Does acquisition of Greeble expertise in prosopagnosia rule out a domain-general deficit?

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A B S T R A C T

According to the expertise account of face specialization, a deficit that affects general expertise mechanisms should similarly impair the expert individuation of both faces and other visually homogeneous object classes. To test this possibility, we attempted to train a prosopagnosic patient, LR, to become a Greeble expert using the standard Greeble expertise-training paradigm (Gauthier & Tarr, 2002). Previous research demonstrated that LR’s prosopagnosia was related to an inability to simultaneously use multiple features in a speeded face recognition task (Bukach, Bub, Gauthier, & Tarr, 2006). We hypothesized that LR’s inability to use multiple face features would manifest in his acquisition of Greeble expertise, even though his basic object recognition is unimpaired according to standard neuropsychological testing. Although LR was eventually able to reach expertise criterion, he took many more training sessions than controls, suggesting use of an abnormal strategy. To further explore LR’s Greeble processing strategies, we assessed his ability to use multiple Greeble features both before and after Greeble training. LR’s performance in two versions of this task demonstrates that, even after training, he relies heavily on a single feature to identify Greebles. This correspondence between LR’s face recognition and post-training Greeble recognition supports the idea that impaired face recognition is simply the most visible symptom of a more general object recognition impairment in acquired prosopagnosia.

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1. Introduction

Patients with prosopagnosia are characterized as showing a disproportional impairment in recognizing faces as compared to other types of objects, however, the specificity of this impairment is a matter of some debate. On the one hand, some researchers suggest that prosopagnosia involves damage to mechanisms that are specific to faces (e.g., Duchaine, Yovel, Butterworth, & Nakayama, 2006; Farah, Levinson, & Klein, 1995). Under this account, damage to face-specific mechanisms should leave recognition ability for all other object classes intact. On the other hand, other researchers suggest that the apparent face-selectivity associated with prosopagnosia is due to factors such as the insensitivity of the methods used to assess object recognition and the (typically) greater demands of face individuation both in the laboratory and in everyday life (e.g., Damasio, Damasio, & Van Hoesen, 1982; Gauthier, Behrmann, & Tarr, 1999). In particular, the expertise account of face specificity (Diamond & Carey, 1986; Gauthier & Tarr, 1997) hypothesizes that face recognition is a particular example of more domain-general mechanisms that potentially support expert-level within-category individuation across most visually homogeneous object categories. Under this account, impairments of the mechanisms that are necessary for expert face recognition should also affect the acquisition of expertise for non-face homogeneous object classes. The nature and specificity of category-selective deficits such as prosopagnosia therefore provides some constraints for theories of normal object recognition. Here, we scrutinize the specificity of impairment in one case of acquired prosopagnosia – with a deficit that appears specific to faces as assessed by standard neuropsychological tests – and find that similar deficits are present for faces and for non-face objects of expertise.

By definition, individuals with prosopagnosia have a disproportionate impairment in recognizing faces compared to other types
of objects. From the earliest reported cases, the disproportionate deficit in face recognition has been interpreted as evidence for neural mechanisms that are specific to faces (e.g., Bodamer, 1947 as cited by Ellis, 1996). However, some researchers have questioned the specificity of the impairment, pointing out that face recognition requires within-class discrimination of individual exemplars that are visually similar, whereas most other types of objects require only between-class discrimination of visually dissimilar objects (Damasio et al., 1982; Faust, 1955, as cited by Heacox, 1981). The evidence for face–specificity in prosopagnosia has been quite mixed, with several cases reported to have completely spared within-class discrimination (Bruyer et al., 1983; Busigny, Graf, Mayer, & Rossion, 2010; de Renzi, 1966; Farah et al., 1995; McNeil & Warrington, 1993; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008), and several others reported to have impaired within-class discrimination (Blanc-Garin, 1984; Bornstein, 1963; Bornstein, Sroka, & Munitz, 1969; Damasio et al., 1982; Gauthier, Behrmann, et al., 1999; Gloning & Quatember, 1966; Lhermitte & Pillon, 1975). Recently, a novel approach that used preserved semantic knowledge to estimate pre-morbid car expertise level of six prosopagnosic participants found that all six had car recognition impairments compared to matched controls (Barton, Hanif, & Ashraf, 2009).

Studies of neurologically typical individuals have likewise produced mixed evidence for the specificity of face recognition (for a recent review, see Bukach & Peissig, 2010). Supporting the face–specificity stance, faces recruit an area in the fusiform gyrus more than any other class of objects (Kanwisher, McDermott, & Chun, 1997), show an N170 component greater for faces than for other types of objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996), and show more evidence of holistic and relational processing than other types of objects (Leder & Carbon, 2006; Young, Hoddell, & Hay, 1987). Supporting a more general expertise stance, studies of real-world expertise (such as car, bird, and fingerprint experts) show patterns of neural and behavioral markers similar to those seen for faces (e.g., Bukach, Phillips, & Gauthier, 2011; Busey & Vanderkolk, 2005; Gauthier, Curran, Curby, & Collins, 2003; Gauthier, Skudlarski, Gore, & Anderson, 2000; Righi, Tarr, & Kingon, in press; Tanaka & Curran, 2001; Xu, 2005).

Most saliently, much of the support for the expertise hypothesis has relied on data from the acquisition of expertise using “Greebles” (Gauthier & Tarr, 1997): novel homogeneous objects that share a common configuration of parts—a property that according to Diamond and Carey (1986), makes faces distinct from other object classes. Like faces, which have eyes above nose above mouth, Greebles also have three primary parts in a stable configuration: Greebles above Quiff above Dunth (Fig. 1). Identification of individual objects with a common overall configuration of parts is thought to recruit more metric aspects of shape as well as their second order spatial relationships.

Greebles can be classified at a “family” level as well as an “individual” level. In the typical training paradigm with Greebles (Gauthier & Tarr, 2002), subjects practice both levels of classification until response times for individual judgments (typically slow to begin with) are statistically equivalent to response times to family level judgments. This criterion is based on findings that experts tend to be as fast to make a subordinate level judgment as a more superordinate level judgment (Tanaka, 2001). Greeble studies have found that, as expertise is acquired, subjects show similar behavioral and neural patterns as those thought to be specific to face recognition, including holistic and relational processing, recruitment of the FFA, and a strong N170 when viewing novel Greeble exemplars not used during training (Gauthier & Tarr, 1997; Gauthier & Tarr, 2002; Gauthier, Tarr, Anderson, & Gore, 1997; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gauthier, Williams, Tarr, & Tanaka, 1998; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002). Thus, there is some evidence that Greeble expertise recruits computational and neural mechanisms that are common to those mechanisms recruited by face recognition.

