

Opinion

Origins of food selectivity in human visual cortex

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Several recent studies, enabled by advances in neuroimaging methods and large-scale datasets, have identified areas in human ventral visual cortex that respond more strongly to food images than to images of many other categories, adding to our knowledge about the broad network of regions that are responsive to food. This finding raises important questions about the evolutionary and developmental origins of a possible food-selective neural population, as well as larger questions about the origins of category-selective neural populations more generally. Here, we propose a framework for how visual properties of food (particularly color) and nonvisual signals associated with multimodal reward processing, social cognition, and physical interactions with food may, in combination, contribute to the emergence of food selectivity. We discuss recent research that sheds light on each of these factors, alongside a broader account of category selectivity that incorporates both visual feature statistics and behavioral relevance.

Visual cortex regions selective for food

Visually identifying nutritious and safe foods is critical to our survival. Yet, despite the ecological importance of food, decades of research on human higher visual cortex, which led to the discovery of areas selective for faces, places, bodies, tools, and words (Figure 1A) [1-6], failed to identify neural populations with selectivity for food (Box 1). While previous neuroimaging research has observed food-related responses in the visual cortex, such responses were typically attributed to the motivational saliency of food, rather than to selectivity for food as a visual stimulus [7]. Recently, however, three groups independently reported the existence of ventral stream regions that respond preferentially to natural scenes containing food [8-10] (see also [11], Figure 1 and Box 2). These convergent studies were facilitated by a large-scale fMRI dataset, the Natural Scenes Dataset (NSD; [12]). Validating these reports, one group reproduced the identified pattern of food selectivity in an independent, hypothesis-driven fMRI study with new stimulus images and a new population of participants [8]. As further support, a recent study used an unbiased diffusion model to similarly demonstrate a preference for food images for these regions of the ventral stream [13]. By generating images that maximized responses in previously identified foodselective voxels, the study produced plausible images resembling food. This finding strengthens the interpretation of these voxels as selectively responsive to food-related visual stimuli.

The specific factors that drive ventral responses to food images are not yet well understood [14]. In particular, there is currently no clear account for how, either evolutionarily or developmentally, food-selective populations might arise and come to be situated in these particular cortical areas. In contrast to visual categories such as faces, bodies, and words, which each have a great deal of consistency in their low-level visual features and/or relationship to the spatial visual field [15], the appearance of food is highly variable [16,17]. Due to this variability, nonvisual properties related to the behavioral relevance of food may play a particularly important role in driving the emergence of food selectivity.

In this article, we focus on possible contributions of both visual factors and nonvisual factors to the emergence of food selectivity in the visual cortex. First, we assess evidence for a role for

Highlights

Using fMRI, a region of ventral visual cortex has been identified as displaying preferential responses to food images in both natural and isolated contexts. These findings begin to resolve previous inconsistencies in reporting selective visual responses to food.

Color is likely to be an important visual feature contributing to the emergence of food selectivity, with color-biased neural populations tending to overlap with food selective populations.

Cross-modal interactions between visual cortex and areas involved in feeding behavior, such as the insula, may shape functional processing within food-selective visual areas.

Social observation is likely to be an important contributor to early learning about food, with food and social processing potentially interacting in the brain.

Physical affordances of food items recruit a set of regions to manipulate food and these can further interact with the visual processing of food.

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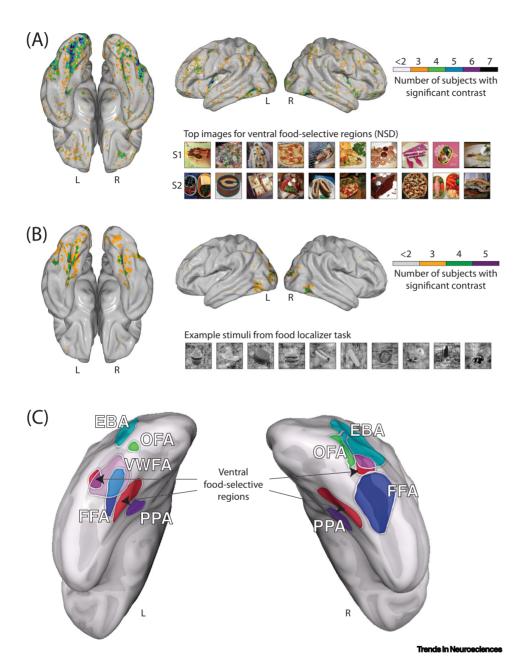


Figure 1. Cortical areas where food selectivity has been observed in recent fMRI studies. (A) Voxels showing selective responses to food-containing natural scene images [8], estimated using data from the Natural Scenes Dataset (NSD) [12] and a generalized linear model. Values are shown on a partially inflated standard surface (Montreal Neurological Institute; MNI) and reflect the number of participants in which a contrast between food and other categories yielded a significant t -statistic. The images shown (bottom right of panel) are the top ten images associated with highest activation in the food-selective regions within ventral visual cortex (shown for two example NSD participants). It can be observed that these images all depict food, in a range of natural contexts. Adapted from [8]. (B) Results of an independent localizer experiment that identifies food-selective voxels in ventral visual cortex, validating the data-driven result in (A) [8]. A visual category localizer [78] was adapted to presented grayscale images of food along with other standard categories (faces, houses), on a phase-scrambled noise background to participants. Values are shown on a partially inflated surface as in (A) and depict the number of participants in which a contrast between food and other categories yielded a significant t -statistic. Adapted from [8]. (C) Average locations of category-selective regions in ventral visual cortex,

(Figure legend continued at the bottom of the next page.)



