N170 face specificity and face memory depend on hometown size

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ABSTRACT

Face recognition depends on visual experience in a number of different ways. Infrequent exposure to faces belonging to categories defined by species, age, or race can lead to diminished memory for and discrimination between members of those categories relative to faces belonging to categories that dominate an observer's environment. Early visual impairment can also have long-lasting and broad effects on face discrimination – just a few months of visual impairment due to congenital cataracts can lead to diminished discrimination between faces that differ in their configuration, for example (Le Grand et al., 2001). Presently, we consider a novel aspect of visual experience that may impact face recognition: The approximate amount of different faces observers encountered during their childhood. We recruited undergraduate observers from small (500–1000 individuals) and large communities (30,000–100,000 individuals) and asked them to complete a standard face memory test and a basic ERP paradigm designed to elicit a robust N170 response, including the classic face inversion effect. We predicted that growing up in a small community might lead to diminished face memory and an N170 response that was less specific to faces. These predictions were confirmed, suggesting that the sheer number of faces one can interact with during their upbringing shapes their behavioral abilities and the functional architecture of face processing in the brain.

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1. Introduction

Visual experience has an impact on face processing, leading to measurable effects early in infancy. Young infants generally prefer female faces to male (Quinn et al., 2002), for example, an effect which appears to follow from the biased exposure to female faces most infants receive early in life (Rennels and Davis, 2008). Infants with male primary caregivers show a different behavioral profile, suggesting that face preference reflects experience rather than innate mechanisms. Visual preferences for own- vs. other-race are also evident early in the first year of life (Kelly et al., 2005) and later in the first year, infants "narrow" their face discrimination abilities to exclude other-race faces (Kelly et al., 2007). Perhaps the most striking evidence that this developmental trajectory depends on experience is Sugita's (2008) elegant study that demonstrated that non-human primates reared without exposure to faces could develop face recognition abilities specific to human faces or monkey faces depending on which faces they were exposed to after an initial period of face deprivation.

Face processing also exhibits some plasticity during childhood that reflects experience. The use of specific visual features (e.g. surface pigmentation vs. 3D shape) for own- and other-race faces

changes between 5–6 years of age and adulthood, for example (Balas et al., 2014). Also, the direction of the other-race effect can be reversed following a substantial change in the faces children are exposed (Sangrigoli et al., 2005). While some results suggest that some aspects of the development of face recognition during childhood really reflect more general developmental processes (Crookes and McKone, 2009), there also appear to be many examples of face recognition being sensitive to experience during infancy and childhood.

Besides the effects described above that depend on the statistics of experience (the number of faces an individual encounters belonging to intuitive sub-groups defined by sex, race, or species), there are also several results that speak to the impact of deprivation on face recognition abilities. The effects of deprivation are interesting to consider alongside the effects of biased experience since in this case we have the chance to see how globally-impoverished experience (rather than category-specific impoverished experience) shapes face processing. Face deprivation does turn out to have intriguing effects on perception and recognition. One particularly striking result is the finding that congenital monocular cataracts (removed during the first year of life) lead to specific deficits in face processing later in development (Le Grand et al., 2001). This result suggests that early experience with faces may be critically important for later processing, a subsequent lifetime of face exposure notwithstanding. However, this is not to say that early or extended deprivation represents an

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insurmountable obstacle to face processing-patients born with congenital cataracts that were not removed until late in life have been shown to be able to achieve useful face recognition abilities (Ostrovsky et al., 2006), though the information they use for recognition may differ from typical observers.

In the current study, we chose to investigate face processing in a population of observers that we suggest occupy an interesting place somewhere between the biased experience that nearly all observers have of human facial appearance and the visual deprivation that a far smaller number of people endure. Specifically, we examined how growing up in a depopulated region affects face processing in adulthood.