This correspondence between Greeble expertise and face recognition has been questioned on the basis that a developmental prosopagnosic patient, Edward, was able to individuate Greebles after training (Duchaine, Dingle, Butterworth, & Nakayama, 2004; Duchaine et al., 2006). Duchaine et al. reported that Edward met criterion in sessions one, three, four, six and eight. Unfortunately, there were several differences in data analysis that make it difficult to conclude whether in fact Edward reached criterion according to the traditional standard used in earlier studies. Nonetheless, it is clear that Edward’s learning trajectory was within normal age-matched limits, and had training continued, he may have reached the stricter criterion used in previous studies. However, we hold that this finding alone is insufficient to invalidate the conclusions of previous expertise studies and to conclude that face recognition and Greeble recognition rely on separate mechanisms as Duchaine et al. claim. In particular, evidence for separate mechanisms would require a demonstration that Edward could learn to individuate 20 Greebles, but be unable to learn to individuate 20 faces using the same task. Moreover, the potential sensitivity of the acquisition of expertise to prosopagnosia may depend on the underlying cause of the prosopagnosia; that is, whether the specific mechanisms used in the acquisition of expertise are concomitantly impaired (for a similar argument, see Bukach, Gauthier, & Tarr, 2006). Thus, specific predictions for the acquisition of Greeble expertise, and likewise, performance on any test with nonface objects, should depend on the particular deficit that underlies the face recognition impairment. Consequently, the “space” of neuropsychological

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1 For a discussion of the issue as to whether Greebles “look like” faces, see Sheinberg, Tarr, Gauthier, and Bub (2010).

2 Traditionally, only response time data to verification hits (correct trials in which the label and Greeble match) from the 20 known Greebles are analyzed after the initial introduction to all 20 Greebles has been accomplished. Thus we do not test for criterion before session five, and verification data from the 10 “unknown” Greebles are excluded. In addition, to assure that response time estimates are reliable and expertise criterion is not met prematurely due to high variability, data are binned across two verification blocks (called “sessions” by Duchaine et al.), and a dependent t-test is carried out on the average response times by stimulus (df = 19). It is not clear whether Duchaine et al. excluded data from hits to “unknown” Greebles, nor what type of statistical test was used as they did not report df. More importantly, they did not bin data from multiple blocks, and thus criterion may have been reached due to high variability, rather than because the means were close. In fact, the last training session plotted in Edward’s graph suggests that average response time to individual trials was at least 500 ms longer than average response time to family judgments.
deficits should be explored as widely as possible (Plaut, 1995) in order to understand the relationship between face recognition and nonface expertise. In this vein, we present a prosopagnosic case, LR, who, following Greeble expertise training, exhibits correspondence in the strategies he employs in both Greeble and face recognition.

2. Case description of LR

LR’s etiology and symptomology have been described in detail elsewhere (Bukach, Bub, Gauthier, & Tarr, 2006; Bukach, Le Grand, Kaiser, Bub, & Tanaka, 2008). Born in 1953, LR acquired prosopagnosia following a vehicle accident in which the anterior temporal lobe on the right side was damaged when the shaft of the gearshift penetrated the left cheek. CT scans pictured in Fig. 2 reveal the extent of the damage (MRI is not possible due to a clip on the internal carotid artery), mostly impacting the anterior and inferior right temporal lobe, including the amygdala, but apparently sparing more posterior regions such as the fusiform face area and occipito-temporal junction commonly damaged in other prosopagnosic patients. The severity of LR’s impairment in face processing is evidenced in both his every day life and in specially tailored laboratory tests: not only does he fail to recognize his own daughter when encountered unexpectedly, he also successfully identified only 23 out of 121 famous faces from their photographs.

LR’s performance on a variety of standardized neuropsychological tests is presented in Table 1. These tests indicate a severe impairment of face recognition. In contrast, he shows normal performance on a variety of non-face object recognition tests. Most impressively, he scored in the 95th percentile on the Doors task of the Doors and People Test (Baddeley, Emslie, & Nimmo-Smith, 1994), a very stringent test of visual object recognition. There are two sets of trials, varying in difficulty. The doors in the most difficult set are very similar, with just a few features that vary (e.g. doorknobs or planters). After studying 12 doors for 3 s each, targets are presented with three distractors. This test is sensitive to impairments related to temporal lobe damage, including Alzheimer’s disease, stroke, and temporal lobectomy (e.g., Morris, 1995). It has also been used to demonstrate impairments in object recognition that were not evident in other standardized object recognition tests, and performance parallels that of experimental tests of within-category recognition that have been used to compare face and object recognition (Germine, Cashdollar, Duzel, & Duchaine, 2011). LR’s superior performance on this task confirms the overtly selective nature of his face recognition deficit.

A thorough investigation of LR’s face recognition abilities (Bukach, Bub, et al., 2006) resulted in an intriguing pattern of spared and impaired performance: LR showed excellent fine-level discrimination of faces when subtle changes affected the entire face. In the composite task, where subjects make a same-different judgment to the top or bottom of a pair of faces while ignoring the other half, LR showed a normal pattern of interference from the uncued half. This interference was reduced when the face halves were misaligned, indicating a normal pattern of holistic processing, at least for coarse-level information. He also showed preserved relational processing: he could detect changes in the spacing of features in an upright face. Importantly, however, he showed normal performance only for mouth judgments, but was severely impaired at detecting both featural and relational changes to the eye region. This pattern of performance suggested that LR’s ability to make fine-level judgments is limited to small regions of the face (typically