Box 1. The enigma of visual food preferences

While food has been a long-standing domain of neuroscience inquiry [49,79], food selectivity has not been consistently reported within visual neuroscience. Researchers used food images in paradigms similar to those used to identify selectivity for faces, places, bodies, tools, and words, but reported not finding visual food selectivity [80]. This may be surprising given multiple reports of visual responses to food [7,16,33,34,46,49,50,79]. Here we briefly outline our perspective on why visual neuroscience research often dismissed or failed to report food selective visual areas.

When visual food responses were observed, they have typically been attributed to other properties such as saliency, rather than to food as a visual category. For instance, food responses in left fusiform visual cortex, comparable in magnitude with those for faces, were interpreted as being due to the reward value of food and not to its visual properties [7]. Similarly, higher responses to food images were interpreted as a consequence of increased attention to food in hungry participants rather than to any specialization of visual cortex [49,79]. More generally, in contrast to faces, bodies, and places, the visual appearance of food as ecologically critical has not been a preferred explanation. Instead, visual food responses have been assumed to reflect ecologically important low-level or nonvisual properties of food.

Failures to report food selectivity may also have been compounded by standard fMRI methodologies which often identify responsive regions by averaging across individuals: responses to one category are compared with others, and data from individual statistical maps are combined. Aggregating across participants rests on the assumption of good spatial overlap across individuals. By contrast, other approaches, including those leveraging large-scale neuroimaging datasets [11,12,81,82], allow for analyses to be performed at the single-participant level, which can be particularly critical for identifying regions with variable locations [83,84]. Aggregating across participants was identified as a likely explanation [8] for why previous work did not find robust visual food selectivity [7], as food areas showed greater spatial variability among participants than other category-selective

Recent reports of food selectivity [8-10] may be attributed, in part, to a 'cultural' shift in cognitive neuroscience [11], characterized by at least four methodological advances; larger-scale datasets using natural scenes [11,12,81,82]; better data processing pipelines [85]; innovation in predictive modeling [86,87]; and individual level analyses with greater sensitivity.

low- and mid-level visual features (particularly color) that may be informative for food-related tasks. Second, we evaluate the possible contributions of three key nonvisual factors; a brain network related to eating and reward, of which visual food responses are but one component; social contexts that may influence the acquisition of visual food selectivity during development; and the functional affordances arising from interactions with food (e.g., grasp or substance).

We propose a theoretical framework in which visual food selectivity emerges and is maintained through the interactions of these visual and nonvisual factors. Our proposal is in line with perspectives emphasizing the role of higher visual cortex within wider brain networks that support ecologically critical behaviors [18-23]. Here, we apply the same framework to the category of food, as has been done previously with categories such as words [24] or faces [25]. We suggest that food-selective visual regions, like areas selective for other categories, are shaped by connectivity to domain-relevant systems [25-30]. In this context, the category of food provides an informative case study for how visual properties interact with behaviorally-relevant signals from nonvisual sources as part of ecologically critical processing networks.

Do visual feature statistics contribute to food selectivity?

Due to the topographic organization of the visual cortex, food selectivity may arise as a result of spatially clustered neuronal populations encoding visual features that are statistically more likely to be found in food images. While these features may vary with food category, subgroups of features may support tasks such as food/edibility detection or discrimination among different foods

identified using the localizer task in (B) [8]. Regions were delimited by considering voxels for which the respective contrast is significant for a majority of the participants and are shown on an inflated MNI surface. The newly observed 'foodselective' regions are shown in red. For comparison, we also include regions previously established as selective for faces, (occipital face area, OFA; fusiform face area, FFA), human bodies, (extrastriate body area, EBA), places (parahippocampal place area, PPA), and words (visual word form area, VWFA). Created using the results from [8].



Box 2. Is food selectivity dependent on natural contexts?

Some evidence suggests visual cortex responses to food images may be dependent on the context in which food is presented. Namely, while naturally contextualized food images within natural scenes were reported to elicit responses in the dorsal visual stream and the insular cortex ('taste cortex') as well as in ventral areas, context-free food images only elicited responses in ventral areas [8] (compare Figure 1A and 1B in the main text). One explanation for this observation is that natural context may better invoke the multimodal experience of interacting with food, compared with isolated objects on simple backgrounds. That is decontextualized food images, because of the absence of 'extrafood' information, might not engage the entire network of neural processes in play during everyday food perception. This effect could lead to stronger interactions between visual cortex and other brain regions, including the insula and dorsal visual stream, when viewing food images in natural context.

