Perceptual interference supports a non-modular account of face processing

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The perception of faces and of nonface objects share common early visual processing stages. Some argue, however, that the brain eventually processes faces separately from other objects, within a domain-specific module dedicated to face perception. This apparent specialization for faces could, alternatively, result from people's expertise with this category of stimuli. Here we used behavioral and electrophysiological measures of interference to address the functional independence of face and object processing. If the expert processing of faces and cars depend on common mechanisms related to holistic perception (obligatory processing of all parts), then for human subjects who are presumed to be face experts, car perception should interfere with concurrent face perception. Furthermore, such interference should increase with greater expertise in car identification, and indeed this is what we found. Event-related potentials (ERPs) suggest that this interference arose from perceptual processes contributing to the holistic processing of both objects of expertise and faces.

To date, few studies have directly addressed the question of the domain-specificity of face processing[1,2]. Face-selective parts of the visual system[3,4] can be recruited by expertise with other objects[5,6]. And in experts, similar electrophysiological responses can be obtained at the scalp for faces and for objects of expertise[7,8]. The possibility remains, however, that the perception of faces and objects might recruit nearby neural networks with similar timing, yet proceed in parallel. If the spatial and temporal proximity of face and object processing stem from a common processing stage, it should be possible to detect interference in a dual task requiring simultaneous processing of both categories. Here we use a dual task to assess interference between faces and cars on a measure of holistic processing (HP). Measures of HP are taken to indicate obligatory processing of all features of an object, even when subjects are instructed to attend selectively to one feature while ignoring others. This measure was chosen because it should engage processing stages thought to be domain-specific for faces[1,2] and those influenced by expertise with non-face objects[9,10].

We found that car expertise was directly associated with HP for cars; that is, experts found it more difficult to ignore certain features of cars, as compared with other objects. Car expertise was also associated with a higher-amplitude N170 (an early face-selective ERP component) to cars. Not only did subjects with greater car expertise show more holistic processing of cars, but they also showed less holistic processing of faces that were presented among images of cars, indicating a common functional substrate for HP of cars and faces. This interference lowered the amplitude of the N170 response to faces seen in the context of cars, suggesting that it has a perceptual basis.

RESULTS

Car expertise was measured with a sequential matching task (**Fig. 1a** and Methods). An expertise score was calculated for each subject by subtracting sensitivity (d') for bird judgments from the sensitivity for car judgments ($\Delta d' = d'_{\mathrm{cars}} - d'_{\mathrm{birds}}$)[6].

Interference between car and face processing was measured during a two-back task with alternating images of face and car composites (**Fig. 1b** and Methods). Subjects pressed a key to indicate whether the bottom of the current image is the same or different from the bottom of the previous image of the same category. HP was estimated as in previous studies[2,9,10] by measuring the degree to which judgments about the bottom of the image were influenced by the top. Consistent trials were those in which processing the top of the image would lead to a response congruent with the correct response to the bottom (top and bottom were both the same or both different, as compared to the previous face/car). Inconsistent trials were those in which processing the top of the image would lead to a response incongruent with the correct response to the bottom. HP for cars and faces was calculated by subtracting the d' for consistent versus inconsistent trials ($HP = d'_{\mathrm{consistent}} - d'_{\mathrm{inconsistent}}$). Thus, larger HP scores reflect a greater tendency to process the whole stimulus rather than just the bottom half. Holistic interference was manipulated in two blocked contexts: faces among normal cars (**Fig. 1b**, top row) and faces among transformed cars (bottom row). We expected that HP by car experts would be greater for normal than transformed cars, so holistic interference between cars and faces should be greater for faces among normal cars than for faces among transformed cars. To quantitatively assess this

