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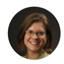
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Beyond faces and modularity: the power of an expertise framework

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Studies of perceptual expertise typically ask whether the mechanisms underlying face recognition are domain specific or domain general. This debate has so dominated the literature that it has masked the more general usefulness of the expertise framework for studying the phenomenon of category specialization. Here we argue that the value of an expertise framework is not solely dependent on its relevance to face recognition. Beyond offering an alternative to domain-specific accounts of face specialization in terms of interactions between experience, task demands, and neural biases, expertise studies reveal principles of perceptual learning that apply to many different domains and forms of expertise. As such the expertise framework provides a unique window onto the functional plasticity of the mind and brain.

> 'Perhaps the most serious barrier to resolution of the nature–nurture dilemma is the dearth of efforts to manipulate both components in the ontogenetic equation underlying the development of complex behaviors.' [1]

Introduction

Many studies of perceptual expertise were initially motivated by the domain-specificity debate. Supporting domain-general arguments, we found that putatively face-specific cognitive and neural mechanisms are recruited for skilled individuation of non-face homogeneous categories, such as birds, cars, dogs, and even novel object classes such as Greebles [2–6]. However, in recent years the expertise framework has evolved to address broader issues of perceptual categorization despite the fact that critiques of our approach still focus on domain-specificity [7–10].

While not diminishing the importance of questions regarding modularity, we argue that it is a mistake to limit discussion of expertise to this one issue. Such a view polarizes researchers into opposing camps, limiting the relevance of findings to one perspective. We prefer to view the expertise approach as an *extension* of the face processing literature, rather than an alternative to it. Moreover, the usefulness of studies of expertise does not hinge upon whether expert mechanisms are isomorphic to those supporting face recognition. Indeed, we doubt whether all types of expertise recruit the same processes used for face recognition. In short, we feel that the preoccupation with the domain-specificity debate masks the potential of the expertise framework to address general issues related to category specialization and cortical plasticity.

To that end, we emphasize the value of the expertise approach as a tool for examining fundamental issues related to category specialization. We also highlight how this approach can be used to study types of expertise that are quite different from the visual recognition of homogeneous object classes. Finally, we discuss outstanding issues concerning the relationship between different types of expertise. We hope to stimulate research that goes beyond questions of faces and modularity, thereby gaining a better understanding of cortical function and the cognitive mechanisms underlying category specificity and perceptual skills.

The expertise framework: addressing fundamental questions

We have used manipulations of expertise to examine questions that are of general relevance to the function and plasticity of the visual system, including questions on the acquisition, generalization and loss of expertise. The experimental framework we have developed provides converging evidence from many stimulus domains and varying methodologies. For example, we have studied both real-world and laboratory-trained experts, the latter having the advantage of providing control over variables that would not otherwise be possible.

Acquisition of expertise

Studies with adults allow us to investigate cortical plasticity in the mature brain, presumably after any 'critical period' for the acquisition of perceptual expertise has passed. Expertise training typically involves discrimination practice at both categorical and individual levels, continuing until response times are equivalent [11]. The 10 h of Greeble laboratory training our subjects usually receive is far shorter than the 10+ years once thought to be necessary for the acquisition of real-world expertise [6], yet such training has produced striking behavioral and neural changes. At least two brain regions become