With this perspective in mind, we note that all three recent studies identifying food selectivity in visual cortex relied on a common dataset collected using natural scene images taken from the COCO dataset [88]. Thus, it is possible that food selectivity itself is more likely to be observed when food appears in natural contexts. Indeed, a recent experiment has failed to find a selective response in ventral visual cortex for 'cutouts' of food images. This possibility suggests that some prior studies of category selectivity may have failed to observe selectivity for food because they relied on images of isolated objects on simple backgrounds [1-6] rather than objects embedded in natural scenes. At the same time, food representations in the adult brain do appear to persist in the absence of contextual information, as food selectivity can be observed using images that either omit or do not include context, color, or grasp affordances [7,8,14]. One possibility is that placing food in appropriate contexts may better recruit the broader multimodal food network, leading to increased signal in food-selective visual areas via feedback connections, and thus increasing the likelihood that food selectivity can be detected with neuroimaging techniques.

on the basis of taste, freshness, nutritional benefit, or level of processing [31]. Across evolution and development, the visual feature statistics of food may plausibly interact with feature-biased neural populations, ultimately influencing the neural localization of food selectivity in the adult brain [32]. This sensory-based visual account predicts a functional and/or anatomical association between high-level responses to food and lower-level visual responses to food-associated features. To be clear, this account does not imply that visual food selectivity is exclusively a consequence of the statistical structure of visual inputs. Rather, statistical regularities in low-level visual features may account for a portion of food-related visual responses in the adult brain. Visual features may also play a more critical role during development when children are learning which natural objects are edible and which foods are associated with their culture and geographical location.

Consistent with this account, an extensive behavioral literature has shown that low- and mid-level visual properties influence observers' judgments of food. Features such as shape, size, texture, variety, and color are associated with taste categories as well as human food preferences and the consumption of food products [33,34]. Among these visual properties, color appears to be particularly important. For example, color facilitates the rapid detection of food during visual search [35] and when identifying food, adults and young children (but possibly not infants) prioritize information about substance, such as color, over other properties [36,37], a phenomenon first observed in macaques [38]. Further supporting a link between color and food perception, men that self-reported as color blind on an online crowd-sourcing platform indicate lower aversion to novel foods as compared with men that self-reported as having normal color vision [39] and findings from another study suggest that observers rely on color as a cue to the calorie content of food, with redder foods tending to be judged as higher in energy than greener foods [40]. The importance of color in signaling edibility also appears central to the eating behavior of non-human primates, where it has been hypothesized that trichromatic color vision was evolutionary selected for based in part on the usefulness of color in estimating the ripeness of fruits [41], although recent work has provided mixed support for this theory [42]. More broadly, according to one hypothesis, color serves as a 'trainable system' that facilitates rapid recognition of behaviorally-relevant object categories [43,44].

Neuroimaging results also implicate color in learning about and detecting food. Notably, preferential responses to food images in the human brain have been observed to overlap with color-sensitive patches previously identified in humans and macaques [10,45]. One possibility is that this overlap



reflects an association between warm, saturated hues and the presence of food. However, a more detailed analysis revealed that color saturation and warmth are encoded independently of food [10], consistent with color metrics only accounting for a portion (sic) of the response variance in food-selective visual areas [9]. Further demonstrating independence between food and color, an independent localizer task revealed that food-selective regions are also identifiable using decontextualized, grayscale images [8] (further work is necessary to better understand responses to decontextualized food). Thus, although color does not appear to be a prerequisite for foodselective visual responses, color may contribute to inferences about substance or material. Consistent with this view, it has been hypothesized that the left medial fusiform gyrus (collateral sulcus), which is roughly the same region of visual cortex that has been identified as sensitive to both color [45] and food [8-10], encodes features related to surface texture and material [27].

Other neuroimaging evidence suggests the role of color in food perception is restricted to particular tasks or contexts. Food-selective responses in visual areas were observed during a color estimation task, but not during an edibility estimation task [46]. Additional studies suggest a secondary role for color in food perception. Individual differences in domain-specific food recognition abilities were identified in the absence of color [39], and while differences have been identified in magnetoencephalographic (MEG) responses to food and non-food images, these responses were not discriminable on the basis of low-level visual features, including color [47]. Relatedly, a recent fMRI study showed that multivariate food representations could not be accounted for by low-level visual properties".

In toto, visual properties such as color or texture may play a role in the emergence of food selectivity and the perception of food (Figure 2). However, associations between food and sensory-based visual properties appear to be insufficient to fully account for the emergence of food-selective neural populations during evolution or development [19]. Thus, we next turn to the potential contributions of nonvisual factors.

A multimodal reward network for food processing

Food engages taste, smell, touch, and sight, making it a uniquely multisensory stimulus. Food consumption also provides immediate reward signals related to flavor, nutritional content, and hunger reduction. In this context, the visual areas with preferential responses to food may be part of a larger functional network related to eating. Within this network, the visual, gustatory, and olfactory properties of food are primarily processed by the visual cortex, the insula, and the piriform cortex, respectively [48]. In addition, the orbitofrontal cortex (OFC) and insula contribute to the multimodal integration of taste information with other sensory modalities [16,49,50], while the amygdala and striatum are involved in integrating sensory properties of food with internal states such as hunger, attention, and reward [49,51,52].