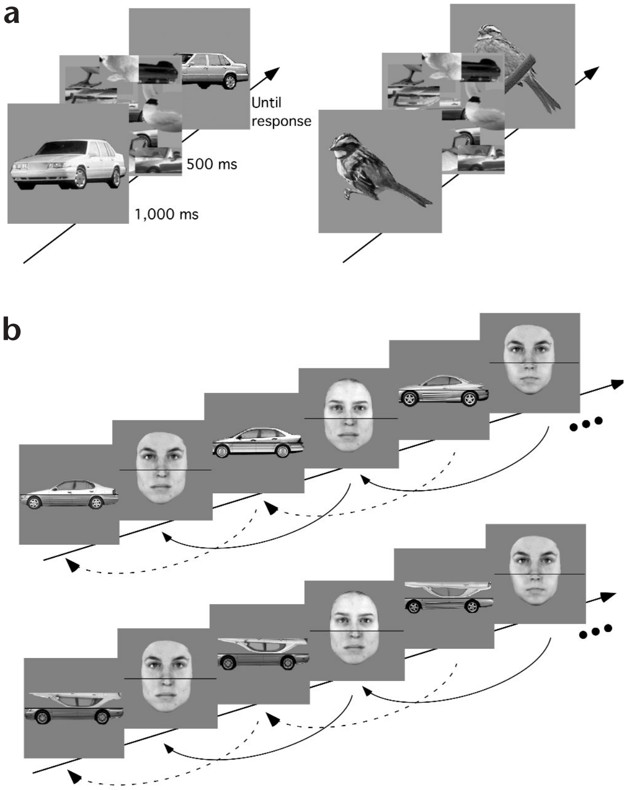


Fig. 1. Experimental design. (**a**) Example of trials used to measure car expertise. Subjects performed 112 trials of a sequential matching task with contemporary cars, and the same number with images of passerine birds. (**b**) Example trial used to measure interference effect of cars on face processing. Composites of faces and cars made of the top and bottom of different objects were alternately presented. Subjects were instructed to attend only to the bottom half of all objects for the entire experiment and, for each one, to make a two-back judgment on whether the bottom part matched that of the last object of the same category. Normal faces were interspersed with either normal cars (top row) or cars in a transformed configuration with the top half upside-down (bottom row).

prediction, we calculated a face interference index (FII) by subtracting the amount of HP for faces among normal cars from the amount of HP for faces among transformed cars ($\mathrm{FII} = \mathrm{HP}_{\text{faces among normal cars}} - \mathrm{HP}_{\text{faces among transformed cars}}$).

Behavioral performance on the two-back task replicated previous research (K.M.C. & I.G., unpub. data). An ANOVA on HP for cars revealed a significant interaction between expertise and car condition (normal versus transformed) ($F_{1,37} = 3.96$, $P = 0.05$). Indeed, the difference between HP for normal and transformed cars increased with expertise ($r = 0.33$, $P < 0.05$). Furthermore, the FII correlated with car expertise (**Fig. 2**; $r = 0.38$, $P < 0.05$), indicating that HP of faces was influenced by the car context and that this interference increased with car expertise. Reaction times are not reported because their interpretation is ambiguous given the compromise between the need to encode the current stimulus and the pressure to minimize the retention interval for the concurrent task. This behavioral interference of car expertise on face processing suggests that HP of faces and objects are not supported by functionally independent systems.

The goal of this study was to investigate at which stage this interference occurs in the visual system. Therefore, we considered the activity reflected in the brain's earliest face-selective component of the event-related brain potential, the N170 potential. The N170 is a negative-going potential, which is maximal at occipitotemporal electrodes with generally larger amplitude for faces than other objects[11]. The N170 is thought by some to reflect the activity of a face-specific processing module[12]. However, expertise affects the N170 response to non-face objects, as shown by a larger amplitude N170 potential in bird and dog experts[7]. The N170 potential is larger and delayed by 10 ms when faces (but not objects) are shown upside-down[13], although this inversion effect can also be obtained with novel objects after expertise training[8].

We measured the N170 potential in response to cars and faces during the two-back interference task. Consistent with prior work[7], we found that car experts had a larger-amplitude N170 in response to seeing cars than did car novices (**Fig. 3**). These findings are consistent with an influence of expertise on the earliest ERP correlate of face-selectivity. However, despite the striking similarity between the N170 potentials to faces and cars, an important question remains: do these two responses reflect the workings of the same neural network? On the basis of scalp topography, it has been suggested that the N170 peaks more medially for objects than for faces[12], and a similar topographic difference was found here (**Fig. 3c**). Studies using functional magnetic resonance imaging (fMRI), which affords much better spatial resolution (but poorer temporal resolution) than ERPs, have revealed at least one large region in the parahippocampal gyrus (medial to face-sensitive areas) that responds much more to objects than to faces[14]. Thus, it is possible that the activity in the more lateral areas that respond to both faces and objects is confounded at the scalp with activity in other areas that respond only to objects, resulting in misleading differences in scalp topographies. Therefore, the typical analysis of condition differences in ERPs cannot assess the extent to which categories are processed by independent brain substrates.