<table>
<thead>
<tr>
<th>Neuropsychological test</th>
<th>LR’s performance</th>
</tr>
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<tbody>
<tr>
<td>Intelligence (WAIS)</td>
<td>High average (114)</td>
</tr>
<tr>
<td>Wechsler Adult Intelligence Scale (3rd ed.)</td>
<td>Normal (20/20)</td>
</tr>
<tr>
<td>Visual acuity</td>
<td></td>
</tr>
<tr>
<td>General memory</td>
<td>Normal (107)</td>
</tr>
<tr>
<td>Wechsler Memory Scale (3rd ed.)</td>
<td></td>
</tr>
<tr>
<td>Working memory</td>
<td>Normal (111)</td>
</tr>
<tr>
<td>Wechsler Memory Scale (3rd ed.)</td>
<td></td>
</tr>
<tr>
<td>Color perception</td>
<td>Normal</td>
</tr>
<tr>
<td>American Optical Handy Rand Rittler</td>
<td></td>
</tr>
<tr>
<td>Benton judgment of line orientation (Benton, Sivan, Hamsher, Varney, &amp; Spreen, 1994)</td>
<td>Normal</td>
</tr>
<tr>
<td>Visual object and spatial perception (Warrington &amp; James, 1991)</td>
<td>Normal</td>
</tr>
<tr>
<td>Object recognition</td>
<td></td>
</tr>
<tr>
<td>(Snodgrass &amp; Vanderwart, 1980)</td>
<td>Normal</td>
</tr>
<tr>
<td>Recognition memory for words (Warrington, 1994)</td>
<td>Normal</td>
</tr>
<tr>
<td>Recognition memory for faces (Warrington, 1994)</td>
<td>Severeley impaired (38/50)</td>
</tr>
<tr>
<td>Benton’s face recognition test (timed) (Benton et al., 1994)</td>
<td>Severeley impaired (12/54)</td>
</tr>
</tbody>
</table>
the mouth region), and he is unable to integrate high-resolution information from multiple facial regions.

Bukach, Bub, et al. (2006) further tested the integration deficit hypothesis by creating a conjunction set of faces in which the values of the eyes, nose, and mouth each had two possible values such that all three parts of the face had to be identified in order to differentiate the faces. The identification task involved briefly viewing a face for variable exposure durations, and then selecting the face from a template of all eight possible faces. LR's performance was well below that of controls, and, in fact, was equivalent to what would be expected had he based his decisions on a single feature (25%). Further analysis revealed that LR consistently based his identification on the mouth region, regardless of exposure duration. On the basis of LR's performance across all tasks, Bukach et al. concluded that LR has a spatially limited expertise for faces, tending to favor the mouth region, and preventing him from integrating fine-level details across a wider spatial region. They suggested that the extraction of fine-level details may require additional processing that is mediated by attention to local face regions and that LR may either be unable to move this attention rapidly to different parts, or may be unable to create a unified percept from these outputs for the purpose of comparison.

Here we test how this pattern of impaired feature integration with preserved fine-level discrimination impacts the acquisition of Greeble expertise to determine whether the inability to integrate details from multiple features is specific to faces or whether it will also be evident for other homogeneous object classes.

3. Experiment 1. Greeble training

3.1. Method

3.1.1. Subjects

LR was aged 49 at the time of testing, and experiments were conducted around the same time that previously published experiments in face recognition were administered (Bukach, Bub, et al., 2006; Bukach et al., 2008). In addition to LR, who is described above, 5 age-matched controls (mean age 47.6 years, 3 males) participated. One of these controls participated at the time that LR was tested; the other four were tested at a later time and were screened to match LR's preserved visual recognition skills as assessed by the Doors test from the Doors and People test (Baddeley et al., 1994). This was important because visual skills decline with age (Frazier & Hoyer, 1992; Read, 1988). Age-matched controls could therefore perform poorly with Greebles because of visual discrimination and memory declines that are not specific to feature integration and that did not characterize LR at the time of testing. LR recognized 23 out of 24 doors (95th percentile), indicating preservation of general visual processing. Controls were included in the study if they scored in the 75th percentile or above according to standardized norms. Scores for controls included in the study ranged from 20 to 22 out of 24. All participants received monetary compensation for their time.

3.1.2. Materials

Stimuli consisted of 30 Greebles (Gauthier & Tarr, 1997; stimuli are available at http://www.tarrlab.org/stimuli/novel-objects/). Each Greeble has four appendages that share a common configuration around a central body (see Fig. 1). The Greebles can be grouped into five different families on the basis of the shape of the central body, and each Greeble can be distinguished at the individual level from all other Greebles on the basis of the shapes of its appendages. Although the appendages are very similar to one another, each shape is unique in the entire set of Greebles. Images were displayed on a computer screen and were 6.5 cm high × 3.25 cm. Subjects sat approximately 60 cm from the computer screen, although distance was not fixed. Experiments were conducted on Macintosh computers equipped with color monitors (72 pixels per inch), using RSVP software (© Michael J. Tarr, Brown University).

3.1.3. Procedure

The training was based on that used by Gauthier and Tarr (2002) with minor modifications. Subjects, including LR, learned to classify all 30 Greebles according to the family level, but only 20 of the Greebles at the individual level (4 individuals from each of the 5 families). Training occurred in 1-h sessions over a period of several weeks. The training consisted of two main phases: a learning phase and a criterion phase. In the learning phase, individual names were gradually introduced over four sessions. In Session 1, all five family names were introduced, in addition to the names of five individual Greebles. Each of the following three sessions provided a brief review of the family names and the individuals learned previously, and in addition introduced five new individual Greeble names. Because LR had initial difficulty learning the individual names, Session 4 was administered a total of four times to LR before proceeding to the next phase. Controls completed two administrations of Session 4. The criterion phase was designed to continue naming practice and to test for expertise criterion using a name verification task. These sessions provided no review of names at either family or individual level. Controls were given a minimum of 4 sessions of the criterion phase. Typically two criterion sessions were conducted on each day, as they were quite short. The details of the task procedures used over the course of training can be found in Table 2.

3.1.4. Expertise criterion

For each subject, correct response times for family and individual “yes” judgments in each session were assessed by a paired t-test (one-tailed) on average response times by stimulus. Only the 20 stimuli that had been trained at both individual and family levels were included in this analysis, yielding a df of 19. Each session of interest contained 80 eligible trials, two trials for each stimulus for each of the two judgment levels. Traditionally, a subject is considered to have reached criterion when family and individual level verification response times are statistically equivalent. This criterion was developed for a younger neurologically intact population. However, variability in response times can be an issue for neurologically impaired and older adults, and thus criterion could be reached prematurely due to large variances. To determine a reasonable upper limit for response time differences at criterion, we re-examined data from a previous Greeble training study (Gauthier & Tarr, 2002). Differences between family and individual level response times for the last 80 eligible trials in this previous study ranged from 74 ms to −89 ms (negative values indicate faster individual level judgments). The average absolute response time difference between family and individual level verification trials was 41 ms, with a standard deviation of 27 ms. To avoid prematurely ending Greeble training, we adjusted the criterion for the current study as statistically equivalent response times and no greater than a 95 ms difference between family and individual level judgments in the verification task (2 standard deviations above the previously established mean). We note that extending training past criterion should only improve LR’s likelihood of showing feature integration after training, and thus makes any observed deficit relative to controls even more striking.

