Domain specificity in face perception

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Is face perception carried out by modules specialized only for processing faces? Or are faces perceived by domain-general mechanisms that can also operate on non-face stimuli? Considerable evidence supports the domain-specific view.

A primary goal in scientific research is to 'carve nature at its joints.' This is emphatically true in cognitive science, where philosophers and psychologists have sought for centuries to discover the fundamental components of the human mind. In his influential book *Modularity of Mind*, Fodor[1] contrasts two competing views on the functional organization of the mind. One view holds that the mind is divided according to the content of the information processed. Proponents of this approach seek distinct mechanisms for functions like voice recognition, spatial navigation and perception of visual motion. In the alternative view, the mind is organized instead around the kinds of processes it carries out. Accordingly, mechanisms might exist for functions like judgment, volition and categorization.

The current discussion of the nature of face perception is a microcosm of this long-standing debate[2]. Is face perception carried out by domain-specific mechanisms, that is, by modules specialized for processing faces in particular? Or are faces handled by domain-general mechanisms that can operate on nonface visual stimuli as well?

Evidence for domain-specificity

Many behavioral studies suggest that domain-specific mechanisms are involved in processing faces. For example, face recognition is more disrupted by inversion (turning the stimulus upside down) than is object recognition[3]. Accuracy at discriminating individual face parts (such as the nose) is higher when the entire face is presented than when the parts are presented in isolation, whereas the same 'holistic' advantage is not found for parts of houses or inverted faces[4]. These and other findings[5–7] suggest that face recognition involves special mechanisms that are more inversion-sensitive and more holisitic (that is, less part-based) than those involved in object recognition. Perhaps the strongest evidence that distinct mechanisms may be involved in the recognition of faces comes from the neuropsychological literature. In the syndrome of prosopagnosia[8], patients are unable to recognize previously familiar faces, despite a largely preserved ability to recognize objects. Even more striking are patients with the opposite syndrome. Patient CK is severely impaired at reading and object recognition, yet completely normal at face recognition[9]. Importantly, CK's face-recognition abilities are much more disrupted than those of normal subjects when faces are inverted or fractured into pieces, consistent with the idea that face-specific mechanisms are holistic and inversion-sensitive. Thus the neuropsychology literature contains evidence for a double dissociation between face and object recognition.

Functional brain imaging investigations of the normal human brain have complemented the evidence from neuropsychology. Many studies show that a region in the fusiform gyrus is not only activated when subjects view faces[10,11], but activated at least twice as strongly for faces as for a wide variety of nonface stimuli, including letter strings[12], assorted objects[13,14], animals without heads[15] (but see also ref. 16) and the backs of human heads[17]. Similarly, selective responses to faces are reported using scalp ERPs[18] and MEG[19], as well as direct electrical recordings from the surface of the human brain[20–22]. As this brief overview of the literature shows, considerable evidence supports the domain-specific view: face perception seems to involve different cognitive and neural mechanisms from those involved in the recognition of nonface objects. Note, however, that the question of the domain specificity of face-processing mechanisms is independent from the question of the innateness of such mechanisms, which is not the focus of the present discussion.

Evidence for domain-generality

Faces differ from other objects in several important respects. Whereas it is often sufficient to identify common objects at the 'basic level' (for example, chair, coat, pen), without determining the specific exemplar of the category (my chair, Joe's coat), for faces we usually proceed beyond the general category 'face' to determine the identity of the particular individual. Second, we probably look at and discriminate between faces more than any other class of visual stimuli (with the possible exception of words, discussed later). We are all face experts. Is it possible that the mechanisms we use to process faces are not specialized for face processing *per se*, but rather for making fine-grained discriminations between visually similar exemplars of any category? Or might the putative face-specific mechanisms actually be specialized for making any discriminations for which we have gained substantial expertise? That is, might a domain-general account of face perception be possible?

A seminal study of the behavioral consequences of visual expertise[23] found that expert dog judges show inversion costs when recognizing dogs, much like the inversion costs all subjects show in recognizing faces. On the basis of these results, the authors inferred that it is unlikely that a neural substrate dedicated to face encoding exists. Instead, they hypothesized that the mechanisms involved in face recognition are also engaged when subjects make discriminations between structurally similar exemplars of a category for which they have gained substantial visual expertise. The authors of this study[23] and another[24] propose that face recognition and expert exemplar discrimination both involve extracting 'second-order relational features,' that is, computing the distinctive features of the presently seen exemplar compared to the average of the category. Note however, that these important results[23] are consistent either with a unitary mechanism for the processing of both faces and dogs in dog judges, or with two distinct mechanisms (one for faces and one for dogs) that function in similar ways, at least with respect to inversion. Although it is difficult to choose between

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these two hypotheses based on behavioral data alone, brain-based evidence can provide clues.