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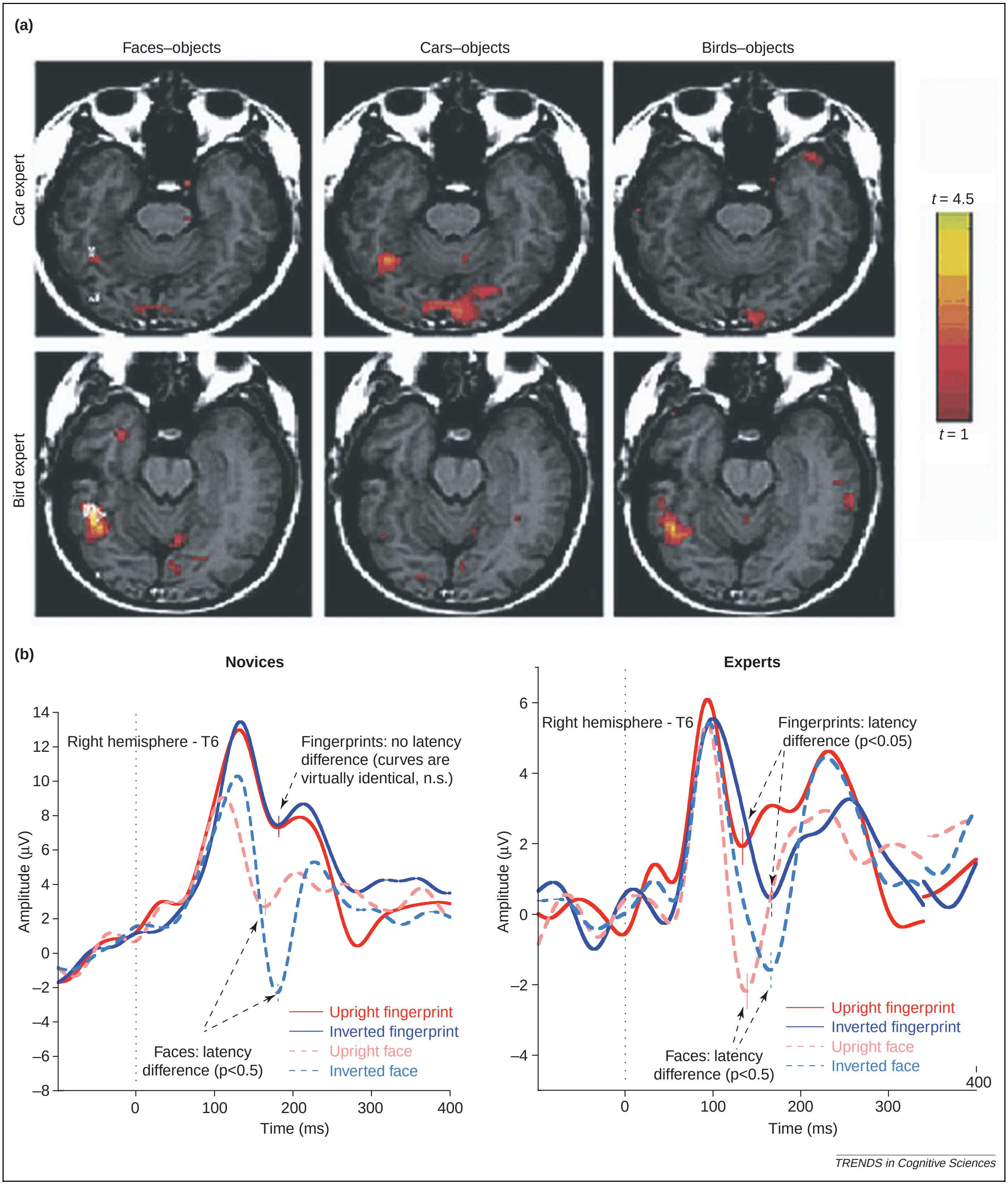

Figure 1. Neural markers of expertise for homogeneous objects. (**a**) Example of expertise-related activity in the right FFA [2]. The t-maps compare activation for faces, cars and birds with activation evoked by objects in a one-back location task for a representative car expert (top row) and bird expert (bottom row). Car experts showed an expertise effect in the right FFA for faces and for cars, but not for birds, whereas bird experts showed an expertise effect in the right FFA for faces and birds, but not for cars. (**b**) Example of expertise-related responses of the N170 component. The N170 is an electrophysical component that shows an inversion effect (delayed for inverted relative to upright orientation) for objects of expertise. Pictured here are the results of a study on fingerprint expertise. Fingerprint novices (left panel) showed an inversion effect for faces but not for fingerprints, whereas fingerprint experts (right panel) show a delayed N170 to both inverted faces and inverted fingerprints relative to their upright counterparts. Panel (b) reprinted with permission from [48].