Fargo, North Dakota, is not a big city. Boston, Paris, Sydney – these are big cities. By comparison, the approximately 200,000 people who call the Fargo–Moorhead metropolitan area home do not constitute what you might think of as an overwhelmingly dense urban environment. However, while Fargo may seem diminutive in comparison to the largest cities in the world, it also looms very large in comparison to other towns in ND. North Dakota is 47th out of the 50 states in terms of population density with approximately 10.5 people/sq. mile (Fig. 1), (http://en.wikipedia.org/wiki/List_of_U.S._states_by_population_density), which means that many undergraduates in North Dakota have grown up in towns with extremely small populations. Anecdotally, students who arrive in Fargo from communities with populations in the neighborhood of a few dozen frequently report that their initial experience of Fargo is overwhelming. A freshman at NDSU may easily find themselves sitting in a lecture hall that has many more people in the room than there are people in their hometown – an experience which can be disquieting for some students.

Aside from the broad challenges associated with the transition between a rural upbringing and a more urban environment in adulthood, the visual experience of individuals who live in depopulated areas poses an intriguing question regarding the impact of experience on visual recognition. Specifically, does growing up in an environment that contains a relatively small set of faces affect face recognition at behavioral and neural levels? These individuals obviously don't suffer from true deprivation. Their visual environment in general is quite rich, and while their communities are small, they are not insulated from faces the way Sugita's monkeys were. Nonetheless, the "face space" that these students maintain may be sufficiently different from that of other observers to lead to interesting differences in how faces are processed. For example, Valentine's (1991) argument that other-race faces are hard to recognize because they are tend to occupy a small outlying clump relative to the faces observed more frequently may apply on a broader scale to these individuals. Given the small sample of faces these observers have seen over a lifetime, *all* faces may end up hard to discriminate or recognize because of the statistical properties of their experience. We hypothesized that limited experience with faces (induced by living in a very small community) might therefore lead to measurable deficits in face recognition and measurable differences in basic neural responses that are sensitive to faces.

We tested individuals from both small and large hometowns on a simple behavioral task requiring robust memory for faces and also a basic ERP paradigm comparing responses to faces and objects. Our overarching hypothesis was that face recognition abilities should be poorer in individuals with a history of limited face experience and also that face recognition may not be as functionally distinct from object recognition in these individuals. Briefly, we found evidence supporting both of these predictions: participants from very small hometowns performed more poorly in our behavioral task and exhibited less face-specificity in their ERP responses to faces and objects. We discuss our results in terms of a synthesis of biased experience and deprivation.

2. Methods

2.1. Participants

We recruited two groups of participants to take part in both the behavioral and ERP studies described here. The first group (11 females) was comprised of 19 undergraduate students at NDSU who reported that the population of their hometown was either 0–500 persons or 500–1000 persons. These individuals were between the ages of 18 and 21 years old ($M=18.6$ years, sd$=0.77$) and all of them were right-handed as assessed by the Edinburgh Handedness inventory (Oldfield, 1971). The second group was comprised of 18 undergraduate students (13 females) at NDSU who reported being from hometowns with a population greater than 30,000 persons. These individuals were between the ages of 18 and 24 ($M=19.2$ years, sd$=1.5$) and 17 of them were right-handed. All participants reported either normal or corrected-to-normal vision and also reported that they were free of any neurological impairments. All participants received course credit in exchange for their participation.

There are several important limitations to acknowledge regarding our recruitment procedures. We did not ask participants to report the exact size of their hometown, nor estimate day-to-day interactions. Participants had also been living on the NDSU campus in Fargo for varying amounts of time. We also did not ask students to report other potentially relevant variables like the extent of their travel to large cities. While such data is undeniably valuable in providing a rich picture of face experience (see Rennels and Davis, 2008 and Sugden et al., 2014), we opted for a relatively coarse division between participant groups based on a very simple dimension of their face experience. Overall, we suggest that the
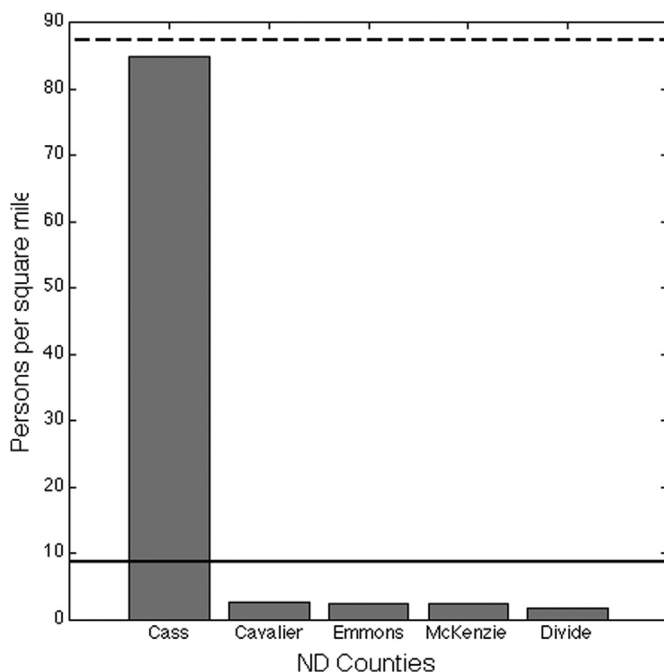