By our present design, we were able to test directly whether the face-N170 and object-N170 reflect the activity of functionally independent neural networks. An electrophysiological FII expressed in terms of the amplitude of the face-N170 (the difference in amplitude of the N170 response to faces among transformed cars relative to faces among normal cars) correlated significantly with car expertise (**Fig. 4b**). The scalp topography for this electrophysiological FII on the N170 is shown in **Fig. 4a**. The magnitudes of the behavioral and neurophysiological FII

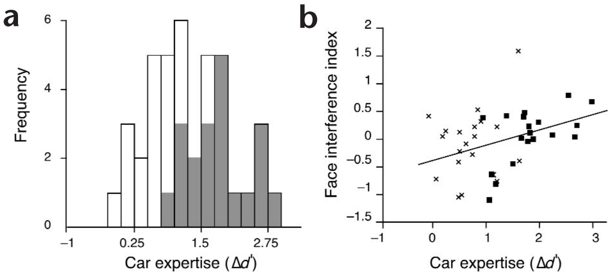
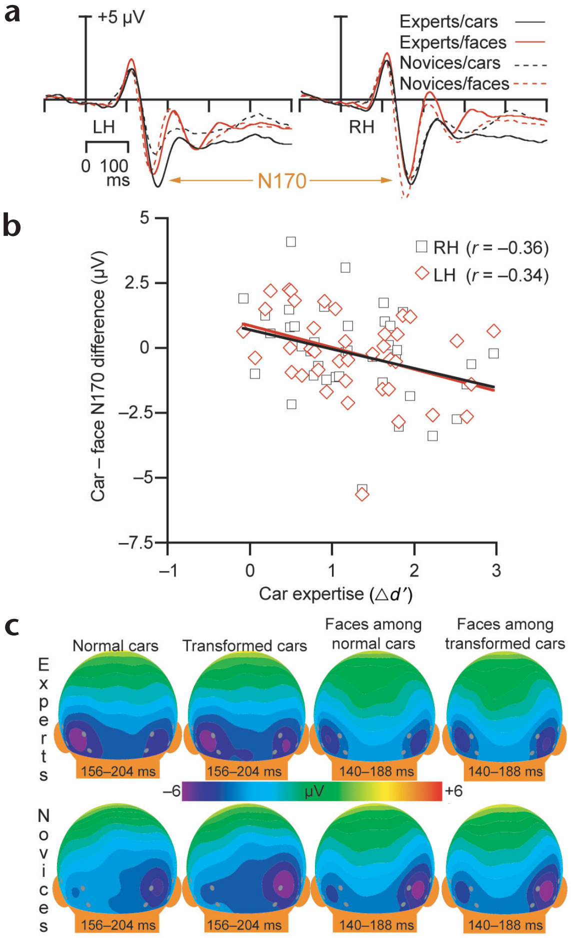


Fig. 2. Car expertise correlates with behavioral interference. (**a**) The frequency histogram for car expertise reveals a continuum of expertise. Our behavioral measure of car expertise is highly consistent with self-reported car expertise (dark bars). (**b**) An ANOVA on the behavioral FII showed a significant effect of expertise ($F_{1,37} = 7.51$, $P < 0.01$). A scatter plot shows the correlation between the behavioral face interference index and car expertise ($r = 0.38$, $P < 0.05$). Subjects with self-reported car expertise are shown with filled squares.

Fig. 3. Expertise effects on the N170. (**a**) An ANOVA (including channels P7/8, mastoid, P07/8, IM1/2) showed a significant group × stimulus type interaction ($F_{1,37}$ = 7.00, P = 0.01). Experts and novices were separated according to a median split of their expertise scores. The N170 to cars was higher amplitude in experts (–4.41 µV) than novices (–3.57 µV), but was similar across groups for faces (experts, –3.56 µV; novices, –3.95 µV). ERP plots from normal conditions are averaged across the right hemisphere (RH) and left hemisphere (LH) channels. (**b**) A scatter plot shows correlations between car expertise and the voltage difference between the N170 to cars and faces (averaged across the normal and transformed conditions). (**c**) Each plot shows average ERPs interpolated over a map of the back of the head. Small circles represent the P7/8, mastoid, P07/8 and IM1/2 locations included in ANOVAs. A stimulus (car, face) × location (medial, lateral) interaction suggested that the N170 to cars was more negative over medial than lateral locations, whereas the N170 to faces had a similar amplitude across these regions, $F_{1,37}$ = 26.14, P < 0.001.



on the N170 were also significantly correlated (**Fig. 4c**). Interestingly, the electrophysiological FII was significant at right-hemisphere electrodes, whereas the expertise effect on the N170 was bilateral. HP is related to expertise in the right but not the left FFA[5,10], consistent with our finding that interference in HP is greater on the right side. Importantly, this interference on the face-N170 cannot be explained by difficulty on the face trials because car experts and novices did not differ in their performance on these trials (**Table 1**).

