Similar exemplar pooling processes underlie the learning of facial identity and handwriting style: Evidence from typical observers and individuals with Autism

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Highlights

- The learning of facial identity and handwriting style from exemplars was compared
- Recognition of learned facial identities and handwriting styles correlates closely
- Observers with ASD are poor at learning facial identities and handwriting styles
- The ability to pool multiple exemplars of a common source may be impaired in ASD
Abstract

Considerable research has addressed whether the cognitive and neural representations recruited by faces are similar to those engaged by other types of visual stimuli. For example, research has examined the extent to which objects of expertise recruit holistic representation and engage the fusiform face area. Little is known, however, about the domain-specificity of the exemplar pooling processes thought to underlie the acquisition of familiarity with particular facial identities. In the present study we sought to compare observers’ ability to learn facial identities and handwriting styles from exposure to multiple exemplars. Crucially, while handwritten words and faces differ considerably in their topographic form, both learning tasks share a common exemplar pooling component. In our first experiment, we find that typical observers’ ability to learn facial identities and handwriting styles from exposure to multiple exemplars correlates closely. In our second experiment, we show that observers with autism spectrum disorder (ASD) are impaired at both learning tasks. Our findings suggest that similar exemplar pooling processes are recruited when learning facial identities and handwriting styles. Models of exemplar pooling originally developed to explain face learning, may therefore offer valuable insights into exemplar pooling across a range of domains, extending beyond faces. Aberrant exemplar pooling, possibly resulting from structural differences in the inferior longitudinal fasciculus, may underlie difficulties recognising familiar faces often experienced by individuals with ASD, and leave observers overly reliant on local details present in particular exemplars.

Key words:
Autism spectrum disorder; face learning; handwriting; exemplar variance; averaging
1. Introduction
Contrary to intuition, familiar and unfamiliar faces are thought to recruit different types of visual processing (Hancock, Bruce, & Burton, 2000; Jenkins & Burton, 2011; Megreya & Burton, 2006). As faces become more familiar, observers develop the so-called internal feature advantage; they are better able to match targets using the eyes, nose, and mouth (Ellis, Shepherd, & Davies, 1979; Osborne & Stevenage, 2008; Young, Hay, McWeeny, Flude, & Ellis, 1985). In contrast, unfamiliar face matching is frequently based on external features, such as hairstyle and face shape. Relative to unfamiliar faces, familiar faces may also place lower demands on visual working memory (Jackson & Raymond, 2008) and are easier to detect under conditions of reduced attention (Jackson & Raymond, 2006). However, the most striking difference between familiar and unfamiliar face perception is arguably the ease with which we can recognise individuals across encounters. Matching strangers’ faces across different photographic images can be surprisingly difficult (Bruce et al., 1999; Megreya & Burton, 2008; White, Kemp, Jenkins, Matheson, & Burton, 2014). For example, when asked to sort photographs of individuals according to the identity of those depicted, observers frequently overestimate the number of individuals present (hereafter the overestimation effect; Jenkins, White, Van Monfort., & Burton, 2011; Murphy, Ipser, Gaigg, & Cook, 2015). In contrast, recognising familiar faces (e.g., celebrities, colleagues, friends, family) across multiple encounters appears effortless, despite substantial differences in pose, hairstyle and lighting.

Differences in the visual processing of familiar and unfamiliar faces have prompted considerable interest in face learning, the process by which unfamiliar faces become familiar. Previous evidence suggests that face learning is determined, at least in part, by the time observers spend viewing faces. Participants allowed to observe faces for 45 secs each outperform those who view the same faces for 15 secs on subsequent recognition tests (Memon, Hope, & Bull, 2003). Similarly, simple repetition of single facial images can improve subsequent recognition of actors in dynamic video stimuli (Roark, O'Toole, Abdi, & Barrett, 2006). Crucially, however, experiencing a given face in different poses, situations, and lighting conditions (so-called exemplar variation), also contributes to face learning, independently of viewing time. Observers exposed to many variable exemplars during training, outperform observers repeatedly presented with a limited number of exemplars on recognition tests, when viewing time is equated (Murphy et al., 2015). The
pooling of multiple exemplars appears to be integral to the acquisition of facial familiarity and underlies robust recognition performance.

Exemplar-database and averaging accounts have been proposed to explain how exemplar pooling; i.e., the process of identifying and combining exemplars of a common source, facilitates the acquisition of facial familiarity. According to exemplar-database models, familiar faces are recognised through comparison with previous encounters with that face (Longmore, Liu, & Young, 2008). Having encountered a given face on many occasions, in different poses, lighting and viewing conditions, observers are able to densely sample the potential instance space. Thereafter, the likelihood of a close match between a novel encounter and a previously stored instance is high, yielding superior recognition performance. Familiarization has also been modelled as an averaging process (Benson & Perrett, 1993; Burton & Jenkins, 2011; Jenkins & Burton, 2011). According to this view, multiple encounters with a face allow the visual system to form a robust average of that facial identity. Transient differences in lighting, shadow, hairstyle, expression are discounted, leaving a stable representation of permanent, reliable features.