Fig. 1. Population density data from the 2010 census for counties in North Dakota. The dashed line at the top of the figure indicates the average population density for the entire country (∼87.4 persons/sq. mile) and the solid line near the bottom indicates the same for ND (∼9.7 persons/sq. mile). Individual bars describe the density in just a few counties in ND, including Cass county (leftmost bar) which includes Fargo and NDSU. We have chosen just a few illustrative examples of depopulated counties in ND (all with densities close to 2 persons/sq. mile) to highlight the likely difference in visual ecology, faces in particular, that we consider here.

potential heterogeneity within each of these groups in terms of their face experience at smaller scales than we are considering should only negatively impact our ability to measure group effects, making any effects we do report here all the more meaningful.

2.2. Procedures

2.2.1. Face memory

To measure participants' ability to correctly recognize and re-member new faces, we administered a web-based version of the Cambridge Face Memory Test (CFMT) (Duchaine and Nakayama, 2006). Briefly, the CFMT requires participants to study several fa-ces one at a time, and then subsequently select previously studied individuals from an array of three faces. Study and test faces are not identical, so participants must not only remember the facial appearance of each individual in the study set, but be able to generalize across changes in appearance. The version of the CFMT we use was comprised of 72 items and typically took participants approximately 15–20 min to complete. We administered the CFMT on a 14 in. LCD monitor and participants were seated at a com-fortable viewing distance ($\sim$40 cm) with no constraints placed on their head or eye position during the task.

2.2.2. Electrophysiological recording

Participants also completed a short ERP experiment so that we could examine the selectivity of their P100 and N170 response to face vs. non-face images. During the task, we recorded continuous EEG using a 64-channel Hydrocel Geodesic Sensor Net (version 1.0, Electrical Geodesics, Inc.). The raw EEG signal (referenced to electrode Cz) was amplified using the EGI NetAmps 200 amplifier and filtered using a bandpass filter with low and high frequency cut-offs at 0.1 and 100 Hz respectively. Before recording began we established impedances at all sensors below a threshold of 50 kΩ. Recording took place within an electrically-shielded and sound-attentuated chamber, minimizing contamination of the EEG signal by outside sources.

Participants were seated approximately 50 cm away from a 1024×768 LCD monitor where stimuli were displayed. At this viewing distance the images used in this experiment (grayscale images of faces and chairs) subtended approximately 5.5° of visual angle, though this varied somewhat across items. Our stimulus set was comprised of grayscale images of faces (Righi et al., 2012) and chairs, which were presented either upright or inverted. During the task, participants were presented with these images in a pseudo-randomized order, and were asked to categorize each image according to category (face or chair) using two buttons on a small response box. Participants were asked to use their right and left thumbs to respond and the orientation of the button box was flipped for half of our participants so that the assignment of ca-tegories to the left and right hand was balanced across participants in each group. Each image was presented for 500 ms, with an ISI that varied randomly between 700–1500 ms. We presented par-ticipants with 60 images per category (upright/inverted × faces/chairs) for a grand total of 240 images during the entire session. All stimulus timing and display routines were implemented using EPrime v2.0.

3. Results

3.1. Face memory

We described participants' performance in the CFMT using their accuracy (the proportion of correctly identified faces from the study set). Participants in our small-town sample achieved an average accuracy of 72.9% (sd=9.4%), while participants in our large-town sample achieved an average accuracy of 79% (sd=10.6%). This difference was significant ($t(35)=1.98$, $p=0.028$, one-tailed independent samples t-test, Cohen's $d=0.67$), sug-gesting that participants from small towns had poorer face memory than participants from larger towns.

