = 52.9605% $p = 0.170$
	LG	CA = 51.9737% $p = 0.241$	CA = 52.6316% $p = 0.218$
CSI2	mOFC	CA = 54.9505% $p = 0.008$	CA = 54.2904% $p = 0.033$
	AMYG	CA = 54.7855% $p = 0.025$	CA = 52.4752% $p = 0.132$
	LG	CA = 50.1650% $p = 0.442$	CA = 50.0000% $p = 0.513$
CSI3	mOFC	CA = 56.7797% $p = 0.034$	CA = 56.4659% $p = 0.031$
	AMYG	CA = 56.0812%	CA = 54.2471%

		$p = 0.048$	$p = 0.137$
	LG	CA = 45.7627% $p = 0.844$	CA = 49.5763% $p = 0.519$
CSI4	mOFC	CA = 53.3898% $p = 0.220$	CA = 49.1525% $p = 0.544$
	AMYG	CA = 45.7627% $p = 0.719$	CA = 49.1525% $p = 0.573$
	LG	CA = 49.1525% $p = 0.485$	CA = 52.5424% $p = 0.279$

Note. mOFC: medial orbitofrontal cortex, AMYG: amygdala, LG: lingual gyrus.

SVM Classification of Visual Category in mOFC, AMYG, and LG

A second control analysis in the form of SVM classification of visual category (natural versus man-made) was conducted to explore whether the medial OFC and amygdala distinguished the two visual categories. Such an observation would be meaningful for the interpretation of the valence analysis. In addition, the same classification analysis was performed in the lingual gyrus to confirm that the lingual gyrus, as part of the primary visual cortex, accurately classifies the visual categories. For subjects CSI1, CSI2, and CSI3, the medial OFC reliably distinguished between the two visual categories (all p-values under 0.04), while the amygdala failed to distinguish between the two visual categories (p-values ranging between 0.17 and 0.48) (Table 2). Again, subject CSI4 acted as an outlier in that the medial OFC did not distinguish between natural versus man-made images but did follow the pattern observed in the other three subjects by failing to distinguish visual category in the amygdala. The representation of visual categories present in only the medial OFC and not in the amygdala is intriguing, given that valence was represented in both visual categories in the medial OFC but of nature images only in the amygdala. Additionally, the lingual gyrus for all four subjects reliably categorized natural versus man-made images, as expected by the region's being a part of the primary visual cortex.

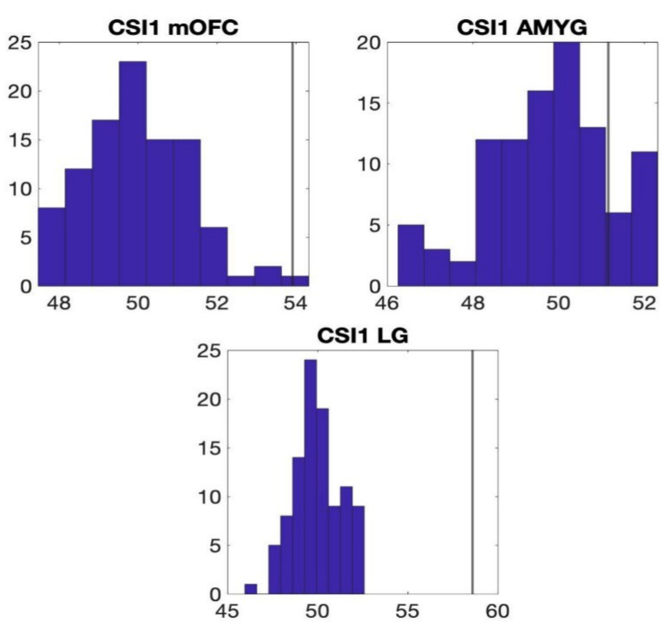

Figure 4. Null distribution histograms and observed classification accuracies of the SVM classifying nature versus man-made images (indicated by vertical lines) for subject CSI1.

Table 2. Classification accuracies and *p*-values for categorical SVM

Participant	ROI	CAs and *p*-values
CSI1	mOFC	CA = 53.9171% p = **0.01**
	AMYG	CA = 51.1521% p = 0.17
	LG	CA = 58.5829% p **< 0.01**
CSI2	mOFC	CA = 53.0530% p **< 0.01**
	AMYG	CA = 50.3456% p = 0.30
	LG	CA = 56.3364% p **< 0.01**
CSI3	mOFC	CA = 52.1009% p = **0.04**
	AMYG	CA = 49.8272% p = 0.48
	LG	CA = 54.9539% p **< 0.01**
CSI4	mOFC	CA = 51.0577% p = 0.26
	AMYG	CA = 48.3654% p = 0.82
	LG	CA = 55.2885% p **< 0.01**

Note. mOFC: medial orbitofrontal cortex, AMYG: amygdala, LG: lingual gyrus.

Discussion

The motivation of the current study was to determine if the valence of stimuli of different visual categories with differing adaptive values from an evolutionary perspective would be represented differently in the brain. Specifically, the orbitofrontal cortex was hypothesized to represent the valence of evolutionarily newer stimuli while the amygdala was hypothesized to represent the valence of evolutionarily older stimuli. The result that the medial orbitofrontal cortex represents the valence of both natural and man-made images but the amygdala only represents the valence of natural images supports the hypothesis with some caveats. The amygdala represented solely the valence of natural stimuli, as predicted, yet the medial orbitofrontal cortex represented the valence of both nature and man-made categories, going beyond the prediction that it would solely represent the valence of man-made category. As such, the amygdala appears to be primed to respond to stimuli of "immediate" adaptive value, or immediate and direct natural threats from an evolutionary standpoint, while the orbitofrontal cortex seems to be reactive to a varying array of potential threats or affective stimuli.