Box 1. Behavioral markers of expertise

Entry-level shift: Novices identify objects at the basic level more efficiently than at a more specific, subordinate level [44] but expertise can lead to faster responses at the subordinate level [45] as training progresses (Figure I). This entry-level shift has been demonstrated for faces, birds, dogs and Greebles [5,18,45,46].

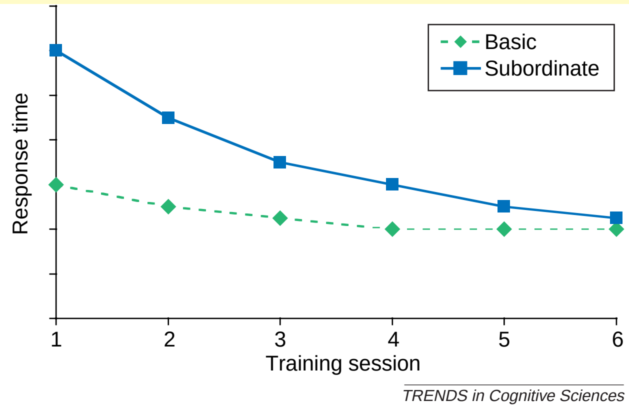

Figure I. Hypothetical data showing the entry-level shift across training sessions. Statistical equivalence between response times for basic and subordinate judgments is used as a criterion for expertise in many training studies.

Holistic processing: Experts encode information over a wider spatial extent than do novices. As such, information across the entire object is likely to affect their behavior and they are less able to attend selectively to single parts [13] (Figure II). Holistic processing has been demonstrated for expertise with faces, Greebles, cars and fingerprints [11,13,41,47–51].

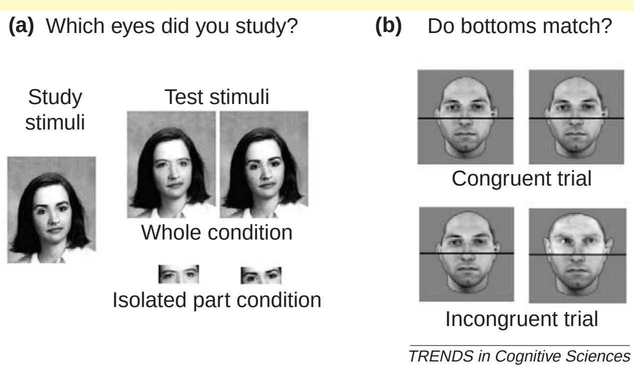

Figure II. Two tasks used to assess holistic processing. **(a)** The part/whole task. Holistic processing is indicated by a greater advantage for part recognition when the test stimuli are wholes, than when the test stimuli are isolated parts. **(b)** The composite task. Holistic processing is indicated by greater interference from the irrelevant half in a parts-matching task: performance is poorer when responses to the bottom and top halves are mismatching (incongruent) than when the responses to bottom and top halves are matching (congruent).

Relational processing: Experts are more likely to encode information about the spatial relations between the parts of an object [13] (Figure III). Relational processing has been demonstrated for expertise with faces and Greebles [11,13,52–55].

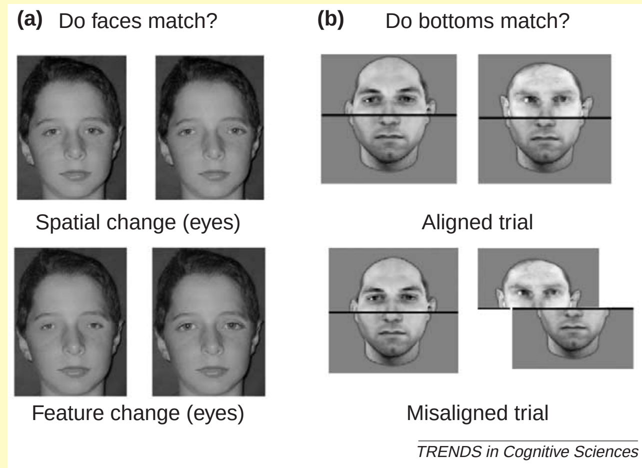

Figure III. Two tasks used to assess relational processing. **(a)** The isolated change task. Sensitivity to *local* spatial information can be measured by a matching task in which the spatial relations between parts have been manipulated. Sensitivity to spatial changes is usually compared with sensitivity to feature changes (a change in feature size or shape). **(b)** The composite task. Sensitivity to *global* spatial information can be measured by a release from interference when object parts are misaligned: there is more interference when the parts are aligned than when misaligned.