The participation of the food-selective visual areas in a larger network may be mediated by links to these food-associated nonvisual brain regions through long-range neural connectivity. For example, there are anatomical and functional connections between the higher visual cortex and regions involved in the processing of reward and taste, including the insula [53] and OFC [54]. Underscoring a possible functional role of these long-range connections, in individuals with obesity, greater connectivity is found between the midbrain ventral tegmental area and a ventral region overlapping with food-selective visual areas, compared with participants without obesity [55]. Furthermore, the posterior insula, which has been shown to respond to food images with a magnitude inversely proportional to peripheral blood glucose level [56], is more strongly connected in human neonates to the medial portion of the ventral visual cortex than the lateral portion [57]. The boundary between the medial and lateral areas of visual cortex roughly corresponds to



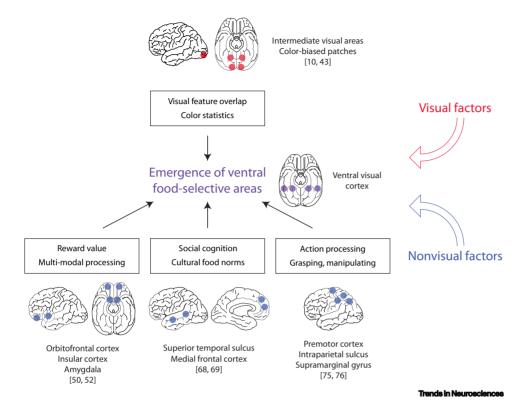


Figure 2. Proposed theory of how visual and nonvisual factors may have contributed - over evolutionary and/or developmental time - to the emergence of food category selectivity in ventral visual cortex. We argue that both the shared visual properties of food inputs (red), as well as signals from areas involved in reward, multi-modal processing, social cognition, and grasp/action (blue) may be contributors to the observed phenomenon of food selectivity in ventral visual cortex (purple). This model provides several predictions that can be empirically tested in future work. See [10,43], [50,52], [68,69], [75,76].

the mid-fusiform sulcus, which has been identified as a dividing line between category-selective regions [29]. This anatomically-based connectivity aligns well with the neuroanatomical locations of the recently identified visual food-selective regions, with the more medial region falling just to the medial side of this sulcus [8-10].

Given the existence of long-range connections between visual and nonvisual areas of the brain, the functional properties of food-selective visual areas may be influenced by nonvisual signals from other brain areas participating in a larger food network. Supporting this possibility, visual responses to food in the fusiform gyrus are modulated by hunger state and hunger-related hormones [58-60]. Additionally, the fusiform gyrus may be involved in estimating the energy content of food [61] and in reinforcement learning of visual-taste associations [62]. Multimodal interactions within a larger food network are also evident in the activation of the insula, an area associated with taste processing, when people view food images [16]. Interestingly, these image-evoked insula responses differentiate between stimuli on the basis of taste [50,63], suggesting experiencing a food stimulus in one modality leads to automatic retrieval of its properties from other modalities [50,63].

We propose that long-range connectivity between visual and nonvisual brain areas involved in eating behaviors may act as a constraint on the development of food-selective visual regions (see also [19]). More specifically, this innate connectivity instantiates a developmental bias that



interacts with incoming visual information to influence where preferential visual responses to food emerge. This proposal aligns with existing theories on other category-selective brain areas, such as those for tools or words [24,26,30]. Under this view, visual food selectivity may be bootstrapped by the formation of associations between food-relevant visual and nonvisual representations (e.g., social cueing, taste, motor interactions with food for eating), as well as signals from other sensory modalities (gustatory and olfactory). At the same time, nonvisual connectivity does not appear to be sufficient to elicit food selectivity within visual cortex. In particular, congenitally blind individuals (who experience normal taste and reward for food) do not show neural responses in visual cortex during taste processing [64]. This finding contrasts with observations made in haptic, auditory, and olfactory tasks, and raises intriguing questions about the relative importance of visual cortex connectivity across different sensory modalities (see Outstanding questions).

Social cues bootstrap the visual representation of food

The high variability of food appearance presents a challenge to the child learner. Failures to identify dangerous foods, foods of low nutritional value, or inedible objects may have serious consequences. Because adults have already acquired both food safety and nutrition knowledge, early food-related knowledge may come from social observation in both passive and active forms [65,66], as well as from explicit language and action instruction during social interactions. Indeed, it has been long observed that food labels can interact with people's enjoyment and appraisal of foods by acting as cues that create expectations of taste, which can be relevant when learning about new foods or foods that are visually ambiguous [67]. Thus, the proposed multimodal network for food processing may incorporate interactions with the social processing network in the brain, including areas in the superior temporal sulcus (STC) and medial frontal cortex (MFC) [68,69].

Studies show that infants process food images differently than young children and adults, providing some evidence for a developmental timecourse in the formation of food representations: in preferential looking tasks, adults tend to prioritize substance-related properties, such as color, over functional properties, such as shape, when reasoning about food; in contrast, infants do not appear to make this distinction [37,65]. These results suggest that infants may lack a preexisting mechanism for generically detecting food, instead relying on social observation, social guidance, and social cues. This early dependence on social cues to detect appropriate nutrition does not pose a threat to survival - human infants are altricial and therefore not responsible for selecting their own food sources [65,66]. Consistent with this point, infants appear to reason socially about food, inferring shared food preferences among adults who socially affiliate with one another and who share a common language [66]. Similarly, adults modeling eating a specific food item increase the acceptance of this item by infants and young children [70,71]. Social learning about food sources has also been documented in non-human primates and rodents [72]. The strong association between food perception and social behaviors extends in the other direction as well: infants infer close relationships between people who share food [73].