Indeed, prosopagnosia is often accompanied by deficits in discriminating between similar exemplars of other nonface categories[25–27], consistent with the hypothesis that a single common mechanism may underlie the discrimination of faces and of different exemplars of nonface categories. On the other hand, this finding is also consistent with the possibility that face recognition and recognition of other expert categories go on in distinct but nearby cortical regions that are frequently damaged together. After all, the chance that a stroke or head trauma to visual cortex will obliterate all of the hypothesized face-processing region of cortex without affecting nearby cortical areas is similar to the chance that an asteroid hitting New England would obliterate all of the state of Rhode Island without affecting Massachusetts or Connecticut. However, brain-imaging studies of normal subjects can contribute importantly here because they have the potential to distinguish between the activation of nearby but distinct cortical areas.

Two neuroimaging studies[28,29] show increased activation of face-sensitive regions of the fusiform gyrus as subjects become experts at discriminating novel categories. However, the 'greeble' stimuli used in these studies are facelike in several important respects. First, they look like animate figures. Second, subjects are trained to identify them using proper names, which is likely to encourage an animate and possibly human interpretation. Third, their key distinguishing features consist of two horizontally displaced parts arranged symmetrically above two vertically displaced parts in a facelike configuration. Thus, activation of face-selective mechanisms by greeble expertise is consistent with the conclusion that face-specific mechanisms may only be recruited for expert subordinate-level discrimination of stimuli that share numerous properties with faces in the first place.

These authors also present stronger evidence[30] for the domain-general hypothesis: in bird experts and car experts scanned with fMRI while viewing birds, cars, faces and objects, the activity in a face-selective region of the fusiform gyrus is weakest during viewing of assorted objects, next strongest for the nonexpert category (cars for bird experts and vice versa), stronger yet for the expert category (cars for car experts, and birds for bird experts) and strongest for faces. Note however that when the fusiform face area was defined using the standard criteria adopted in my lab, face areas could be found in the right hemisphere in only 5 of the 19 subjects in this study; of these, the magnitudes of the expertise and categorization-level effects are quite small, and the response to faces remain at least twice as strong as that to the expert category. Further studies will be necessary to resolve this apparent dependence of effect size on the precise criteria used to localize the FFA. In any event, these findings suggest that both within-category discrimination and visual expertise may account for part of the apparent face selectivity of regions in the fusiform gyrus.

Problems for domain-generality

How far can domain-general accounts go? Can all the behavioral and neural evidence for the 'specialness' of faces be accounted for in terms of the fine-grained nature of face discrimination and the expertise we have with faces? Although a resolution of this question will require considerable further research, reported findings already pose substantial challenges for the domain-general view.

Brain imaging studies provide evidence against a variant of the domain-general hypothesis[23], according to which distinguishing between objects within a category (as opposed to making between-category discriminations) can engage purported face-specific mechanisms even without expertise[31]. The response of the fusiform face area (or FFA) during discrimination of individual faces is over four times as high as that measured during discrimination of individual hands[14]. Further, the response in the FFA when subjects discriminate between hands is no higher (measured in percent signal change, or as a ratio of the response to faces) than when such fine-grained discrimination is not required (that is, when the same subjects passively viewed either hands or assorted objects). Similar results are obtained when discrimination between individual faces is compared to discrimination between individual houses[17]. These data show that within-category discrimination is not sufficient to strongly engage the FFA. Note further that there is substantial evidence that the FFA may not be involved (exclusively) in face recognition, but may instead (or in addition) be involved in face detection[17,32]; if these arguments are right, then they also refute the (exclusive) role of this area in expert within-category discrimination.

Concerning the role of visual expertise, alphanumeric characters are the only visual stimuli for which visual expertise is on a par with expertise for faces (at least for academics!). Yet the response of face-selective regions in the fusiform gyrus is extremely low during viewing of letter strings[12]. One might also argue that another category of stimuli for which we do expert discrimination is places or scenes, yet the FFA responds only very weakly to photographs of indoor and outdoor scenes[33].

Thus considerable evidence shows that the FFA does not consistently produce a strong response during either discrimination between similar exemplars of a nonface category or during viewing of nonface stimuli for which the subject has gained visual expertise. Instead, numerous findings support the domain-specific view: the presence of faces *per se* seems to be an important determinant of the FFA response.