The present study sought to compare the exemplar pooling processes that underlie the acquisition of facial familiarity with those recruited by non-face stimuli. The specificity of the perceptual processing recruited by faces has been long debated. Some authors have argued that cognitive and neural representations are face-specific; that they are qualitatively different to those recruited by objects (McKone, Kanwisher, & Duchaine, 2007; McKone & Robbins, 2011). For example, upright faces may recruit stronger holistic representation – whereby features are integrated into a unified whole – than objects (Robbins & McKone, 2007), and may preferentially engage regions of the fusiform gyrus (Kanwisher, 2000). Other authors have argued that faces and other ‘objects of expertise’ – categories of objects i) with which the observer has extensive visual experience, and ii) which comprise exemplars that share a common prototypical feature arrangement – are processed in similar regions (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999) and recruit similar types of representation (Diamond & Carey, 1986; Gauthier, Williams, Tarr, & Tanaka, 1998).
Despite the interest in the domain-specificity of face perception more broadly, there is currently a dearth of evidence addressing the nature of the exemplar pooling process recruited during face learning\(^1\). Authors have therefore avoided strong claims about domain-specificity (Burton & Jenkins, 2011). In the present study, we compared the acquisition of familiarity for facial identities and handwriting styles, from exposure to multiple exemplars. Despite considerable differences in topographic form, neuroimaging suggests that both faces (Kanwisher, McDermott, & Chun, 1997) and handwritten words (Barton, Fox, Sekunova, & Iaria, 2010) engage bilateral portions of fusiform gyrus. Although reading is predominantly a left hemisphere process (e.g., Price, 2012), some prosopagnostic patients with right lateral fusiform damage also exhibit impaired perception of handwriting style (Barton, Sekunova et al., 2010; Hills, Pancaroglu, Duchaine, & Barton, 2015). Crucially, a similar variance structure is present within a set of facial photographs depicting the same individual, and a pool of hand-written examples of the same word produced by the same author. A given exemplar drawn from either of these sets contains a common source signal present across exemplars, and exemplar-specific variation; for example, associated with lighting conditions, viewpoint, hair-style (in the case of faces), or writing implement, pressure, speed of production, hand position (in the case of handwriting).

We describe two experiments that address the same question – whether similar exemplar pooling processes underlie the learning of facial identity and handwriting style – but do so using different complementary approaches. In our first experiment, we examine the covariation of individual differences in the typical population. In our second experiment, we use developmental neuropsychology to examine whether the learning of faces and handwriting styles dissociates in ASD.

2. Exemplar pooling in typical observers
The aim of our first experiment was to compare typical observers’ ability to learn facial identities and handwriting styles from exposure to multiple exemplars. The covariation of individual differences has previously been used to examine whether two tasks recruit common social perception processes (e.g., Wang, Li, Fang, Tian, & Liu, 2012; Yovel & Kanwisher, 2008; Yovel, Wilmer, & Duchaine, 2014). Should the learning of facial identity and handwriting style recruit common exemplar pooling processes, we reasoned that typical
observers’ recognition of familiarized identities and styles should correlate, despite the gross differences in their form.

2.1 Methods

Participants
Forty-eight healthy adults ($M_{\text{age}} = 24.7$ years; $SD_{\text{age}} = 6.8$ years; 11 males) participated in the first experiment in return for a small honorarium. All participants had normal or corrected-to-normal vision, gave informed consent, and were fully debriefed upon task completion. Ethical clearance was granted by the local ethics committee, and the study was conducted in accordance with the ethical standards laid down in the 6th (2008) Declaration of Helsinki.

Training procedure
The facial stimuli employed during training were taken from the set constructed by Murphy and colleagues (2015). This set of 768 photographic images comprises 96 images of eight to-be-learned identities. The images sample a broad range of poses, expressions, hairstyles, lighting conditions, and camera parameters (Figure 1a). In each image, the to-be-learned identity is the only face visible and appears central and prominent. In all other respects, the raw photographic images are unaltered. None of the facial images depict individuals wearing glasses or sunglasses. A parallel set of handwriting stimuli were purposely created for the present study. Individuals were asked to write the same word (“backgrounds”), repeatedly, in different colours and textures, using different pens and pencils, employing different pressures, at different speeds (Figure 1b). We elected to use a single word to ensure that the stimuli had a prototypical arrangement. By selecting a word (“backgrounds”) comprising 11 unique characters, we hoped to encourage exemplar variation. The handwritten words were digitized, positioned centrally within the image, and saved as .bmp files. The final set of 768 images comprised 96 exemplars of eight handwriting styles. All training images were cropped to square aspect ratios subtending 3° vertically when viewed in the array at a distance of 60 cm.