An interaction between the food and social domains is also suggested by the recent finding that food-selective regions are adjacent to a region that is involved in face processing [8–10]. Although these food and face areas are mostly nonoverlapping and likely subsume distinct cytoarchitectonic portions of the fusiform gyrus [29], their adjacency may nevertheless suggest a localized functional connection or local 'computation constraint' [19], as the nearby areas may plausibly influence each other's representations. Supporting the proposal that this food/ face adjacency is functional, a principal components analysis across the ventral food-selective regions revealed a dominant component capturing the presence of human figures in images concurrent with food [8]. This component, projected on the brain, reveals a spatial gradient across



food regions, suggesting a smooth transition between areas with sensitivity to only food to areas with sensitivity to social scenes of food, consistent with previous suggestions that semantic selectivity varies smoothly [74]. Functionally, proximity between food- and face-selective areas may enable the food regions to encode mixtures of food and social information [9]. Other work using the same fMRI dataset, but with different analysis methods, found associations between the representation of food and socially important stimuli including faces and bodies [22]. Representational overlap of this kind may serve to integrate visual and social properties of food, facilitating both online inferences and mechanisms for learning about food from social cues. One important open question is whether long-range connectivity to areas like STC and MFC may constitute additional computational constraints on these overlapping representations of food and social information in visual cortex (see Outstanding questions) and how this mechanism may relate to the emergence of face-selective cortical areas [25].

Physical interactions with food facilitate its representation

Many foods are associated with specific actions, such as carefully grasping an ice cream cone or twirling spaghetti around a fork. While the nature of these associated actions can vary widely across individual foods, and even across cultures, information related to food affordances may nonetheless exert a strong influence on how key food visual properties such as size, shape, or material properties are represented in the visual system. In this regard, food bears a high-level similarity to another category of objects whose visual processing has been more extensively studied: tools. Like food, tools are a category with high visual variability, whose similarity is defined primarily based on function and shared affordance properties.

A leading current hypothesis is that visual tool selectivity arises due to connectivity between dorsal pathway computations involved in grasp and ventral pathway computations related to visual properties that influence grasp [30,75,76]. Supporting this claim, patients with parietal lesions showed reduced responses to tool images in the fusiform gyrus [27]. However, the same patients did not show reduced responses to place images, indicating that there is not a generic effect of parietal lesions impacting ventral processing. That is, the interactions between visual and nonvisual systems can be limited to a specific class depending on the information content that is shared [27]. Extending this idea to food, there is some evidence that graspable foods (i.e., banana, hamburger), and tools recruit similar patterns of responses of visual cortex [14]. Thus, one possible source of 'downstream' connectivity driving visual representations of food may be dorsally-mediated information about how foods are prepared or eaten.

Commonalities between the neural responses to images of tools and images of food might appear to offer an alternative explanation to 'ecological importance' for why food selectivity is observed in visual cortex [14]. However, the ecological importance of category selectivity is not an explanation in and of itself; rather it is a high-level constraint that helps understand why such selectivity (and connectivity) exists in the first place. Any complete theory of a functionallydefined system in the brain requires accounts of its origins (e.g., how functionality was acquired over evolution or during development) and its computations (e.g., the nature of the representations and processes over them). The framework proposed here provides an initial step toward such a theory, with action-related representations as one of many contributing factors.

Other lines of evidence suggest that action-related information may not fully account for foodselective visual cortex responses. In the aforementioned study [14], the pattern of neural responses arising from images of tools does not encompass the full pattern of regions activated in response to graspable foods, which include areas in the insula and OFC. Additionally, an account based solely on 'graspability' fails to explain the responses of visual cortex to food



images that cannot be grasped. Indeed, the pattern of food-selectivity in ventral visual cortex persists even when excluding images where the depicted food was not within 'reach' space [8], which suggests that affordance information may not be required to activate these areas. Additionally, information related to actions may not entirely account for the organization of multivariate food representations in the brain. Therefore, action-related information may not provide a complete account for the emergence of food selectivity, instead interacting with the other factors outlined here to give rise to the emergence of food-selective visual areas.

The conceptual link between food and tool representations makes testable predictions for how food representations might be subdivided within visual cortex. For example, within the identified food-selective regions, food representations may be organized in part by their associated actions, such as a distinction between foods that are directly graspable versus those requiring additional objects (e.g., silverware) to manipulate. Another prediction concerns the effects of dorsal stream lesions: patients with parietal lesions who show reduced responses to tool images might likewise show reduced responses to food images, and such effects may vary between foods depending on their associated actions.

Concluding remarks and future perspectives

We endorse a unified framework to reconcile the visual and nonvisual accounts of the hypothesized food selectivity in ventral visual cortex. In this framework, visual properties such as color, nonvisual food properties such as reward value, taste, or grasp, and social cues interact both evolutionarily and developmentally to support the emergence of visual food selectivity. Within this model, sensory-based, visual constraints may be realized as a warm color bias in the regions of the visual cortex where food-selective areas eventually develop; these color-biased regions provide a form of scaffolding that enables more efficient acquisition of behaviorally relevant object representations [43]. However, nonvisual constraints, such as the reward value of food [52], taste [50], hunger state [77], or physical interactions [14], impact visual cortical representations via connectivity between different neural systems [30]. Food representations and processing may also be impacted early in development through social signals that serve to modulate these circuits, thus providing further information on how to identify and select food based on associated visual properties [65,66]. In summary, food selectivity appears to emerge through a confluence of visual and nonvisual factors that include the importance of color for detecting and reasoning about food, the behavioral relevance of food as a rewarding stimulus, the physical manner in which we prepare and eat particular foods, and the tight link between food and social contexts. This model accounts for a wide range of phenomena and raises many unresolved questions that offer promising avenues for future research (see Outstanding questions). More broadly, the model provides a case study for how sensory-based visual inputs and, through connectivity, nonvisual behaviorally-relevant signals jointly constrain the emergence and the organization of ecologically important processing systems in the human visual cortex.