3.2. ERP results

We analyzed ERPs in response to upright and inverted images of faces and chairs by first applying a 0.1–30 Hz bandpass filter to the continuous EEG collected for each participant. The EEG data was then segmented into categories corresponding to our stimulus conditions by extracting a 100 ms pre-stimulus interval before each image appeared, as well as the 900 ms following image onset. The 100 ms pre-stimulus interval for each segment was used to baseline correct each segment by subtracting the average ampli-tude in this interval from every subsequent timepoint. We then applied routines for ocular artifact detection and removal and re-placed bad EEG channels using spherical spline interpolation. Fi-nally, ERP segments were averaged within each condition, yielding a single waveform per condition at each sensor. We excluded a total of 3 participants from the final sample (1 from our "Large town" group and 2 from our "Small town" group) based on poor data quality or hardware failures during recording.

We chose to examine the P100 and N170 components at six sensors (three per hemisphere) positioned over occipito-temporal regions. These sensors included T5/T6 and were selected based on previous literature describing the N170 (Rossion and Jacques, 2008) and based on visual inspection of the grand average wave-form. We selected a time window between 110–143 ms to char-acterize the P100 component and a time window between 150–210 ms to characterize the N170 component, again, based on in-spection of the grand average across participants at the sensors of interest. Within this time window, we described both components using the mean amplitude measured within that interval and the latency at peak amplitude, both of which were averaged across sensors within the left and right hemispheres. We submitted these values to separate $2 \times 2 \times 2 \times 2$ mixed-design ANOVAs, with sti-mulus category (face/chair), stimulus orientation, (upright/in-verted), hemisphere (left/right), as within-subject factors and participant group (small/large town) as a between-subjects factor. Grand average waveforms for the right and left hemisphere for both groups and all stimulus conditions are displayed in Fig. 2 (a) and (b).

3.3. P100 mean amplitude

We found that the mean amplitude of the P100 was sig-nificantly affected by stimulus category ($F(1,32)=25.8$, $p<0.001$) and participant group ($F(1,32)=5.51$, $p=0.025$). The former effect was the result of larger mean amplitudes for faces ($M=4.182$, std. error=0.42) relative to chairs ($M=3.16$, std. error=0.28), while the latter was the result of larger mean amplitudes for large town participants ($M=4.47$, std. error=0.5) compared to small town participants ($M=2.87$, std. error=0.47). We observed no other main effects or interactions that reached significance.

3.4. P100 latency

The P100 latency was significantly affected by stimulus or-ientation ($F(1,32)=9.22$, $p=0.005$) such that inverted images eli-cited slower latencies ($M=123$ ms, std. error=1.63) than upright images ($M=121$ms, std. error=1.60). This main effect was quali-fied by a significant interaction between stimulus orientation and stimulus category ($F(1,32)=13.4$, $p=0.001$) and also by a sig-nificant interaction between hemisphere and stimulus orientation
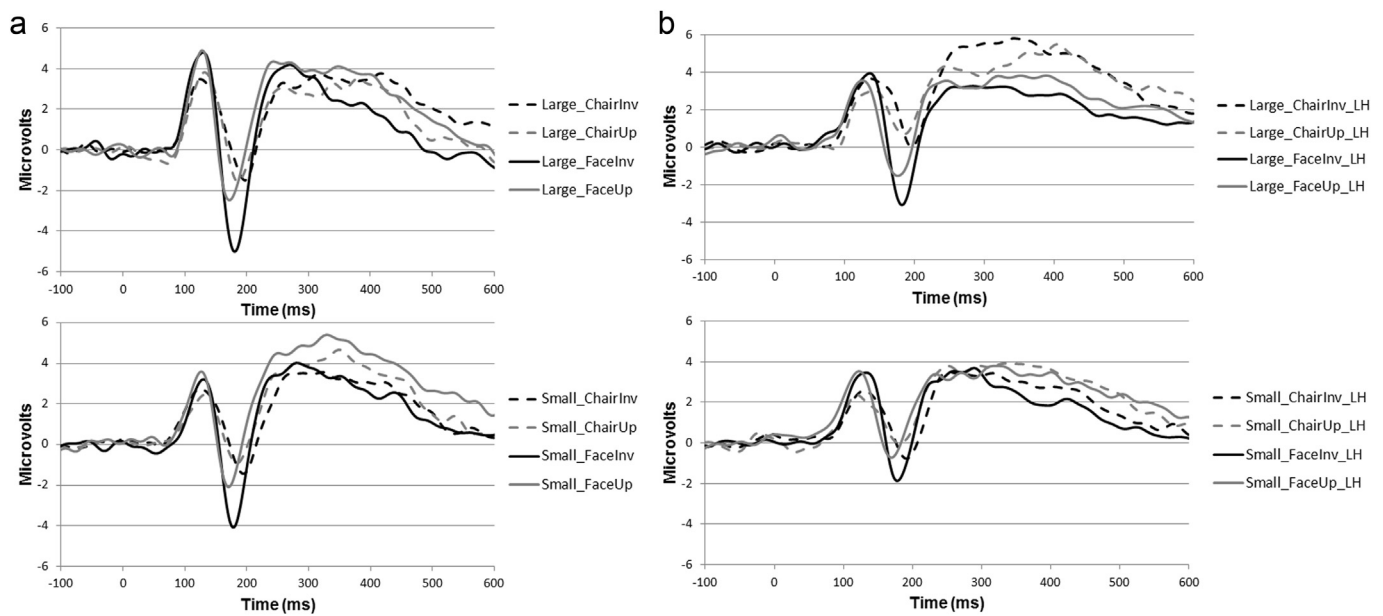
Fig. 2. (a) Average ERP waveforms for upright and inverted faces and chairs in the right hemisphere of participants in both our "small-town" sample and our sample of participants from larger towns. (b) Average ERP waveforms from the left hemisphere of participants in both groups.