Although it is not clear how the bird and car expertise results[30] can be reconciled with these earlier studies, one possibility is that the expertise effects in this study may in part reflect the greater interest and attentional engagement the subjects may have had in the category for which they were expert, compared to the category for which they were not expert. This hypothesis is consistent with prior demonstrations that the fusiform face area can be strongly modulated by visual attention[34,35] and that in this study expertise produced activations that extended well beyond the FFA[30] even into one area (the parahippocampal place area, or PPA) that is completely unresponsive to faces[33,36]. (The complete failure of the PPA to show any activation for faces above that for fixating on a point argues against a similar attentional account of the FFA activation for faces.) Note, by the way, that this activation of the PPA for expert within-category discrimination of nonfaces, but not for faces, shows that the two processes produce different activations, and a single domain-general mechanism cannot account for both.

Thus, conflicting neuroimaging data raise questions for the claimed roles of both expertise and within-category discrimination in the activation of face-specific regions of cortex. Further, even if the activation of the FFA by expertise and/or within-category discrimination is found more consistently in the future, such imaging data leave two important questions unanswered. First, activation of the same area in an fMRI study by faces and by stimuli for which the subject has gained expertise is consistent (as the authors of ref. 30 note) with the possibility that the response of this area reflects two distinct but physically interleaved neural populations (for example, one for faces and one for cars in car experts). Second, activations of a given cortical area in any imaging study need not reflect neural computations necessary for the task. Next I consider evidence from neurophysiology bearing on the first question, and evidence from neuropsychology bearing on the second.

In two recent studies, monkeys were intensively trained over several months to discriminate between visually similar stimuli, and neurons selectively responsive to stimuli from the trained set were found in inferotemporal cortex after training[37], in greater proportion than those found before training[38]. A critical question is whether these neurons tuned to the newly trained stimuli were the same or different as the face-selective neurons reported previously[39,40]. Although these two studies were not designed to systematically test this question, responses both to the trained stimuli and to faces were collected in both studies. Neither study found a tendency for cells responsive to the trained stimuli to also be particularly responsive to faces[41] (K. Tanaka, personal communication), and anatomical information from one study[41] suggests that the two populations are even physically segregated.

Indeed, the possibility that individual neurons might be tuned to two very different stimulus types (for example, faces and stimuli from the trained set) seems implausible given the known response properties of inferotemporal neurons[40]. It seems more likely that a distinct neural population would be tuned to the features of each visual category for which the monkey or person had gained expertise. If, as this preliminary evidence from monkeys suggests, distinct neural populations and cortical loci are involved in face recognition and in making expert discriminations within a (nonface) category, then it would be difficult to argue for a single domain-general mechanism for all expert within-category discrimination.

Observing neural activations with fMRI or single-neuron physiology can provide information about the neural populations that respond in a particular task, but these techniques cannot determine which of these activations reflect computations that are necessary for the task. Neuropsychological studies are particularly helpful here, and indeed they raise the greatest challenge to domain-general accounts of face processing.

First, although several prosopagnosic patients are impaired at both face recognition and at discriminating between visually similar exemplars of nonface categories (see above), the deficit in other prosopagnosic patients is more specific. For example, although patient MT[42] is prosopagnosic, he is nonetheless normal at discriminating between brands and models of cars, as well as between different fruits and vegetables. Further, the severely prosopagnosic patient WJ[43], who became a sheep farmer after his stroke, learned to recognize and name many of his sheep, and performs much better on tests of sheep recognition than on comparable tests with human face stimuli. Another patient is profoundly prosopagnosic despite showing an excellent ability to discriminate between different models of the same make of car, a category for which he had previously gained visual expertise[44]. Cases such as these suggest that prosopagnosia is not simply a general loss of expert subordinate-level discrimination.

Most of these patient studies report only accuracy measures, so it is possible that very slow reaction times occurred in some conditions, suggesting a subtle deficit that eluded detection when only accuracy measures were used[45]. Indeed, it will be important for future patient studies report both accuracy and reaction time data to avoid such ambiguities. Nonetheless, preliminary evidence from developmental prosopagnosic subject BC indicates that despite his severely impaired performance in the recognition of faces[46], his d' and reaction time are no different from controls in an analogous task in which the stimuli were shoes, (B. Duchaine, personal communication). It will be of particular interest to test the ability of patients like BC to make discriminations on categories for which they have gained expertise.

The converse case is even more striking. Patient CK, who has selectively preserved face recognition, is unable distinguish between individual airplanes or tin soldiers, despite being an expert at both before his accident[9,47]. Thus mechanisms that are sufficient for face recognition are evidently not sufficient for expert subordinate-level identification of nonfaces.

In sum, double dissociations between face recognition and expertise and/or within-category discrimination of nonfaces in the neuroimaging, neurophysiology and neuropsychology literature provide strong evidence that distinct neural substrates underlie these processes. Further, the evidence from patient studies shows that even if face-specific mechanisms are sometimes activated by nonface stimuli, such activations are apparently neither necessary nor sufficient for the expert discrimination of exemplars of those categories.