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Declarations of interests

The authors declare no competing interests in relation to this work.

Resources

C. X. Fang, M. Khosla, and N. Kanwisher (2024). Reassessing the food selective component in human visual cortex. Journal of Vision, 24, 1188. doi: 10.1167/jov.24.10.1188.

Outstanding questions

Within ventral food selective areas, are representations of different food subcategories organized topographically, or are they spatially intermingled?

What are the key dimensions that organize the food representational space in the brain, and how do these relate to perceptual and conceptual similarity?

How does food selectivity arise despite the high visual variability of food, particularly across cultures and geographical regions?

How do representations of food differ across cultures and depend on which foods are eaten (e.g., fish-based versus meat-based diets) and how they are eaten (using fingers versus cutlery)?

Other than color, what mid-level visual properties are most critical for food detection and discrimination, and how are they encoded in visual cortex?

How are the co-occurrence statistics of food with related objects, such as utensils, dishes, faces, or hands, reflected in the representation of food?

What role does social context play in food processing across development?

How do task goals and physiological states related to food (e.g., hunger or craving) impact the representation of food?

What is the relationship between food and tool representations in visual cortex, and why do they partially colocalize?

What factors account for the spatial variability in the neuroanatomical location of food-selective regions across individuals?

How early in development do food selective areas arise? How are they connected to other regions, and how does this connectivity constrain their anatomical location?

Why are two areas in ventral visual cortex apparently selective for food images, and what role is played by each?





ⁱⁱC. Coricelli, K.M. Stubbs, R.I. Rumiati, and J.C. Culham (2020). Decoding representations of food images within the ventral visual stream. Journal of Vision, 20, 267. doi: 10.1167/jov.20.11.267.

References

- 1. Sergent, J. et al. (1992) Functional neuroanatomy of face and object processing: A positron emission tomography study. Brain 115, 15-36
- 2. Kanwisher, N. et al. (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci, 17, 4302-4311
- 3. Epstein, R. and Kanwisher, N. (1998) A cortical representation of the local visual environment. Nature 392, 598-601
- 4. Downing, P.E. et al. (2001) A cortical area selective for visual processing of the human body. Science 293, 2470-2473
- 5. Mahon, B.Z. et al. (2023) Higher order visual object representations: A functional analysis of their role in perception and action. In APA Handbook of Neuropsychology (Volume 2: Neuroscience and Neuromethods) (Brown, G.G. et al., eds), American Psychological Association
- 6. McCandliss, B.D. et al. (2003) The visual word form area: expertise for reading in the fusiform gyrus. Trends Cogn. Sci. 7, 293-299
- 7 Adamson K, and Trojani, V. (2018) Distinct and overlapping fusiform activation to faces and food, Neurolmage 174, 393-406
- 8. Jain, N. et al. (2023) Selectivity for food in human ventral visual cortex. Commun. Biol. 6, 175
- 9. Khosla, M. et al. (2022) A highly selective response to food in human visual cortex revealed by hypothesis-free voxel decomposition. Curr. Biol. 32, 1-13
- 10. Pennock, I.M. et al. (2023) Color-biased regions in the ventral sual pathway are food selective. Curr. Biol. 33, 134-146
- 11. Bannert, M.M. and Bartels, A. (2022) Visual cortex: Big data analysis uncovers food specificity. Curr. Biol. 32, R1012-R1015
- 12. Allen, E.J. et al. (2022) Amassive 7T fMRI dataset to bridge cognitive neuroscience and artificial intelligence. Nat. Neurosci. 25, 116-126
- 13. Luo, A. et al. (2023) Brain Diffusion for Visual Exploration: Cortical Discovery using Large Scale Generative Models. 36, 75740-75781
- 14 Ritchie J.B. et al. (2024) Graspable foods and tools elicit similar responses in visual cortex. Cereb. Cortex 34. bhae383
- 15. Hasson, U. et al. (2002) Eccentricity bias as an organizing principle for human high-order object areas. Neuron 34, 49
- 16. Simmons, W.K. et al. (2005) Pictures of appetizing foods activate gustatory cortices for taste and reward. Cereb. Cortex 15, 1602-1608
- 17. Aslan, S. et al. (2020) Benchmarking algorithms for food localization and semantic segmentation. Int. J. Mach. Learn. Cybern. 11, 2827-2847
- 18. Bi, Y. et al. (2016) Object domain and modality in the ventral visual pathway. Trends Cogn. Sci. 20, 282-290
- 19. de Beeck, H.P.O. et al. (2019) Factors Determining Where Category- Selective Areas Emerge in Visual Cortex. Trends Cogn. Sci. 23, 784-797
- 20. Bi, Y. (2020) Concepts and object domains. In The Cognitive Neurosciences (6th edn) (Poeppel, D. et al., eds), pp. 785-792. MIT Press
- 21. Arcaro, M.J. and Livingstone, M.S. (2021) On the relationship between maps and domains in inferotemporal cortex, Nat. Rev. Neurosci. 22, 573-583
- 22. Wang, A.Y. et al. (2023) Better models of human high-level visual cortex emerge from natural language supervision with a large and diverse dataset. Nat. Mach. Intell. 5, 1415-1426
- 23. Contier, O. et al. (2024) Distributed representations of behaviourderived object dimensions in the human visual system. Nat. Hum. Behav. 8, 2179-2193
- 24. Vin, R. et al. (2024) Visual word processing engages a hierarchical, distributed, and bilateral cortical network. iScience 27,
- 25. Powell, L.J. et al. (2018) Social origins of cortical face areas. Trends Cogn. Sci. 22, 752-763