($F(1,32)=14.3$, $p < 0.001$). The former interaction was driven by a significant difference ($p < 0.01$, post-hoc two-tailed paired-samples t-test) between upright ($M=120$ms, std. error$=0.36$) and inverted faces ($M=124$ms, std. error$=0.39$) that was not observed for upright and inverted chairs. The latter interaction was apparently the result of a null difference between orientations in the right hemisphere, while latency values differed by orientation in the left hemisphere significantly.

3.5. N170 mean amplitude

Our analysis of the mean amplitude across participants yielded main effects of stimulus category ($F(1,32)=7.48$, $p=0.010$), stimulus orientation ($F(1,32)=21.5$, $p < 0.001$), hemisphere ($F(1,32)=10.73$, $p=0.003$), but no main effect of participant group ($F(1,32)=0.32$, $p=0.54$). These main effects were driven by more negative amplitudes to faces ($M=0.20$, std. error$=0.42$) relative to chairs ($M=0.89$, std. error$=0.35$), inverted stimuli ($M=0.14$, std. error$=0.39$) relative to upright stimuli ($M=0.95$, std. error$=0.36$), and right hemisphere responses ($M=0.03$, std. error$=0.38$) relative to left hemisphere responses ($M=1.06$, std. error$=0.41$). The direction of all of these main effects is consistent with prior reports of face-sensitive responses at the N170 (Rossion et al., 2000).

Our main effects were qualified by two interactions. Critically, we observed a two-way interaction between stimulus category and participant group ($F(1,32)=4.05$, $p=0.05$), suggesting that the population size of participants' hometowns did influence face-sensitive responses at the N170. Post-hoc tests revealed that this interaction was the result of a significant difference between the face ($M=-0.28$, s.e.m.$=0.62$) and chair ($M=0.91$, s.e.m.$=0.51$) conditions for individuals from larger towns, but no such difference between faces ($M=0.68$, s.e.m.$=0.58$) and chairs ($M=0.86$, s.e.m.$=0.48$) in the small town population (Fig. 3). We also observed a significant three-way interaction between stimulus category, orientation, and hemisphere ($F(1,32)=6.84$, $p=0.013$). This interaction appeared to be driven by particularly large negative amplitudes to inverted faces in the right hemisphere, consistent with a hemisphere- and category-specific face inversion effect, but since the focus of our analysis was the impact of small vs. large town experience on these components, we chose not to explore
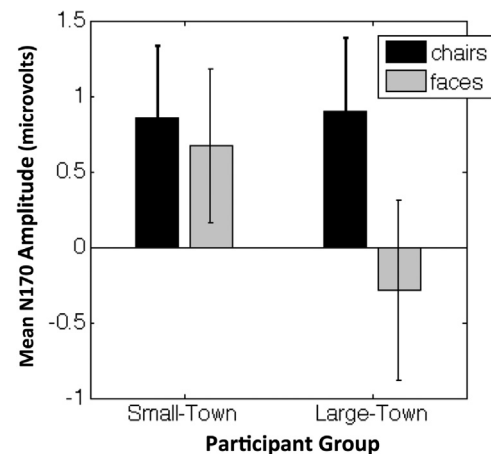