DISCUSSION

Our experiment was designed to test the effect of manipulating HP for cars on the HP of faces seen among cars. In principle, we would expect the interference to run in both directions (that is, for face expertise to influence holistic processing of cars as well as vice-versa). But as the method requires the context domain to be associated with a range of expertise, and there is much less variability in the general population for face than for car expertise, we could only test for interference in one direction. It would be interesting to develop interference paradigms that do not rely on variability in face expertise. Nevertheless, our results are informative, as they indicate interference from car expertise on the presumably much stronger expertise our subjects had for faces. On the basis of our findings, we reject the hypothesis of functional independence between the mechanisms responsible for the face and object N170 potentials. In addition, given the early time course and occipitotemporal distribution of the N170, the common bottleneck seems to be of a perceptual nature, likely originating from extrastriate cortex.

Holistic effects, as measured here, reflect a failure of selective attention: despite instructions to do so, subjects could not ignore the top of images presented to them. Although holistic effects are occasionally taken to indicate the existence of holistic perceptual representations (in which there is no explicit representation of individual parts)[4], some authors suggest a more decisional locus to these effects[15] and others remain agnostic as to their computational implementation[10]. Our data that relate expertise effects on holistic processing to the N170 are more consistent with a perceptual locus because of the early timing of this ERP component.

Visual selective attention can be influenced by perceptual load: a higher load reduces failures of selective attention, as priority in a limited-capacity system is allocated to relevant

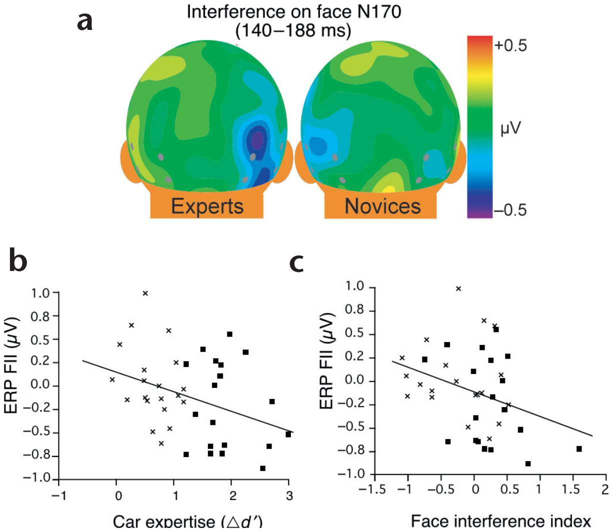


Fig. 4. ERP interference effects. (**a**) An ANOVA on the N170 to faces showed a significant three-way interaction: expertise × condition (normal versus transformed cars) × hemisphere ($F_{1,37}$ = 8.20, P < 0.01). The form of this interaction can be seen by calculating an electrophysiological face interference index (ERP FII): the difference between the N170 amplitude to faces among normal cars and the N170 amplitude to faces among transformed cars. These differences are interpolated over maps of the back of the head. (**b**) A scatter plot shows the correlation between car expertise (Δd′) and the right-hemisphere ERP FII (r = –0.35, P < 0.05). (**c**) A scatter plot shows the correlation between the behavioral and the right-hemisphere FII (r = –0.33 P < 0.05). In (**b**) and (**c**), experts according to the median split are indicated by filled squares.

Table 1. Sensitivity (d') for the sequential matching task used to define expertise and for the two-back task, for groups defined by a median split.