selectively more active to Greebles as expertise is acquired: the 'fusiform face area' (FFA; see Figure 1a), and the 'occipital face area' (OFA) [11]. Three behavioral markers have also been obtained with the onset of Greeble expertise: a subordinate-level shift, holistic processing, and relational processing [11–13] (Box 1). We have also begun to uncover the relationship between these behavioral changes and concurrent neural changes. We found that changes in FFA activity correlated with behavioral measures of holistic processing, but not relational processing, suggesting that the two forms of 'configural' processing might be dissociable [13]. This conclusion is supported by the recent finding that FFA activity is not correlated with relational face processing [8]. Such conclusions are enabled in part because expertise studies are able to examine the relationship between cognitive and neural mechanisms over time as well as over individual differences.

Box 2. When experts perform like novices

Despite numerous studies demonstrating that expertise with various homogeneous categories modulates FFA response [3,5,56], the expertise hypothesis continues to be controversial. For example, some studies fail to find expertise effects in the FFA for certain non-face object categories [7–9]. However, such studies fail to show any expertise-related neural activity, even outside face-selective areas, a result that can be difficult to interpret. This raises the interesting possibility that experts sometimes perform like novices within their nominal domain of expertise. Two factors might prompt such behavior. First, although it has been hypothesized that experts engage expertise mechanisms automatically, recent evidence suggests that task demands can affect the degree to which these mechanisms are engaged. For example, the FFA is more active during an old/new recognition task than during a passive viewing task, for both expert and non-expert categories (including objects, lepidoptera and faces) [9]. Second, recruitment of expert mechanisms is also dependent on stimulus properties: Expert effects do not fully generalize across different races of faces, [17] dog species, [6] bird species [18,57] or Greeble sets with different geometric properties [11]. Such limits in the generalization of expertise suggest an explanation for why some studies have failed to replicate expertise-related FFA activation in real-world experts. Specifically, a study of Lepidoptera experts [9] used Lepidoptera species that were unfamiliar to the experts and a study with modern car experts [8] used, in the fMRI tasks, mostly antique cars. A better understanding of the conditions under which expert mechanisms are engaged or not helps to explain why these particular studies did not obtain effects of expertise, and enhances our understanding of object recognition more generally (Figure I).

Figure I. Will modern car experts show an 'other-race effect' for modern versus antique cars, similar to the 'other-race effect' for faces?

Generalization within object domains

We are also interested in how perceptual skills generalize to new exemplars. It is often held that it is the efficient generalization to new exemplars within a trained category that distinguishes expertise from stimulus-specific perceptual learning [14]. Thus an important characteristic of our training studies is that the behavioral and neural effects of expertise training are assessed using untrained (unfamiliar) exemplars. At the same time, it is crucial to define carefully what counts as a valid object domain for generalization.

Research on perceptual skill acquisition often conceptualizes object categories according to basic-level definitions (e.g. faces, dogs, cars, butterflies), but it is not the case that perceptual skills necessarily generalize to all exemplars within such wide domains [6]. For example, we are much better at remembering faces of our own race than faces of other races [15] and the FFA and other face-selective regions show higher responses to own-race than to other-race faces [16]. Such effects can be explained by differences in experience that lead to different processing styles for own- versus other-race faces. For example, the degree of holistic processing for other-race faces is related to the amount of exposure to these races [17]. Thus, even within the highly expert domain of faces, experience affects how different exemplars are processed and, consequently, how well expertise generalizes to new exemplars.