3.2. Results

3.2.1. Learning phase

Fig. 3 illustrates LR’s performance for the naming task during the initial learning phase. As discussed above, LR had significant
difficulty learning the names of 20 Greebles, and therefore was run in Session 4 repeatedly before continuing to the criterion stage (Session 4 is the last session in which review and feedback are given). His accuracy and response times were well outside of the range of normal performance. During Session 4.2, LR noted that he began to use a strategy of narrowing down the alternatives on individual trials by first identifying the family to which the Greeble belonged. Thereafter his naming accuracy rapidly improved, such that by Session 4.5 he had learned all of the Greeble names, though his response times were still substantially slower (2686 ms) than the control mean for this stage (1500 ms). Note that the naming task required subjects to type in the first letter of a Greeble’s name, and so other factors, for example, familiarity with the keyboard layout, also influence response times in the naming task, probably accounting for variability among controls. Verification trials are typically not analyzed for expertise.

Table 2

<table>
<thead>
<tr>
<th>Tasks (# of Greeble exemplars)</th>
<th># of trials (# of exemplars with known individual labels)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Session 1</td>
</tr>
<tr>
<td>Family examples (10)</td>
<td>1</td>
</tr>
<tr>
<td>Family viewing (25)</td>
<td></td>
</tr>
<tr>
<td>Family naming (30)</td>
<td></td>
</tr>
<tr>
<td>Individual viewing (5)</td>
<td></td>
</tr>
<tr>
<td>Individual naming with feedback (5)</td>
<td></td>
</tr>
<tr>
<td>Individual naming (30)</td>
<td></td>
</tr>
<tr>
<td>Verification (30)</td>
<td></td>
</tr>
<tr>
<td>Family naming (30)</td>
<td></td>
</tr>
<tr>
<td>Individual viewing (review of previously learned)</td>
<td>10 (5)</td>
</tr>
<tr>
<td>Individual naming (30)</td>
<td></td>
</tr>
<tr>
<td>Verification (30)</td>
<td></td>
</tr>
<tr>
<td>Individual viewing (5)</td>
<td></td>
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<tr>
<td>Individual naming with feedback (known only)</td>
<td></td>
</tr>
<tr>
<td>Individual naming (30)</td>
<td></td>
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<td>Verification (30)</td>
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<td>Individual naming (30)</td>
<td></td>
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<tr>
<td>Verification (30)</td>
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Note: Task descriptions:
(i) Family examples: Unlimited passive viewing of a sample of 10 simultaneously presented exemplars (2 exemplars from each family) with family labels.
(ii) Family viewing: Passive viewing of a single exemplar with family label. Exemplar and label are presented for 2500 ms, with 500 ms ITI.
(iii) Family naming: A fixation cross appears for 750 ms, followed by a Greeble. Subject must press the key corresponding to the first letter of the Greeble’s family name. Unlimited response time, a beep indicates incorrect response. 250 ms ITI.
(iv) Individual viewing: Passive viewing of a single exemplar with individual label. Exemplar and label are presented for 2500 ms, with 500 ms ITI. After first block, subjects are encouraged to press key corresponding to first letter of the Greeble’s individual name.
(v) Individual naming with feedback: A fixation cross appears for 750 ms, followed by a Greeble. Subject must press key corresponding to the first letter of the Greeble’s individual name. Unlimited response time. The computer beeps and the Greeble with correct label appears for 750 ms following incorrect response. 250 ms ITI. Only Greebles with known individual names are included in this task.
(vi) Individual naming: Same as above but incorrect response is followed by beep only. All 30 Greebles are included in this task. The subject must press the space bar when a Greeble appears that does not have an individual name assigned (i.e., the individual name is unknown), otherwise the subject presses the key corresponding to the first letter of the Greeble’s individual name.
(vii) Verification: A fixation appears for 250 ms, followed by a label (either a family or individual level) for 1000 ms. This label is then replaced with a Greeble, which stays on the screen until the subject responds. The subject must decide whether the Greeble matches the label, and responds by pressing the keys labeled “yes” or “no” (”,“; and “,” respectively) as quickly as possible. All 30 Greebles are used in this task. The label “Name Unknown” is used for correct individual level judgments for Greebles whose individual label has not yet been assigned. An incorrect response is followed by a “beep”.

Fig. 3. Accuracy and response times for the naming task in the learning phase of Experiment 1 for LR and five controls.
Fig. 4. Sensitivity and response times for the verification trials in the learning phase of Experiment 1. Performance for family trials is plotted by a dashed line; performance for individual trials is plotted by a solid line. The large plot in the upper left of each panel shows LR’s performance compared to the mean of all control subjects. The smaller plots show performance of each individual control subject.

criterion until all 20 individual names have been learned, so statistical analyses were not conducted on the verification trials during the learning phase. However, for the interest of the reader, Fig. 4 shows sensitivity and response times to the verification trials during the learning phase. Notice that LR’s primary difficulty was with verifying Greeble identity at the individual level, whereas sensitivity for family level judgments was within normal range.

3.2.2. Criterion stage

Subjects continued to practice with naming the Greebles during the criterion stage, although without feedback. Fig. 5 shows the results of the naming task for the criterion stage. After an initial setback in Session 5, LR’s naming accuracy continued to be above 90%, though his response times for Greeble naming continued to be slower than that of the controls. Performance on the verification trials for the Criterion Stage is presented in Fig. 6. Recall that we
adopted a modified criterion for Greeble expertise that requires statistical equivalence between family and individual level response times on the verification trials, and also a maximum difference of 95 ms (2 standard deviations above the mean of previous studies). Individual control subjects reached criterion between the 5th to 8th sessions, in line with previously published Greeble studies (Gauthier & Tarr, 1997; Gauthier et al., 1998). LR, however, did not reach criterion until Session 16, and remained at criterion in Session 17. LR’s response times, though above the mean, were not different from slowest controls.