Fig. 3. The critical interaction between stimulus category and group in our N170 mean amplitude data, collapsed over hemisphere and orientation.

this interaction further. No other interactions or main effects reached significance.

3.6. N170 latency

Our analysis of the latency-to-peak values revealed only two significant main effects. First, we observed a significant effect of stimulus category ($F(1,32)=117.2$, $p < 0.001$) such that peak latencies to chairs ($M=184$ ms, s.e.m.$=1.8$) were slower than peak latencies to faces ($M=173$ ms, s.e.m$=1.6$). We also observed a main effect of stimulus orientation ($F(1,32)=24.9$, $p < 0.001$) such that peak latencies to inverted stimuli ($M=182$ ms, s.e.m.$=1.6$) were slower than those to upright stimuli ($M=176$ ms, s.e.m.$=1.9$ ms). Both of these effects are consistent with known influences of category membership and stimulus inversion on the N170 (Rossion et al., 2000). We observed no other significant main effects or interactions.

3.7. Brain/behavior correlations

We conclude by examining the extent to which behavioral

responses measured in the CFMT are correlated with the ERP responses we have measured electrophysiologically. To simplify our analysis, we chose to examine only correlations between memory performance (percent correct) and the mean amplitude of the N170 in the right hemisphere. While comparisons between memory performance and latency-to-peak values could potentially be of interest, focusing on the amplitude effects seemed warranted because this is where we observed the critical interaction between stimulus category and group and limiting our analysis to the right hemisphere also seemed prudent given the known lateralization of the face-sensitive N170. We carried out separate correlations in each participant group comparing memory performance to upright and inverted faces and chairs. We predicted that better face memory would be associated with either more positive amplitudes to upright faces or more negative amplitudes to inverted faces, consistent with enhanced face-specific neural processing in individuals with good face recognition performance.

We found exactly one correlation (out of 8) that reached significance, specifically the correlation between face memory performance and the mean amplitude of the N170 elicited by inverted faces in our small-town participants ($R = -.44$, $p = 0.034$, one-tailed test). This single result, however, does not stand up to correction for multiple comparisons, meaning that at best it is only suggestive of a possible relationship between behavioral performance and the response properties of the N170. Given the present data, we cannot draw strong conclusions about how brain/behavior correlations may differ as a function of visual experience/visual ecology.

4. Discussion

Our results demonstrate that the overall amount of face experience one has over a lifetime can impact face recognition in adulthood. Critically (and in contrast to prior results) the individuals that comprised our sample of participants from low-population hometowns had no visual impairments, no neurological impairments, and were exposed to a fairly normal visual environment. Aside from the comparatively small number of faces available to them in their community, their visual experience of the world was typical. Nonetheless, these individuals differed from our observers who lived in larger communities both in terms of their face recognition abilities and their neural responses to faces. Memory was poorer in the small-town group and we observed a main effect of group on P100 amplitudes and a significant interaction between stimulus category and group that affected N170 amplitudes. Our results demonstrate that it is not just true deprivation that can have lasting impacts on face recognition-impoverished experience considered in the context of an otherwise healthy visual system can also have a measurable effect on behavior and neural processing. Similarly, these results suggest that the statistical biases all observers are subject to with regard to face categories defined by race, age, etc. are essentially special cases of a more general phenomenon: The density and statistical properties of the "face space" maintained by observers determines what recognition tasks observers are capable of.