Many studies of expertise have addressed generalization by manipulating factors that may or may not contribute to the transfer of skills. Thus far, we have identified two factors important for expertise generalization: (i) The level at which exemplars are discriminated; that is, mere exposure is not sufficient. For instance, subjects showed good discrimination skills for new exemplars and species of bird categories trained at a the subordinate species level (great grey owl versus eastern screech owl), but not for bird categories trained at the basic family level (owl versus wading bird) [18]. (ii) Laboratory training studies have highlighted the importance of geometric similarity for generalization. In particular, perceptual skills generalize to new Greebles that are geometrically similar to those used during training, but not to new Greebles that are distinguishable only by information that was not relevant to training tasks [11]. Such results might help to account for some of the conflicting evidence regarding the relationship between expertise for faces and non-face objects (Box 2).

Loss of expertise

We have used similar methods to investigate the cognitive impairments underlying category-specific visual deficits such as prosopagnosia. A study that manipulated discrimination difficulty *within* object classes revealed that the two prosopagnosics tested had deficits in fine-level discrimination for both faces and non-face objects [3], thereby implicating a domain-general impairment, although the specificity of prosopagnosic deficits continues to be debated [19].

Expertise training in subjects with visual recognition deficits can also lead to novel insights. A recent study found that expert processing is spatially limited in some types of prosopagnosia: discrimination of fine-grained relational and featural information was impaired for the eye region but spared for the mouth region. Although this prosopagnosic subject was eventually able to reach our nominal criterion for expertise following extensive Greeble training, identification of both faces and Greebles was based primarily on a single feature (the mouth for faces, and the upper appendage for Greebles) [20]. This spatially graded loss of expertise raises the interesting possibility that expert mechanisms might also be acquired in a spatially graded manner. Consistent with this hypothesis, Greeble training studies with longer training protocols show holistic processing across the entire Greeble [12], whereas a study with a shorter training protocol resulted in holistic processing for only the upper half of each Greeble [13].

Thinking about visual deficits in terms of expertise can also provide some insight into face processing in autism. Specifically, autistic subject DD shows no evidence of face expertise and no face selectivity in the fusiform gyrus, yet exhibits robust fusiform selectivity in response to cartoon characters for which he is highly familiar [21]. This suggests that DD's face deficit is not due to impaired expertise mechanisms *per se*, but to mechanisms that modulate interest to faces. Similarly, impairments to non-expertise mechanisms could be central in certain cases of developmental prosopagnosia [19]. Such observations raise the possibility that some individuals with impaired face recognition might benefit from face training. That is, a training protocol could supply the external motivation to support the sort of experiences necessary to develop face expertise [22].

Such studies demonstrate how the expertise framework goes beyond questions of domain-specificity to address issues such as the relationship between behavioral and neural mechanisms, principles of skill generalization, and the specific cognitive and neural processes underlying perceptual impairments. Techniques arising from the study of expertise might also provide useful diagnostic and rehabilitation tools in cases where expertise mechanisms are intact. However, the examples we have presented to this point give a somewhat limited view of the usefulness of the expertise framework because they are restricted to visual expertise for homogeneous objects. Next, we discuss how a similar approach can be applied to other types of expertise.

Varieties of expertise

Much of our research emphasizes the fact that visual expertise recruits similar cognitive and neural mechanisms across many different categories. However, it is not the case that all types of expertise rely on identical mechanisms. Expertise with stimuli that vary radically from the geometry and functional goals of homogeneous object individuation do not engage the FFA, but recruit other, functionally appropriate, regions. For example, words, unlike faces, do not share a first order configuration. Rather, the meaning of words depends upon the identity and the serial order of a restricted set of letters.

Moreover, word reading should be invariant across changes in capitalization and font. Thus it is not surprising that expert word reading is not associated with the FFA, but with a different brain area in the left fusiform gyrus, dubbed the 'visual word form area' (VWFA) [23]. Interestingly, *single* letter identification is associated with selective activity in yet another part of the left fusiform [24,25] (Figure 2), and is also associated with enhanced N170 event related potentials (ERPs) bilaterally [26]. Currently, anatomical sources of the N170 are still debated, however such results suggest that this ERP component might be a marker for expert processes for different categories (e.g. faces, objects, fingerprints, letters) that could be localized in different brain areas [27] (Figure 1b).