3.3. Discussion

Several aspects of LR’s performance during Greeble training were abnormal. First, he exhibited quite a bit of difficulty in learning to associate names to the 20 Greebles in the learning phase, taking three extra sessions to reach a high rate of accuracy in the naming task. Second, he also took many more sessions than controls to reach expertise criterion – 16 sessions, compared to 8 for the slowest control. It appears, therefore, that LR’s impairments affect the identification of homogeneous object classes and his acquisition of Greeble expertise. Nonetheless, LR eventually met criterion for Greeble expertise despite the stricter criterion imposed in this study.

One possibility for poorer performance in the Greeble training paradigm is that LR may have difficulty associating names with objects. Although we did not test for this specifically, his pattern of performance in standardized neuropsychological tests suggests that this is unlikely (see Table 1). He scored normally in both tests of verbal intelligence and memory. He had no difficulty in naming an extensive set of objects, and also had intact name recall on the Warrington Name Recall task. In contrast, he was significantly impaired on a timed version of the Benton Face Recognition Memory task, which does not require labels, and failure on such a test is typically taken to indicate an apperceptive form of prosopagnosia (Barton, 2008).

A second alternative is that LR used a different strategy to identify the Greebles. Previous studies have shown that as individuals acquire expertise with Greebles, they process the objects in an increasingly holistic fashion – that is, they rely on information from multiple parts (Gauthier & Tarr, 1997, 2002). However, one need not necessarily use a holistic strategy to identify each Greeble, as the shapes of each individual Greeble’s appendages are unique (in the same manner as each eye or nose is unique, though very similar to many other exemplars). Therefore, it is possible to identify the Greebles on the basis of the shape of one part alone. For LR, this seems like a distinct possibility, as prior research has shown that he relies on a single feature to identify faces (Bukach, Bub, et al., 2006; Bukach et al., 2008). Such a strategy would indicate a difficulty with object representation, rather than naming. We therefore included a pre-test and post-test version of a conjunction task with Greebles, similar to the conjunction task with faces that was previously used to document LR’s face impairment (Bukach, Bub, et al., 2006). More specifically, we were interested in whether Greeble training would improve LR’s ability to use multiple features to identify new Greebles.

4. Experiment 2. Greeble conjunction task

4.1. Method

4.1.1. Subjects

Subjects were the same as those who participated in the Greeble training task (see Experiment 1).

4.1.2. Materials

The stimulus set consisted of 8 grayscale variations of a base Greeble. A single image of a Greeble from the training set was modified such that there were two possible positions for the Boges, two possible positions for the Duth, and two possible shapes of the Quiff. Eight stimuli were created using all possible combinations of these modifications, and each was assigned a unique name. The experiment was conducted on a Macintosh computer equipped with a color monitor using RSVP software (© Michael J. Tarr, Brown University). Labels with the names of the eight Greebles were placed on the number pad of the keyboard (keys 1–4 and 6–9). A template reference sheet (8 × 11) was created with the eight Greebles and associated labels in the same spatial arrangement as that of the number pad (see Fig. 7), so that participants were not required to memorize either the label or key associations to the conjunction Greebles.

4.1.3. Procedure

The conjunction task was administered pre- and post-training to determine whether training improved subject’s ability to use multiple Greeble features. The design was a speeded identification task. Each subject was first given the template to study, and required to explain the differences between each of the eight Greebles before proceeding to the computer task. Each subject was given as much time as necessary to find the differences between

![Fig. 5. Accuracy and response times for the naming task in the criterion phase of Experiment 1 for LR and five controls.](image-url)
the eight exemplars. The template was then placed to the side of the monitor for reference throughout the experiment. On each trial, a fixation appeared for 500 ms, followed immediately by the target Greeble for 750 ms. Subjects were required to press the key that corresponded to the name of the target Greeble. Subjects could consult the template as needed. Following their identification response, subjects indicated their confidence level by pressing the appropriate numerical key, with 1 indicating very low confidence and 6 indicating very high confidence. Subjects pressed the return key when they were ready to continue, and after 200 ms the next trial began. Originally designed as a multi-dimensional signal detection task for normal observers, blocks that included all eight exemplars in randomized order (24 trials) were interleaved with blocks that included only two of the possible eight exemplars (20 trials). Instructions prior to the beginning of each block indicated which Greebles would be included in the next block.
purpose of the current research question – Does Greeble training improve LR’s ability to use multiple Greeble features? – only those blocks including all eight exemplars were analyzed.

4.2. Results

Accuracy and response times for the blocks that contained all 8 Greebles are displayed in Fig. 8. On this task, single feature performance would result in a 25% accuracy rate, two features would result in an accuracy rate of 50%. As expected, LR’s performance prior to Greeble training was quite poor (31%), not much above the level of performance that would be expected if responses were based on a single feature. Although LR performed more poorly than any of the controls during the pretest, some of the control subjects also found the task quite difficult, performing at or below 50%. After Greeble training, LR’s performance was much different from controls: whereas accuracy for control subjects ranged between 55% and 97% indicating that all subjects used two or three features, LR was accurate on only 36% of the trials. One-tailed modified t-tests designed to compare single case studies to small-sample control groups (Crawford & Howell, 1998) confirmed that whereas LR’s overall accuracy was no different from controls before training (p > .05), he was significantly impaired relative to controls after training (t(4) = -2.29, p < .05). His response times did not statistically differ from controls before or after training, ps > .05.

To determine whether LR relied exclusively on one particular feature, as he did with faces, a parts-based analysis was conducted. In this analysis, a trial was considered correct for a particular feature if the response shared the feature value, regardless of the value of the other two features. For example, if the target Greeble was Bill, a response of Bill, Biff, Buck or Bram would be considered correct for the Greeble feature, because all four Greebles have the same Boges. In this type of analysis, chance is 50%, as there are two possible values for each feature. The results of this parts-based conditional analysis are displayed in Fig. 9. Prior to Greeble training, LR was at chance for the central appendage (the Quiff) and appeared to rely most heavily on the Boges and Dunth. This pattern remained unchanged after training. Note that this does not mean that he was able to integrate information from these two features, as his overall accuracy

Fig. 7. Template showing all eight conjunction Greebles with their labels. Differences between Greebles are quite subtle, requiring fine-level discrimination. The Boges can be in either a forward or back position, the Quiff shape can be either curved or straight; the Dunth can be in either an upper or lower position. Whereas Bill has Boges in the forward position, a curved Quiff and up a Dunth in the upper position, Ben has Boges in the back position, a straight Quiff and a Dunth in the lower position.