One intriguing feature of our data is the manner in which more limited experience with faces impacts face processing at the N170. We had included upright and inverted stimuli in our ERP paradigm since one of our initial hypotheses was that limited face exposure might lead to face processing that was less "expert-like." That is, to the extent that indices of face-specific processing like the inversion effect (Yin, 1969), the composite face effect (Young et al., 1987), or the part-whole effect (Tanaka and Farah, 1993) depend on expertise accumulated over developmental time, perhaps our

individuals from small towns might exhibit such effects to a smaller degree. Face expertise (operationalized via the other-race effect) does appear to affect the face inversion effect both behaviorally (Balas and Nelson, 2010) and electrophysiologically (Carahel et al., 2011), so we anticipated that we might measure a smaller face inversion effect at the N170 in small-town participants. Instead, the critical interaction we observed was not between group and orientation, but between group and stimulus category. This is somewhat surprising, since face/object distinctions are rarely considered a hallmark of face expertise (though see McCleery et al., 2009, for evidence that these distinctions are reduced in children diagnosed with Autism Spectrum Disorder), while the inversion effect seems to depend critically on visual expertise, even when we consider non-face objects of expertise (Campbell and Tanaka, 2014). Measuring behavioral indices of face expertise alongside basic face recognition and memory abilities would be an important means of determining what processes appear to be impacted most by globally-reduced exposure to faces. In particular, holistic face processing has been shown to predict face recognition abilities (Richler et al., 2011), meaning that our small-town participants' poor performance in the CMFT may signal reduced holistic processing. Presently, however our current data suggests that face-specific effects like the FIE (and possibly others) may be typical in adults who grew up in depopulated areas, but that category distinctions at the neural level may be fuzzier or simply more distributed. One potentially useful way to address this issue would be to use single-trial classification (Moulson et al., 2011) as a means of evaluating how much information is available in the entire ERP signal for distinguishing between faces and objects. Even though the N170 may not be as strongly category-specific in our small-town participants, it may yet be the case that face/object distinctions can be made on the basis of a distributed response spanning multiple loci in a distributed face network (Haxby et al., 2001). Related to the issue of measuring face-sensitive responses over multiple ERP components, we note that the effects observed at the N170 cannot be easily attributed to the earlier P100 since we observe a different profile of responses at this component. Specifically, the interaction between category and group is not evident at the P100, and we did not observe a main effect of group on the N170 amplitude. We thus suggest that this aspect of category-selectivity appears to be at least somewhat localized in time rather than reflected over multiple components. An intriguing target for further study of this issue with this population would be the N250 component, which appears to be sensitive to subordinate-level training (Scott et al., 2006), as evidenced by measurable differences between own- and other-group face responses in prior studies (Balas and Nelson, 2010; Wiese, 2012). Unfortunately, our participants did not reliably exhibit clear N250 components, precluding a useful analysis of this component in the current study.

Another interesting aspect of our results concerns the heterogeneity of our participant sample, especially with regard to small-town participants. Ideally, one might like to identify participants who have had very limited exposure to faces and measure face-specific and face-sensitive processes before they are exposed to a wider sample of faces (as all of our undergraduate students are as part of the NDSU community). Nonetheless, even though we recruited small-town participants who had been enrolled at NDSU for over a year (and thus exposed to a large community of faces), we were still able to observe differences between this sample and our equally heterogeneous sample of participants from larger towns. Participants in both of these groups also likely have observed faces on television and other media, traveled to other, larger communities on occasion, and had other instances of punctate exposure to a large set of faces. The fact that we observed differences between these two samples suggests that the difference in

community size has an impact on face processing above and beyond the mitigating influence of face exposure via other channels that do not afford either prolonged or repeated exposure to faces within a social context. An important caveat, however, is that we did not measure behavioral performance using a non-face category, leaving open the possibility that some aspects of high-level vision considered very broadly may differ in these groups. The main effect of participant group on the P100 may, for example, reflect some such difference between our small-town and large-town participants. The nature of the interaction we observed on N170 responses suggests to us that there is likely some face-specific impact on performance underlying our results, but we acknowledge that a broader survey of visual abilities in these two groups would be highly useful.