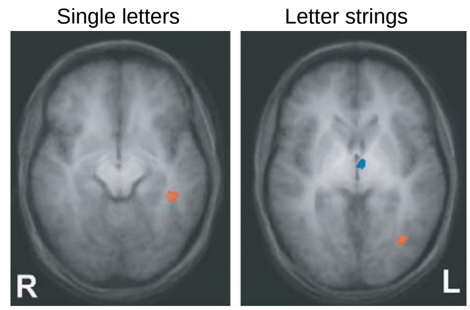

Figure 2. Expertise-related activity for single Roman letters and Roman letter strings during a one-back go-no-go letter-matching paradigm [25]. The single Roman letter area was defined by the conjunction of single Roman letters versus single Chinese characters and single Roman letters versus single digits. The Roman letter-string area was defined by the conjunction of Roman letter-strings versus Chinese character-strings and Roman letter-strings versus digit strings.

Still another type of visual expertise relies on local qualitative shape contrasts rather than configural information [28]. It seems unlikely that such expertise would recruit FFA any more than basic-level object recognition. Chess expertise, sometimes thought of as a cognitive skill, might also have a significant visual component [29]. Indeed, the rapid recognition of the complex spatial relations between pieces is thought to be crucial in playing chess at the expert level. As such, it is not surprising that a recent study found that chess experts, but not novices, show category selectivity for valid chess boards (but not invalid chess boards) in the region of the right fusiform gyrus [30].

Of course, all of these examples still rely on *visual* expertise. A similar approach can be used to study cortical plasticity in other modalities. For example, some birders are able to identify individual bird species through both vision and audition. Consistent with brain organization by modality, bird song elicits selective activity in auditory cortex that is modulated by expertise (Brodmann Area 22). Interestingly, birdsong also elicits expertise-related activation in both lower- and higher-level visual areas as well, including a region in the right fusiform gyrus (Ellis, Chung and Tarr, unpublished). This fusiform activation is adjacent to, but not overlapping with the functionally defined FFA. Similar auditory-related activation in regions adjacent to the FFA has been found for recognition of familiar voices [31]. Such expertise-related crossmodal activation might arise from multimodal representations for specific objects (e.g. a given person or bird species), from visual imagery elicited by auditory stimulation, or from domain-general expertise mechanisms within the fusiform gyrus.

Finally, behavioral markers associated with expert object recognition are also obtained when subjects are trained to identify 2-D and 3-D objects by touch. For example, experts but not novices show better tactile recognition of upright patterns than inverted patterns, and better recognition of object wholes than object parts [32]. At present, the neural substrates recruited by tactile expertise and their degree of overlap with those recruited by expertise in other domains remain to be specified. Worth noting, however, is that the criterion for Greeble expertise (identification as rapid as categorization) is reached with about the same amount of tactile training as visual training - this despite our greater experience recognizing objects visually [33]. Studies that manipulate the levels of expertise with the same object domain across modalities might be used to examine whether expertise in one modality transfers to that domain in another modality [34,35].

The studies reviewed in this section illustrate the usefulness of the expertise framework as it is applied to a variety of stimulus types and sensory modalities. In some instances, we see evidence of common cognitive and neural mechanisms, whereas in others the evidence points to non-overlapping cognitive and neural mechanisms. In the next section, we discuss the importance of studying the relationship between different domains of expertise.

Defining the relationship between types of expertise

One goal of the expertise approach is to identify the cognitive and neural mechanisms necessary to achieve perceptual expertise within a given domain. A second and no less important goal is to define the relationship between the mechanisms recruited by expertise in different object domains. This is significant not simply because it speaks to the question of domain-generality, but because it can help identify principles of cortical organization at the functional level. Several recent studies have addressed this question by quantifying the spatial overlap between the category-selective regions in the fusiform gyrus for faces and other domains of expertise.