After each block, subjects received feedback as to their accuracy for that block. Note that whereas all three features are necessary for identification when the block included all eight exemplars, a single diagnostic feature is sufficient to identify Greebles in blocks that included only two exemplars. Thus, in these two-exemplar blocks, the location of the diagnostic feature could be determined in advance in that the instructions prior to the beginning of each block indicated which two Greebles would appear (i.e., the specific diagnostic contrast could be pre-determined). Therefore, for the

Fig. 8. Overall accuracy and response times for LR and five controls in Experiment 2 before and after Greeble training. The dashed line represents expected accuracy if identification was based on a single part.
indicated that his performance did not differ from what would be expected from reliance on a single feature; rather, LR appears to have favored the Boges on some trials and the Dunth on others. In contrast, all control subjects were able to use at least two features after training. Moreover, unlike LR who alternated between the two extreme features at both pre- and post-test, the control subjects showed nearly perfect performance on the central part following training, and above chance performance on the other two parts. Modified t-tests confirm that LR’s performance on the Quiff was impaired relative to controls at both pretest ($t(4) = -3.68, p < .05, r^2 = .77$), and post-test ($t(4) = -19.84, p < .05, r^2 = .99$). Performance on the other two appendages was not different from controls ($ps > .05$).

4.3. Discussion

The results of the conjunction task confirm that LR is unable to use multiple features for identification of Greebles, similar to his impairment with faces (Bukach, Bub, et al., 2006). Importantly, LR showed this impairment even after Greeble training, indicating that he likely relied on a single feature to reach expertise criterion. Like LR, some controls were also unable to use all three features prior to Greeble training. However, in contrast to LR, all controls improved in their use of multiple features following training, and used all three features above chance following Greeble training. Controls’ near perfect performance for the central appendage is consistent with either a more efficient strategy that integrates the product of rapid sequential processing of two adjoining features (one of which always occurs at fixation), or with a parallel processing strategy that uses the central part of the Greeble as a focal point.

We acknowledge that it is not possible here to distinguish between a parallel and a sequential model of feature integration. If it is accomplished through a parallel process, LR’s processing may be less efficient in that he was unable to achieve a high-resolution holistic representation in the time provided (see Richler, Mack, Palmeri, & Gauthier, 2011 for a similar explanation for the difference in holistic processing between upright and inverted faces).

Another possibility is that the design of the conjunction task may encourage selective attention to multiple parts in order to achieve a high-resolution representation, and LR is unable to rapidly move his attention to multiple parts or cannot integrate multiple outcomes to consider them together. The fact that LR showed normal interference on the composite task (Bukach, Bub, et al., 2006) suggests that he is able to build at least a coarse-level holistic representation of faces, but one that is not sufficient for face identification. He is not able to rapidly integrate multiple fine details to make an identity judgment such that multiple parts are considered together. Rather he appears to consider only a single part, independent of the other parts, when making a decision, whether for faces or Greebles. In contrast, controls used information across all three diagnostic features following Greeble training.

One concern with the design of Experiment 2 is our use of a single, fast exposure duration. In the conjunction task with faces (Bukach, Bub, et al., 2006) we used a range of exposure durations to test whether additional time would improve LR’s ability to integrate facial features. We therefore created a version of the conjunction Greeble task with multiple exposure durations, identical to that used previously with faces. This additional manipulation also allows a somewhat more direct comparison between the processing of faces and Greebles.

5. Experiment 3. Greeble conjunction task with multiple exposure duration

5.1. Method

5.1.1. Subjects

LR and the same 5 controls participated (see Experiments 1 and 2). Because it had been nearly a year since LR and C5 completed Greeble training, both subjects completed seven refresher Greeble training sessions over several weeks prior to testing. In the first session, subjects received a full review of both family and individual names of all 20 Greebles, including passive viewing of Greebles with their labels, and naming and verification tasks. In the following
six sessions, subjects received one block of review of family and individual viewing, followed by naming and verification trials. The details of the retraining can be found in Table 3. The results of the naming and verification trials over the 7 sessions are displayed in Figs. 10 and 11. Again, the strict criterion of statistical equivalence between family and individual level response times with less than a 95 ms difference was used to judge expertise. C5 reached criterion for expertise in all sessions but Session 2. LR, however, did not regain criterion until the final session. Although LR’s response times were slower than C5, by Session 7 LR was responding faster than he did in the final session of the original training procedure.

5.1.2. Materials

The materials were the same as those used in Experiment 2 above.

5.1.3. Procedure

This test was designed to provide a more direct comparison of LR’s ability to use multiple Greeble features with his ability to use multiple facial features. The procedures for this task were therefore identical to those used in Experiment 4 of Bukach, Bub, et al. (2006), with the exception that the stimuli were Greebles as opposed to faces. The conjunction Greeble task was a speeded identification task with variable exposure durations (250 ms, 500 ms, 750 ms, 1000 ms, and 1250 ms). Each subject was first given the paper template to study, and again required to explain the differences between each exemplar. The template was then placed to the left of the computer monitor for consultation during the computer task, avoiding the need to memorize the labels or key associations. There were 4 blocks of 120 trials each, with a total of 96 trials at each of the 5 exposure durations. Exposure duration and identities were randomized throughout the experiment. On each trial, a fixation point appeared for 500 ms in the middle of the screen, followed by

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Details of Greeble expertise retraining across sessions.</th>
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<tbody>
<tr>
<td>Tasks (# of Greeble exemplars)</td>
<td># of trials</td>
</tr>
<tr>
<td></td>
<td>Session 1</td>
</tr>
<tr>
<td>Family examples (10)</td>
<td>1</td>
</tr>
<tr>
<td>Family naming (30)</td>
<td>30</td>
</tr>
<tr>
<td>Individual viewing (20)</td>
<td>80</td>
</tr>
<tr>
<td>Individual naming (30)</td>
<td>60</td>
</tr>
<tr>
<td>Verification (30)</td>
<td>120</td>
</tr>
<tr>
<td>Family examples (10)</td>
<td>1</td>
</tr>
<tr>
<td>Individual viewing (20)</td>
<td>40</td>
</tr>
<tr>
<td>Individual naming (30)</td>
<td>60</td>
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<td>Verification (30)</td>
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<td>Individual naming (30)</td>
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Fig. 10. Accuracy and response times on naming trials for LR and an age-matched control during Greeble retraining in Experiment 3.