- 26. Bouhali, F. et al. (2014) Anatomical Connections of the Visual Word Form Area J. Neurosci, 34, 37034
- 27 Garcea E.E. et al. (2019) Domain-Specific Diaschisis: Lesions to Parietal Action Areas Modulate Neural Responses to Tools in the Ventral Stream, Cereb. Cortex 29, 3168-3181
- 28. Saygin, Z.M. et al. (2012) Anatomical connectivity patterns predict face selectivity in the fusiform gyrus. Nat. Neurosci. 15, 321-327
- 29. Weiner, K.S. et al. (2017) The Cytoarchitecture of Domain-specific Regions in Human High-level Visual Cortex, Cereb, Cortex 27.
- 30. Mahon, B.Z. (2022) Domain-specific connectivity drives the organization of object knowledge in the brain. In Handbook of Clinical Neurology (187 edn) (Miceli, G. et al., eds), pp. 221-244,
- 31. Coricelli, C. et al. (2019) Distinct brain representations of processed and unprocessed foods, Fur. J. Neurosci, 50, 3389-3401
- 32. Arcaro, M.J. and Livingstone, M.S. (2017) A hierarchical. retinotopic protoorganization of the primate visual system at birth. eLife 6. https://doi.org/10.7554/eLife.26196
- 33. Wadhera, D. and Capaldi-Phillips, E.D. (2014) A review of visual cues associated with food on food acceptance and consumption. Eat. Behav. 15, 4159-4171
- 34. Spence, C. (2023) Explaining Visual Shape-Taste Crossmodal Correspondences. Multisens. Res. 36, 313-345
- 35. Sato, W. (2021) Color's Indispensable Role in the Rapid Detection of Food. Front. Psychol. 12, 5442
- 36. Lavin, T.A. and Hall, D.G. (2001) Domain effects in lexical development: learning words for foods and toys. Cogn. Dev.
- 37. Shutts, K. et al. (2009) Core knowledge and its limits: The domain of food. Cognition 112, 120-140
- 38. Santos, L.R. et al. (2001) Recognition and categorization of biologically significant objects by rhesus monkeys (Macaca mulatta): the domain of food, Cognition 82, 127-155
- 39. Sun. J. and Gauthier, I. (2023) Does food recognition depend on color? Psychon Bull Rev. 30, 2219-2229
- 40. Foroni, F. et al. (2016) Food color is in the eye of the beholder: the role of human trichromatic vision in food evaluation. Sci. Rep. 6, 1-6
- 41. Regan, B.C. et al. (2001) Fruits, foliage and the evolution of primate colour vision. Philos. Trans. R. Soc. Lond. B Biol. Sci. 356, 229-283
- 42. Osorio, D. and Vorobyev, M. (2008) A review of the evolution of animal colour vision and visual communication signals. Vis. Res. 48, 2042-2051
- 43. Conway, B.R. (2018) The Organization and Operation of Inferior Temporal Cortex. Annu. Rev. Vis. Sci. 4, 381-402
- 44. Naor-Raz, G. et al. (2003) Is color an intrinsic property of object representation? Perception 32, 667-680
- 45. Lafer-Sousa, R. et al. (2016) Color-Biased Regions of the Ventral Visual Pathway Lie between Face- and Place-Selective Regions in Humans, as in Macagues, J. Neurosci. 36 1682-1697
- 46. Pohl, T.M. et al. (2017) How task demands shape brain responses to visual food cues. Hum. Brain Mapp. 38,
- 47. Tsourides, K. et al. (2016) Neural correlates of the food/non-food visual distinction. Biol. Psychol. 115, 35-42
- 48. Rolls, E.T. (2008) Functions of the orbitofrontal and pregenual cingulated cortex in taste, olfaction, appetite and emotion. Acta Physiol. Hung. 95, 131-164
- 49. Huerta, C.I. et al. (2014) Neural bases of food perception: coordinate-based meta-analyses of neuroimaging studies in multiple modalities. Obesity 22, 1439-1446
- 50. Avery, J.A. et al. (2021) Viewing images of foods evokes taste quality-specific activity in gustatory insular cortex. Proc. Natl. Acad. Sci. 118, e2010932118

Are dorsal visual regions activated by food also consistently selective for food? How does their function differ from the ventral food areas?

Are the ventral food-selective areas necessary for recognizing and/or interacting with food, or can other neural pathways compensate for damage to these areas?