Varieties of domain-generality

Despite the substantial evidence against a domain-general account of face recognition, it is always possible that future work will prove this hypothesis to be right. It is therefore worth stepping back to consider more closely what might be entailed in the domain-general account.

If a common mechanism existed that was necessary for both face recognition and for expert discrimination of visually similar exemplars of a nonface category (but not for 'basic-level' categorization of objects), what would that mechanism do? One hypothesis is that attaining expertise in discriminating faces, cars, or other categories entails the discovery and increased use of the visual features that distinguish different exemplars of that category. However, a key problem here is that the visual features that are diagnostic in discriminating between cars (for example) are bound to be different from those that are diagnostic in discriminating between faces. If the job of the proposed domain-general mechanism is to encode distinguishing features of the exemplars of each category, then in what sense would the mechanisms involved in doing this for two different expert within-category discriminations be any more closely related to each other than either is to the mechanisms involved in basic-level recognition?

One of the classic claims about the way that face recognition differs from object recognition is that face recognition is more holistic or configural[4]. What exactly is meant by configural or holistic processing? One possibility is that holistic processing of faces results from the tendency of face-selective cells to respond to the whole face, rather than to parts of the face. Indeed, work using the stimulus-reduction method[40] shows that the image of a face cannot be simplified without losing maximal activation of face-selective cells. (It is also true, however, that some face-selective cells respond well to a particular face feature or set of features.) In contrast, the preferred stimuli for other nonface-selective cells in inferotemporal cortex are typically simpler, often corresponding to features rather than whole complex objects[48]. Thus, the selectivities of cells in inferotemporal cortex are consistent with the idea that faces are processed in a more configural or holistic fashion than are nonface stimuli. Is the same also true of nonface stimuli for which the person or monkey has obtained expertise? It is argued[49] that although the selectivity of trained cells' responses might be reducible to less-complex feature constellations, these data are more consistent with the hypothesis that these cells respond to the whole object (as seen from a particular point of view). These preliminary data are consistent with the idea that expertise in discriminating exemplars of a category leads to the formation of neurons responding holistically to exemplars of that category. Nonetheless, it would be surprising if individual neurons coded for both whole faces and, for example, whole cars (in car experts). Assuming they did not, it would be strained to argue that the set of all cells, each one tuned to one of two very different kinds of whole objects for categories on which the subject had gained expertise, constitutes a domain-general mechanism for expert within-category discrimination.

Another version of the domain-general story[23] proposes that what is common to face recognition and expert within-category discrimination of nonfaces is that each is done by the extraction of second-order relational features, that is, deviations from the average member of the category. The challenge for this view is to provide an account of how the existence of a common mechanism for the extraction of second-order relational features is not ruled out by the data reviewed above.

Conclusions

Ultimately, the answer to the question of whether face processing is domain specific will require us to decide which of the many possible criteria of domain specificity are central: first, the most common use of the module; second, the possible use the module can be put to under some circumstances (even if these are rare); third, the functions for which the module is necessary (rather than simply involved); fourth, the origins of the module in the development of the individual[50,51] or the evolution of the species or both. Face processing is likely to be domain-specific according to the criteria of common use and origins, because for almost all humans (and probably also for their primate ancestors), faces are the primary if not the only stimulus category for which we are experts at making within-category discriminations. As argued above, existing neuropsychology data argue for domain-specificity of face recognition according to the criterion of necessity.

The car and bird expertise study[30] tests the possible use of a module. However, this criterion is generally considered a weak indicator of domain specificity. Sperber[52] argues that human cognition is likely to be characterized by the flexible use of even domain-specific mechanisms. Pinker[53] argues against the actual use criterion most pointedly: "The only thing that can be special about a perception module is the kind of geometry it pays attention to, such as the distance between symmetrical blobs…If objects other than faces (animals, facial expressions, or even cars) have some of these geometric features, the module will have no choice but to analyze them, even if they are most useful for faces. To call a module a face-recognizer is not to say it can handle only faces, it is to say that it is optimized for the geometric features that distinguish faces because the organism was selected in its evolutionary history for an ability to recognize them" (pp 273–274).

Carving nature at its joints has rarely been straightforward in any scientific field, and the effort to discover and characterize the fundamental components of the mind is no exception. Although Fodor[1] argued that modular organization was restricted to perceptual and language systems, intensive research is now striving to discover the organization of higher-level cognitive functions. A vigorous debate is now addressing the question of whether discrete functional components exist in the frontal lobes, and—to the extent that they do—whether they are organized along process-specific or domain-specific lines, or both[54]. It seems unlikely that all of cognition will be subserved by discrete modular mechanisms, and also unlikely that all modules that exist will be domain specific. A more reasonable hypothesis is that the degree of modularity and the degree of domain specificity within modules will vary across the brain and across aspects of cognition.

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