Two different fMRI studies (one using butterflies, another using cars) found that the overlap in activation for faces and for the expert domain was smaller than the overlap for faces across different blocks or tasks [8,9]. However, because we understand so little about neural coding, it is difficult to know how to interpret these results. First, it is unclear what degree of overlap signifies dependent versus independent mechanisms. Indeed, there is good evidence that neural codes for object categories, as measured by fMRI, are distributed, yet still overlapping. For example, voxels that are maximally active for one object category are also involved in classification of other object categories [36,37]. Second, it is important to distinguish topology of structural properties from topology of cognitive functions. Many visual areas, for example V1, exhibit spatially selective coding for different stimulus properties (e.g. different orientations), yet functional equivalence across a much wider brain region (detection of orientation) [38]. Thus, even completely non-overlapping regions might not necessarily signify independence at the functional level, particularly if they are adjacent. At the same time, we should acknowledge that fMRI has limited spatial resolution. As such, current fMRI methods might reveal overlap between category-specific responses at the population level that are conceivably resolvable at the neuronal level.

An alternative to measuring spatial overlap is examining *functional* overlap through dual task paradigms. If the perception of two objects share overlapping cognitive and neural mechanisms at the functional level, then a task that requires simultaneous processing of both objects should reduce the availability of the shared process