- 51. Tang, D.W. et al. (2012) Food and drug cues activate similar brain regions: a meta-analysis of functional MRI studies. Physiol. Rehay 106 317-324
- 52. Rolls, E.T. (2023) The orbitofrontal cortex, food reward, body weight and obesity. Soc. Cogn. Affect. Neurosci. 18, nsab044
- 53. Dionisio, S. et al. (2019) Connectivity of the human insula: A corticocortical evoked potential (CCEP) study. Cortex 120, 419-442
- 54. Bolls, F.T. et al. (2020) The orbitofrontal cortex: reward, emotion and depression Brain Communications 2 fcaa196.
- 55. Devoto, F. et al. (2023) How images of food become cravingly salient in obesity. Obesity 31, 2294-2303
- 56. Simmons, W.K. et al. (2013) Category-specific integration of homeostatic signals in caudal but not rostral human insula. Nat. Neurosci. 16, 1551-1552
- 57. Barttfeld, P. et al. (2018) A lateral-to-mesial organization of human ventral visual cortex at birth. Brain Struct. Funct. 223, 3107-3119
- 58. Chen, E.Y. et al. (2020) Hunger and BMI modulate neural responses to sweet stimuli: fMRI meta-analysis. Int. J. Obes. 44, 1636-1652
- 59. Siep, N. et al. (2009) Hunger is the best spice: an fMRI study of the effects of attention, hunger and calorie content on food reward processing in the amygdale and orbitofrontal cortex. Behav. Brain Res. 198, 149-158
- 60. Malik, S. et al. (2008) Ghrelin Modulates Brain Activity in Areas that Control Appetitive Behavior. Cell Metab. 7, 400-409
- 61 DiFeliceantonio A.G. et al. (2018) Supra-Additive Effects of Combining Fat and Carbohydrate on Food Reward. Cell Metab. 28 33-44 63
- 62. Sadler, J.R. et al. (2020) Network organization during probabilistic learning via taste outcomes. Physiol. Behav. 223, 112962
- 63. Avery, J.A. et al. (2023) A common neural code for representing imagined and inferred tastes. Prog. Neurobiol. 223, 102423
- 64. Gagnon, L. et al. (2015) Neural correlates of taste perception in congenital blindness. Neuropsychologia 70, 227-234
- 65. Shutts, K. et al. (2013) Understanding infants' and children's social learning about foods: previous research and new prospects. Dev. Psychol. 49, 419-425
- 66. Liberman, Z. et al. (2016) Early emerging system for reasoning about the social nature of food. Proc. Natl. Acad. Sci. 113, 9480-9485
- 67. Pigueras-Fiszman, B. and Spence, C. (2015) Sensory expectations based on product-extrinsic food cues: An interdisciplinary review of the empirical evidence and theoretical accounts. Food Qual. Prefer. 40, 165-179
- 68. Pitcher, D. and Ungerleider, L.G. (2021) Evidence for a Third Visual Pathway Specialized for Social Perception. Trends Coan. Sci 25 100-110
- 69. Amodio, D.M. and Frith, C.D. (2006) Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7 268-277

- 70. Mura Paroche, M. et al. (2017) How infants and young children learn about food: A systematic review. Front. Psychol. 8, 1046
- 71 Mahmood I et al. (2021) The Influence of Parental Dietary Behaviors and Practices on Children's Eating Habits. Nutrients 13, 1138
- 72. Olsson, A, et al. (2020) The neural and computational systems of social learning. Nat. Rev. Neurosci. 21, 197–212
- 73. Thomas, A.J. et al. (2022) Farly concepts of intimacy: Young humans use saliva sharing to infer close relationships. Science 375 311-315
- 74. Huth, A.G. et al. (2012) A continuous semantic space describes the representation of thousands of object and action categories across the human brain, Neuron 76, 1210-1224
- 75. Gallivan, J.P. and Culham, J.C. (2015) Neural coding within human brain areas involved in actions. Curr. Opin. Neurobiol. 33, 141-149
- 76. Mahon, B.Z. and Almeida, J. (2024) Reciprocal interactions among parietal and occipito-temporal representations support everyday object-directed actions. Neuropsychologia 198, 108841
- 77. LaBar, K.S. et al. (2001) Hunger selectively modulates corticolimbic activation to food stimuli in humans. Behav. Neurosci. 115, 493-500
- 78. Stigliani, A. et al. (2015) Temporal processing capacity in highlevel visual cortex is domain specific. J. Neurosci. 35. 12412-12424
- 79. van der Laan, L. et al. (2011) The first taste is always with the eyes: A metaanalysis on the neural correlates of processing visual food cues. Neurolmage 55, 296-303
- 80. Downing, P.E. et al. (2006) Domain specificity in visual cortex. Cereb. Cortex 16, 1453-1461
- 81. Chang, N. et al. (2019) BOLD5000, a public fMRI dataset while viewing 5000 visual images. Sci. Data 6, 1-18
- 82. Kupers, E.R. et al. (2024) Principles of intensive human neuroimaging. Trends Neurosci. 47, 856-864
- 83. Saxe, R. et al. (2006) Divide and conquer: a defense of functional localizers. Neuroimage 30, 1088-1096
- 84. Nieto-Castañón, A. and Fedorenko, E. (2012) Subject-specific functional localizers increase sensitivity and functional resolution of multi-subject analyses. Neuroimage 63, 1646-1669
- 85. Prince, J.S. et al. (2022) Improving the accuracy of single-trial fMRI response estimates using GLMsingle. eLife 11, e77599
- 86. Yamins, D.L.K. and DiCarlo, J.J. (2016) Using goal-driven deep learning models to understand sensory cortex. Nat. Neurosci. 19 356-365
- 87. Naselaris, T. et al. (2011) Encoding and decoding in fMRI. Neurolmage 56, 400-410
- 88. Lin. T.-Y. et al. (2014) Microsoft COCO: common objects in vontext. In Computer Vision - ECCV 2014. Lecture Notes in Computer Science (Vol. 8693) (Fleet, D. et al., eds), pp. 740-755, Springer