Fig. 11. Sensitivity and response times for the verification trials in the Greeble retraining phase of Experiment 3 for LR and an age-matched control. Performance for family trials is plotted by a dashed line; performance for individual trials is plotted by a solid line. Error bars represent 95% confidence intervals. Sessions in which criterion for expertise was reached are indicated by an asterisk.
one of the eight Greebles for a variable duration. Subjects pressed the key whose label matched the Greeble presented, and then gave a confidence judgment. Subjects pressed the return key to initiate the next trial, which began after a 200 ms pause. After each block, subjects received feedback indicating their accuracy for that block.

5.2. Results

The results of the conjunction task across multiple exposure durations are displayed in Fig. 12. In this task, decisions based on a single feature would achieve an accuracy of 25% on average; decisions based on two features would achieve an accuracy of 50% on average. At the lowest exposure durations, the majority of controls were able to use only two features on average, but by 750 ms, controls were using all three features on the majority of trials, as indicated by accuracy levels well above 50%. In contrast, LR was not able to use all three features within the parameters of this task. LR’s performance was below 50% until 1250 ms, indicating that he was unable to consistently use even two of the three available features for all but the longest exposure duration. In line with his poor performance, LR’s confidence rating was quite low across all exposure durations (M = 2). Statistical analyses revealed that both LR’s accuracy and confidence ratings were significantly below that of controls for all but the two lowest exposure durations (see Table 4). LR’s responses were further examined to determine whether he used particular features consistently, or whether his perception was poor across all three features. As in Experiment 2, a conditional by-parts analysis was conducted. In this analysis, chance performance is 50%. As can be seen in Fig. 13, LR consistently favored a single feature (the Bogo) on the vast majority of trials. At 1250 ms, LR appears to have also used the Duth for some responses and the Quiff for others. Consistent with the analysis of overall performance, the control subject showed accurate use of all three features at 750 ms.

5.3. Discussion

LR’s performance on the conjunction task with Greebles indicates that he has difficulty using multiple parts of Greebles in making identity judgments, showing slight improvement with increased exposure duration. This pattern is consistent with his performance on the same task with faces (Bukach, Bub, et al., 2006), and suggests that LR’s impairment affects the recognition of faces and other homogeneous object classes.

6. General discussion

We return again to the question of how we assess and explore the space of different patterns of sparing and impairment that may exist in conjunction with prosopagnosia. In particular, there is an ongoing debate as to whether prosopagnosia is a “pure” syndrome in which face recognition, and only face recognition, is impaired, or whether visual recognition deficits extend to nonface object classes, particularly in cases of individuating between members of a homogeneous object class. Since the number of prosopagnosic cases is relatively small, the likelihood that we have adequately mapped out the breadth of the space is low. This is perhaps best exemplified by the divergence between our present results and the results of Duchaine et al. (2004), who found that Edward, a developmental prosopagnosic patient, was able to learn Greebles normally. Although Duchaine et al. took these latter results as evidence in favor of face-specificity, and notwithstanding the potential pitfalls in comparing acquired and developmental versions of the disorder, we suggest that the visual recognition strategies underlying the attainment of expertise – in this case Greeble expertise – should be carefully examined. Thus, while at first glance LR’s ability to reach expertise criterion appears to support the hypothesis that Greeble training relies on “ordinary object recognition mechanisms” dissociable from those used for face recognition (Duchaine et al., 2004, p. 472), several aspects of LR’s performance argue against this interpretation of the data (and suggest that further examination of Edward’s post-training recognition strategies may be warranted).

First, LR’s acquisition of expertise did not follow the normal trajectory. LR’s performance, particularly in the beginning of training, was well below that of controls, and LR took many more sessions to reach criterion than did the slowest control. This pattern indicates that LR had considerable difficulty learning the Greebles.

Second, and more critically, performance in the conjunction tasks (Experiments 2 and 3) indicates that LR used a qualitatively different strategy for learning the Greebles than did normal controls. Prior to Greeble training, the ability to use multiple features was variable among controls. Following training, all normal controls were able to use three critical features to rapidly identify Greebles, consistent with past evidence for the development of holistic processing following Greeble training (Gauthier & Tarr, 2002; Gauthier et al., 1998). LR, however, continued to rely primarily on a single feature in this task, even after reaching expertise criterion. Thus, it appears that LR may have relied on subtle shape differences in a single feature during Greeble acquisition, whereas controls learned to use all three critical features.

Third, the pattern of performance in the conjunction tasks with Greebles corresponds to LR’s pattern of performance in a similar conjunction task with faces (Bukach, Bub, et al., 2006). For both conjunction faces and conjunction Greebles, impaired recognition was due to an inability to use multiple features to identify individuals. Although the analogy to face learning is somewhat limited by the fact that the specific strategies adopted by LR are inherently unknown to us, the correspondence between LR’s performance on the two conjunction tasks implicates a common mechanism for domains of perceptual expertise and face recognition, one that involves the integration of fine-level details across multiple features. Unlike his performance in the expertise-training paradigm, we note that LR shows preservation of basic level identification. We suggest that this skill is preserved because unlike individuation of homogenous categories, basic level recognition could be accomplished by a coarser representation of an object and/or integration of fewer finely discriminated parts. We would expect that LR’s deficit would impair rapid individuation of any object category that contains many exemplars with multiple diagnostic features that are highly similar, and thus is best described as a domain-general deficit that interferes with a process critical for perceptual expertise. This explanation is consistent with the hierarchical theory of the temporal lobe in which anterior regions of the temporal lobe (specifically the perirhinal cortex) are involved in complex conjunctive object representations (Bussey, Sakida, & Murray, 2005). Of note, Greeble training has been informative for other cases with face recognition difficulty. For example, SM, who has damage to the right hemisphere that includes the temporal–occipital region (an area commonly damaged in prosopagnosia), was shown to have difficulty making fine-level visual discriminations of faces (Gauthier, Behrmann, et al., 1999). In SM’s case, this deficit severely
impaired his ability to effectively acquire Greeble expertise. Even after 31 training sessions, SM was able to identify only 5 of the Greebles (Behrmann, Marotta, Gauthier, Tarr, & McKeeff, 2005). Further training of SM and a second patient with integrative visual agnosia (CR) using another set of novel objects (Fribbles) has shown that inability to integrate multiple parts impairs both face and object recognition (Behrmann & Williams, 2007). Greebles have also been used to explore whether children with Autism who have perceptual

Fig. 12. Overall accuracy and confidence levels for LR and five controls across the five exposure durations in Experiment 3. The dashed line represents expected accuracy if identification was based on a single part.