One question raised by our results, based to some extent on the sample's heterogeneity, is whether or not late exposure to a large sample of faces in adulthood can ameliorate the effects of early impoverished experience. Were this the case, individuals from small towns who had spent sufficient time in a larger community might ultimately be indistinguishable from other observers. Presently, we can only say that we were able to observe differences in behavior and the N170 response despite the fact that some of our participants had been members of the NDSU community for more than a year. Whether or not we should expect this to be sufficient time for behavioral or neural changes to manifest themselves is not clear. The effects of biased exposure in adulthood (the other-race effect, e.g.) do appear to be malleable at least to a limited extent (Goldstein and Chance 1985; Lebrecht et al., 2009), suggesting that perhaps either continued immersion in a face-rich environment, explicit training (Degutis et al., 2011) or incentivizing face recognition in some manner might lead to behavioral and/or neural changes in behavior. However, while the other-race effect is actually reversible in childhood (Sangrigoli et al., 2005), there is as yet little evidence to suggest that true reversibility is achievable in adulthood. The other-age effect does appear to depend on both early and late exposure to face belonging to distinct age groups (Cassia et al., 2009), but to our knowledge it remains an open question whether early biased experience can be compensated for late in life. As a result, we can at present only speculate whether or not late exposure to a wider set of faces can fully compensate for early exposure to a more limited face environment. A longitudinal study of incoming students from very depopulated areas would be the most straightforward way to address this question.

We close by comparing our results to two scenarios from the larger literature describing various kinds of deprivation/impoverished experience that share some qualities with our study of individuals from small towns. First, we consider the results of recent studies describing behavioral and neural responses to face stimuli in children who received impoverished face experience due to their placement in orphanages in Romania. Briefly, these children's experience with faces (among other aspects of their life, visual and otherwise) was very limited as a result of the conditions they were raised in, and in childhood they exhibit globally reduced electrophysiological responses to face stimuli (Moulson et al., 2009a). However, their differential responses to faces that differed by emotion (Moulson et al., 2009b) and by familiarity (personally familiar faces compared to strangers) were not different from observers with richer experience. Obviously, there are crucial differences between these children and our small-town participants, but nonetheless the fact that these children exhibited neural sensitivity to different kinds of faces leads to two important questions: would our participants also show typical differential responses to faces as a function of emotion or familiarity? Also, would this sample of children exhibit decreased selectivity for faces vs. objects? Both of these groups raise important questions

about how face-sensitive and face-specific processes respond to visual experience.

Finally, our results are also interesting to consider in relation to prior reports of differential visual processing of shape in rural populations. Like our participants, the observers in these studies lived in depopulated areas that differed not only in terms of the "face density" we have considered here, but also in terms of the overall visual environment. Specifically, the groups we consider here were selected in large part because their visual environment did not conform to the "Carpentered World" (Switkes et al., 1978) of a typical urban environment. Urban scenes tend to have more vertical orientation energy (Torralba and Oliva, 2003) than rural scenes and also may have fewer cardinal orientations. One hypothesis then is that observers living in such environments may have different shape processing due to the more even distribution of orientations in their natural surroundings. Indeed, some reports conclude that the magnitude of the Muller-Lyer illusion is reduced in rural observers (Segall et al., 1966), suggesting that scene statistics may modulate shape perception at a relatively low level. Similarly, members of the Himba, an African community studied by a number of researchers due to the profound differences between their visual ecology and that of urban observers, exhibit differential processing of some visual illusions (de Fockert et al., 2007) and classify simple shapes differently (Roberson et al., 2002). In both cases, it seems that reduced exposure to a particular set of visual features (orientations and classes of shapes) may lead to meaningful differences in visual perception and recognition. However, in both cases there are also aspects of visual processing that are not different – the Himba appear to use non-accidental properties of shape the same way other observers do (Biederman et al., 2009), for example. Also, neither class of rural observers (thus far) provides us with results that are analogous to the reduced category-specificity we observed in our ERP data. Thus, considered in the context of prior work examining these experiential forms of visual deprivation, the current study is an important contribution to an intriguing literature demonstrating how broad differences in visual ecology can influence visual processing.

In sum, we have found that reduced exposure to faces in early life reduces face recognition abilities and neural face-specificity at the N170 component. Understanding the time-scale of these effects both in terms of their onset (when do observers with different visual ecology start to exhibit these differences?) and their potential amelioration (how much experience is sufficient to erase these effects?) may reveal important properties of how visual learning unfolds across the lifespan.

Acknowledgements

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