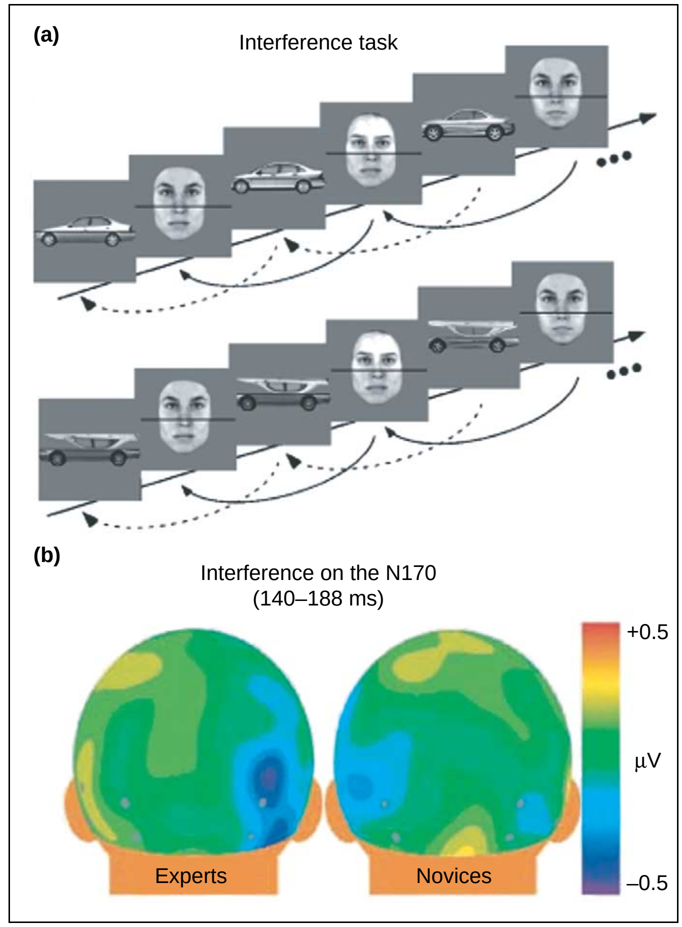

Figure 3. Example of how dual-task interference paradigms can assess independence of cognitive processes related to expertise. **(a)** Experimental design of a two-back task used to measure whether holistic processing of cars interferes with holistic processing of faces [41]. Subjects were instructed to attend only to the bottom half of all objects, and for each one, to make a two-back judgment on whether the bottom matched that of the last object of the same category. Holistic processing is indexed by the amount of interference from the to-be-ignored top, which either matched or mismatched independently of the bottom half. On half of the blocks, cars were presented in their normal configuration (top row) such that car experts (but not novices) would engage holistic processing for both cars and faces. On the other half of the blocks, cars were shown in a transformed configuration in which the top half was inverted (bottom row) such that holistic processing for cars would be disrupted. The amount of holistic processing for faces in the two conditions was compared, to determine whether holistic processing of cars interfered with holistic processing of faces. As expected, the amount of holistic processing for faces depended on the configuration of the cars only for car experts. **(b)** Electrophysical results of the study described above showing *the difference* between the N170 amplitude to faces among normal cars and faces among transformed cars in experts (left) and novices (right). The amplitude of the N170 for faces was dependent on the configuration of cars for Experts, but not for novices. The interference on the N170 correlated significantly with behavioral measures of interference on holistic processing, and both measures of interference correlated with independent measures of car expertise.

applied to either (providing that the mechanisms in question have limited capacities). Although this approach does not directly speak to the underlying neuroanatomical organization of category-specific areas, it does offer means for understanding how behavior is instantiated in neural systems. For example, the efficacy of this approach has been demonstrated in an ERP study that found that the N170 in response to faces was significantly reduced when observers were simultaneously required to process a second face, but was not affected when the second face was scrambled [39]. Simultaneous processing of a Greeble with a face also reduces the N170 response to faces for

Box 3. Questions for future research

- How long-lasting are the effects of expertise training?
- What is the role of decisional processes in expertise?
- What is the role of attention in expertise?
- How does feature saliency change with expertise?
- Can we create feature-based expertise, and how will it differ from holistic expertise?
- What role do semantic features play in perceptual expertise?
- How does expertise for different modalities (visual, auditory, tactile) differ? In what ways are they the same?
- How does expertise affect working memory capacity?
- Can we dissociate FFA activity related to detection from FFA activity related to identification?
- How do interactions between the amygdala and the FFA influence the acquisition of expertise?
- Are there special populations that can benefit from face training?
- How does the age at which expertise is acquired influence its development and potential neural instantiation?
- What neural mechanisms are at work during the acquisition and preservation of expertise? Are there changes in connectivity? If so, at what scale?

Greeble experts [40]. This technique has been used to demonstrate that car experts show lower holistic processing for faces and reduced N170 amplitudes to faces when they process cars and faces simultaneously (as well as greater holistic processing and a higher N170 amplitude for cars) when compared with novices [41]. The degree of interference between faces and cars within an individual was positively correlated with an independent behavioral measure of car expertise. Thus, the neural processes used by car experts in the holistic processing of cars are not functionally independent from those that support holistic face processing (Figure 3).

Although most research in this area has focused on the issue of domain specificity for faces, the same techniques can be used to identify functional similarities and differences between any two domains of expertise. Demonstrations of interference effects in fMRI, ERP, or psychophysical studies would certainly provide better evidence for the functional relationship between different types of expertise than mere spatial overlap. In particular, this approach aids in establishing whether specific cognitive functions are shared or independent, and provides a clearer picture of how related cortical functions are spatially organized in the brain.

Towards a taxonomy of perceptual expertise

The combination of evidence from studies of face-selectivity, of extant expertise for non-face objects, and of expertise acquired in the laboratory, provides a basis for a taxonomy of the cognitive and neural mechanisms engaged by different forms of perceptual expertise. Although much remains to be done (see also Box 3), recent work suggests that this taxonomy is likely to reflect the physical and conceptual properties of the stimulus class (e.g. similarity to other domains, within-domain similarity, modality and functional knowledge), task and/or experiential factors (e.g. level of individuation), as well as inherent biases due to principles of neural organization (e.g. modality, eccentricity, hierarchy [42,43]). The development of this taxonomy will continue to rely on comparisons between cognitive and neural mechanisms for a wide range of domains, as well as across perceptual modalities. Obviously such research remains relevant to the question of domain specificity; however, we believe that the value of the expertise framework has moved beyond demonstrations of isomorphism. Specifically, the approach is useful in its own right as a tool for exploring the cognitive and neural mechanisms underlying expertise acquisition and, more generally, as a means for studying the computational properties and cortical plasticity of the primate brain.

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