Fig. 13. Parts based accuracy for LR and controls across five exposure durations in Experiment 3. Accuracy was calculated for each part separately based only on the value of that part, ignoring the value of the other two parts. Because each part has two possible values, chance performance for a particular part is 50%, as indicated by the dashed line.
discrimination deficits with faces also show difficulty individuating Greebles (Scherf, Behrmann, Minshew, & Luna, 2008).

LR, SM, and Edward demonstrate the heterogeneous nature of prosopagnosia. Face recognition is a complex task that recruits a wide variety of cognitive processes at perceptual, memory, and social levels of cognition. Performance on any particular behavioral test will therefore depend on whether the task in question relies on specific processes also implicated in the subject’s face recognition impairment. LR has damage to more anterior temporal lobe regions in the right hemisphere, leaving fine-level discrimination intact, as well as holistic processing at a coarse level of representation, but preventing rapid integration of multiple finely-detailed features (Bukach, Bub, et al., 2006). In contrast, SM’s damage to more posterior regions affected his fine-level visual discrimination (Behrmann, Marotta, et al., 2005). Importantly, for both LR and SM, the nature of their impairments with Greebles was consistent with their impairments for faces.

In contrast to these two types of acquired prosopagnosia, Edward suffers from developmental prosopagnosia, which involves impairment of face recognition during childhood before the recognition system has matured (for reviews, see Barton, Cherkasova, Press, Intriligator, & O’Connor, 2003; Behrmann, Avidan, Thomas, & Humphreys, 2010). Recent imaging studies of developmental prosopagnosics have found an overall reduction in volume within several face-processing regions, (Behrmann, Avidan, Gao, & Black, 2007; Garrido et al., 2009), as well as reduced white-matter connectivity in right ventral occipito-temporal cortex that is correlated with face recognition impairment (Thomas et al., 2008, 2009), though no abnormalities have yet been reported for Edward. He shows impairments in a variety of tasks with faces, but was able to acquire Greeble expertise in a normal trajectory (Duchaine et al., 2004, 2006). Unfortunately, Duchaine et al. did not probe how Edward recognized the Greebles, so although the trajectory of learning was normal, we do not know if Edward was using an unusual strategy, or if the mechanisms supporting expertise are indeed intact. Both explanations are possible, but without further testing it is impossible to decide between these two alternatives.

It is important to note that the Greeble training paradigm, as with any laboratory-based experiment, does not capture all facets of the acquisition of face-recognition abilities. It is possible to exhibit face recognition deficits and yet acquire expertise for other objects. For example, a deficit in social processing may result in poor face recognition, but spare perceptual processes necessary for face individuation. Such a case has been previously published: DD is an individual with Autism who individuates faces no faster than objects, yet displays a proficiency in identification of Digimon cartoon characters. This finding suggests that DD’s expertise mechanisms are intact, but not, for whatever reason, applied to faces (Grelloti et al., 2005). For DD, it is Digimon, not faces, that recruits the region in the fusiform gyrus where the “fusiform face area” is typically located. Providing Greebles could similarly capture DD’s attention, we would predict he should show a normal trajectory in a Greeble training paradigm.

Similarly, Edward may have an impairment that spares the expertise mechanisms necessary to complete the Greeble training paradigm. If this were also the case for Edward, and if Greeble and face individuation rely on common mechanisms, he should be able to reach expertise criterion for a set of 20 faces in a similar fashion, and may in fact benefit from such training. Thus we argue that it is premature to conclude on the basis of Edward’s success with Greeble training that Greebles merely tap “ordinary object recognition processes”, or that perceptual mechanisms involved in face recognition are domain specific. In fact, other evidence from congenital prosopagnosics who, like Edward, have been impaired since birth but who have been shown to have reduced white fibre tracts in the right occipito-temporal cortex (Thomas et al., 2009) showed impairments of subordinate-level object recognition as well (Behrmann, Avidan, Marotta, & Kimchi, 2005).

Despite the usefulness of the Greeble training paradigm in studying general mechanisms of perceptual expertise and their relation to face recognition abilities and impairments, both studies of LR and Edward point to limitations of the Greeble training paradigm, particularly when applied to a limited number of neuropsychological case studies. In contrast to real-life face recognition, which involves a lifetime of experience with thousands of faces, the Greeble training paradigm requires identification of only 20 exemplars at an individual level over hours of training. Although the mechanisms recruited by post-expertise recognition and face recognition may be similar, the degree of expertise between the two domains is quite different. A second limitation is that all Greebles contain uniquely shaped features, thus a single feature strategy is possible should a subject choose to use such a strategy. To a limited extent, faces may also contain some uniquely-shaped features that may be useful, particularly when individuals are highly familiar, though for faces there are many more competitors and thus when applied broadly a single-feature strategy would likely lead to many false positives. It is therefore important to adopt a wide range of paradigms to assess how observers process objects, both faces and nonfaces alike. Of note is the finding that despite the availability of a feature-based strategy for Greeble individuation, controls typically adopt a more holistic strategy – as do most of us with faces despite the availability of diagnostically single features. In contrast, reliance on single features is predominant in both the Greeble and face recognition strategies of LR, who, for example, can recognize the sideburns of Elvis or Bette Davis’ eyes. Thus, there are obvious benefits to probing the timing and manner of expertise acquisition even when performance is high. Tasks that measure holistic processing and the use of multiple features, such as the composite and conjunction tasks used in the present study, may be particularly informative.

In summary, the correspondence between single-feature use in both face and Greeble conjunction tasks suggest that impaired performance for faces and Greebles are the result of a common deficit. It is worth repeating that the specific strategies adopted by LR in response to Greeble training are inherently unknown to us. To the extent that he is relying on a serial, part-based strategy, our analogy to normal face learning is necessarily weakened. Moreover, no single study could ever resolve the complex issue of whether faces are processed in a domain specific or domain general way. While we do hold that our present results further our understanding of face processing and the question of domain specificity, we acknowledge that it is but one small piece of a much larger puzzle.

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