	Car novices mean d' (s.e.m.)	Car experts mean d' (s.e.m.)	P-value (*one tail)
Whole car matching	1.51 (0.05)	2.68 (0.13)	< 0.0001*
Whole bird matching	0.79 (0.05)	0.85 (0.05)	0.31
Normal cars consistent	1.46 (0.17)	1.97 (0.18)	0.02*
Normal cars inconsistent	0.90 (0.17)	1.27 (0.12)	0.04*
Transformed cars consistent	1.61 (0.18)	2.01 (0.17)	0.06*
Transformed cars inconsistent	1.12 (0.15)	1.71 (0.15)	0.005*
Faces among normal cars consistent	1.87 (0.19)	2.08 (0.17)	0.43
Faces among normal cars inconsistent	0.67 (0.11)	0.81 (0.12)	0.42
Faces among transformed cars consistent	1.81 (0.15)	2.19 (0.20)	0.13
Faces among transformed cars inconsistent	0.73 (0.12)	0.87 (0.13)	0.42

stimuli[16]. Thus experts, who may need to process less information from the relevant bottom part of the stimulus because they have learned from experience which features are most diagnostic, may be left with spared perceptual capacity that is used to automatically encode information from the irrelevant top parts. In addition, selective attention can also be influenced by working memory load, although the effects are different from those of perceptual load: as working memory load increases, failures of selective attention become more likely[17]. In our study, selective attention for faces was more likely to fail in car experts who concurrently showed relatively more holistic processing (measured by failures of selective attention) for cars. Thus, our results seem at odds with an explanation in terms of working memory load, as experts who encoded more irrelevant information would be expected to have a higher working memory load and thus more holistic processing for faces. Any such interpretation, however, must be treated with caution because it depends on intuitive predictions of how working memory may be influenced by perceptual expertise. This should be an important avenue for future research.

A strength of cognitive neuroscience is the recognition that converging evidence from different techniques often strengthens conclusions. Findings of similar patterns for the perception of faces and objects using behavioral[9,18], fMRI[5,6] or ERP[7,8] methods are not by themselves conclusive evidence against domain-specific modules. In contrast, our behavioral results suggest that the neural populations responsible for HP of faces and cars are not functionally independent. Our ERP results reveal that this interference is of a perceptual nature, affecting the earliest face-selective processing stages in the adult human brain. Together, these results are consistent with the perspective that some of the early processes specialized for face perception also contribute to the expert perception of other objects.

METHODS

Subjects. Twenty self-reported car experts and twenty novices with normal or corrected vision gave informed consent and participated in this study, approved by the Human Research Committee at University of Colorado at Boulder, for payment or partial course credit. All subjects were male college students. A single expert was excluded from all analyses because he was an outlier: his ERP FII exceeded the high hinge + 1.5(high hinge – low hinge), where hinges are the 25th and 75th percentiles[19]. His N170 amplitude was more negative than all other subjects, probably because of relatively low numbers of artifact-free trials.

Car expertise test. Subjects' car expertise was tested, yielding a quantitative estimate of their ability relative to their performance with birds (used here as a baseline for novice-level performance). Subjects matched sequentially presented (256 × 256) grayscale images of cars and birds on the basis of their model or species (224 trials.) The first image was presented for 1,000 ms, followed by a mask for 500 ms, and then the second image appeared and remained until either the subject made a response or 5,000 ms had passed (**Fig. 1a**). Matching stimuli were not physically identical, but were different exemplars of the same bird species or the same make/model of car from different years.

Interference task. Sixteen conditions were constructed by varying stimulus category (cars, faces), context (normal cars, transformed cars), response to bottom (same, different) and response consistency (response to bottom consistent or inconsistent with response to top). All stimuli shown in the interference task were composites (64 faces and 64 cars) made out of the top and bottom of different faces or different cars (different make or model). We used 336 grayscale (256 × 256 pixel) composite images of cars (profile) and faces (front view) with a horizontal red line covering the seam between the two parts. In half of the car stimuli, the top part was inverted. In each of 930 trials (30 practice, 900 experimental), a fixation cross was presented centrally for 1,000 ms, followed by the stimulus for 1,500 ms or until the subject made a response. Stimuli alternated between car and face composites (**Fig.1**). Subjects pressed a key indicating whether the bottom of the current stimulus was the same or different from the last stimulus of the same category; their keypress triggered the presentation of the next stimulus.

Electrophysiology. ERPs were acquired with a 128-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, Oregon)[20] using our standard recording and analysis procedures[7]. All ERPs were computed with respect to an average reference. ERPs were analyzed at locations nearest to the left (P7, left mastoid, P07, IM1) and right hemisphere (P8, right mastoid, P08, IM2) channels analyzed in previous N170 experiments[12]. Initial analyses revealed that the N170 peaked earlier for faces (164 ms) than for cars (180 ms). To account for these latency differences, mean amplitude was calculated within temporal windows that were ±2 s.d. from these mean latencies (faces, 140–188 ms; cars, 156–204 ms).

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Competing interests statement

The authors declare that they have no competing financial interests.

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