The control analysis of categorical SVM classification interestingly revealed that the medial OFC, but not the amygdala, distinguishes between natural and man-made categories. This finding seems to be in line with previous research that has determined the OFC's ability to distinguish faces of different social and emotional categories through a special set of face-selective cells, suggesting a categorical capacity of the OFC (Barat et al., 2018). Our results suggest that this cortical area also has the capacity to distinguish visual categories at a different level.

With respect to the main finding of the current study, the difference in categorical valence representation in the medial OFC and the amygdala should, once again, not come as a complete surprise due to their difference in function. For example, the orbitofrontal cortex was found to be much more critically involved in a reward-linked object reversal learning, which stems from basic emotional and valence processes, than the amygdala is (Rudebeck & Murray, 2008). What is more interesting, though, is how exactly the difference in categorical valence representation presented itself; that is, the fact that the orbitofrontal cortex was unexpectedly found to represent the valence of both visual categories, contrary to the amygdala, which represented the valence of only natural stimuli. However, this finding makes more sense in the context of previous works exploring the massive redeployment hypothesis that have found that there is a correlation between the age of a brain region and the number of functions it is involved in, suggesting that an anatomical evolutionary split can translate into a split in functional architecture (Anderson, 2010). Specifically, this would mean that the amygdala has a lesser number of functions than the orbitofrontal cortex does, and the number of visual categories each region represents may be proportional to the complexity of the region itself.

In addition, the amygdala and OFC have been highly implicated in emotional processing, sharing a "bidirectional coupling" relationship in which these two brain regions communicate with each other (Sonkusare et al., 2023). A model for this relationship has been proposed in which the amygdala informs the behavior ultimately expressed by the orbitofrontal cortex through conveying affective information, which may be interpreted as the orbitofrontal cortex collectively containing affective information from both the amygdala and itself, once again reinforcing the larger range of stimuli for which the orbitofrontal cortex represents valence (Murray & Izquierdo, 2007). Furthermore, more studies on the orbitofrontal cortex and amygdala have revealed that the orbitofrontal cortex shares far more neural connections with other cortical regions than the amygdala does, as the OFC itself is a part of the cortical system (Rolls, 2023). The fact that the orbitofrontal cortex is connected to many major sensory cortices -- the gustatory, olfactory, visual, and auditory cortices -- while the amygdala is not helps explain the presence and lack of categorical representation in the OFC and amygdala, respectively, as neural links to the sensory regions would make it far more likely that the sensory information would be represented in the region of interest (Rolls et al., 2023). As such, the strength of connections between the OFC and amygdala to these cortical regions is reflective of the number of visual categories of which the regions represent valence.

Another point of discussion is the sensory modality, vision, used to obtain the data of this study. It seems reasonable to question whether the results found in this current study are specific to the sense of vision or would still hold true if it had used data obtained from the stimulation of different senses such as the olfactory or auditory. There have been previous studies on the neural representation of the valence of stimuli perceived by the four senses other than vision with proposals on how the representations of valence may be different across modalities (Chikazoe et al., 2014; Viinikainen et al., 2012). In one study, the medial and lateral orbitofrontal cortex were found to be supramodal areas associated with valence from both vision and gustation, while the ventral temporal cortex was found to be a modality-specific region representing valence from vision and gustation differently, suggesting to some extent the categorization of valence representation along the lines of sensory modality (Chikazoe et al., 2014). Furthermore, studies have suggested that more primitive modalities like gustation require a lesser degree of processing than do more sophisticated and complex modalities like vision, further implying that valence representation may directly depend on the type of sense stimulated (Chikazoe et al., 2014). In addition, studies on auditory valence have demonstrated a parallel activation of the amygdala and auditory cortex in response to sound stimuli, thus enlisting the sensory region specific to the stimulus (Viinikainen et al., 2012). Such established connections between the sensory modality and valence representation suggest a future study examining the categorical representation of valence, as done here, through comparing different sensory modalities such as gustation, audition, or olfaction.

The current study defined the visual categories, nature and man-made, by adaptive value from an evolutionary perspective considering the important connection between emotion and survival. Nevertheless, visual categories split by other means, such as animacy, could serve as a topic for further exploration in the study of valence categorization. In particular, the amygdala has been shown to demonstrate sensitivity to threatening and approaching animate stimuli as opposed to inanimate stimuli (Coker-Appiah et al., 2013). Similarly, the amygdala has also been demonstrated to differ in levels of reactivity to animal stimuli, which are animate, and object stimuli, which are inanimate, based on different background visual information (Cao et al., 2014). As such, categorizing images by animate versus inanimate and observing the valence representation of these two visual categories seems promising, especially with a focus on the amygdala as a region of interest.

In conclusion, the medial OFC of the evolutionarily newer cortical system is able to distinguish the valence of both man-made and natural images, or stimuli of varying levels of evolutionary adaptive value, but the evolutionarily primitive amygdala is able to distinguish only the valence of nature images, or stimuli of high levels of adaptive value. These findings are expected to serve as a starting point for additional investigations into the neuroscientific research of valence.

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