Figure-1
The training procedure comprised 24 trials. Each training trial presented 48 images, simultaneously in a 6 × 8 array. Twelve training trials presented facial images and twelve presented images of handwriting. Half of the participants started with a faces trial and half started with a handwriting trial. Thereafter, alternating training trials presented exemplars of faces and handwriting. Training arrays were presented for 48 seconds, during which observers were free to inspect the images as they wished. Following array offset, a prompt appeared to judge the number of different individuals represented within the array. Unbeknown to observers, the 48 images were in fact always taken from only 8 individuals, training arrays comprising 6 exemplars from each source. The same 8 to-be-learned identities were shown on every face trial; the same 8 to-be-learned styles were shown on every handwriting trial. On each training trial, observers saw a novel set of 48 images, chosen at random by the program. Across the procedure, they were therefore exposed to 72 novel exemplars (12 trials × 6 exemplars) of each to-be-learned identity and style. The next trial commenced only once a response had been recorded. All experimental programs were written in MATLAB using Psychtoolbox (Brainard, 1997; Pelli, 1997), and presented on a Dell 17-inch Liquid-crystal display (LCD) monitor at 60-Hz refresh rate.

Test procedure
Immediately after training, participants completed a test procedure to assess their ability to recognise new examples of the learned facial identities and handwriting styles. Trials briefly (for 1,000 ms) presented a single face or handwriting stimulus centrally, followed by a prompt to judge whether the source of the exemplar was or was not encountered during the learning phase (‘old’ or ‘new’). The face and handwriting stimuli used at test were presented in greyscale. The test faces were shown in frontal view, with approximately neutral expressions, and were cropped to exclude external features. Half of the stimuli presented during the test depicted learned sources (the 8 identities and 8 styles encountered during training). Crucially, however, none of the exemplars were used during the training phase; recognition therefore required observers to abstract source identities from the exemplars encountered during training. The remaining stimuli were exemplars of 8 novel facial identities and 8 novel handwriting styles, not encountered previously. The allocation of learned and novel identities / styles was the same for all observers. When viewed at 60 cm, facial stimuli subtended 6° vertically and handwriting stimuli subtended 6° horizontally. In total, the test procedure comprised 320 trials: 5 exemplars of the 8 trained
sources and 5 exemplars of 8 novel sources, presented twice each, for both faces and handwriting.

2.2 Results and discussion
The source estimates from the training phase (see Figure 2) were analyzed using analysis of variance (ANOVA) with Trial (1:12) and Stimulus (faces, handwriting) as within-subjects factors. The analysis revealed a significant main effect of Stimulus \([F(1,47) = 7.184, p = .010, \eta^2_p = .133]\), indicating that source estimates for facial identities \((M = 12.23, SD = 3.94)\) tended to be higher than those for handwriting styles \((M = 10.93, SD = 3.49)\). Importantly, however, the source estimates for facial identities \([t(47) = 7.463, p < .001]\) and handwriting style \([t(47) = 5.808, p < .001]\) both exceeded eight, the true number of sources. The analysis also revealed a significant linear trend of Trial in the source estimates \([F(1,47) = 75.529, p < .001, \eta^2_p = .616]\) that varied as a function of stimulus \([F(1,47) = 4.590, p = .037, \eta^2_p = .089]\). Although the linear trend observed for handwriting estimates was highly significant \([F(1,47) = 40.260, p < .001, \eta^2_p = .461]\), a stronger trend was observed for facial identities \([F(1,47) = 63.152, p < .001, \eta^2_p = .573]\).

Figure-2

Analysis of the test performance (Figure 2) indicated that observers’ discrimination of the facial identities \((M = 76.3\%, SD = 10.91\%)\) and the handwriting styles \((M = 68.0\%, SD = 7.92\%)\) differed significantly \([t(47) = 6.242, p < .001]\). Strikingly, however, a highly significant correlation \([r = .564, p < .001]\) was observed between observers’ recognition of the learned handwriting styles and facial identities (Figure 3).

Figure-3

The results from our first experiment suggest a degree of overlap between the exemplar pooling processes underlying the acquisition of familiarity for facial identities and handwriting styles. Observers’ ability to learn facial identities and handwriting styles, from exposure to multiple exemplars, correlated closely. Moreover, observers over-estimated the number of sources represented within arrays of unfamiliar exemplars of facial identities and handwriting styles, particularly at the start of the procedure when the sources were
unfamiliar. This phenomenon was first reported with unfamiliar faces (Jenkins et al., 2011) and is known to decline with increasing facial familiarity (Murphy et al., 2015). The finding of parallel effects with handwriting styles suggests that exemplar pooling may operate in a similar way in these two domains.

3. Exemplar pooling in Autism Spectrum Disorder

Neuropsychological dissociation paradigms (e.g., Duchaine, Yovel, Butterworth, & Nakayama, 2006) have been used to provide complementary evidence that tasks recruit common processes, convergent with evidence derived from individual differences (e.g., Yovel & Kanwisher, 2008; Yovel et al., 2014). Should the learning of facial identities and handwriting styles recruit similar exemplar pooling processes, observers who exhibit impaired face learning may also experience difficulties learning handwriting styles. We sought to test this hypothesis in our second experiment by comparing the learning of facial identities and handwriting styles in adults with Autism Spectrum Disorder (ASD), a neurodevelopmental condition characterized by social-communicative atypicalities, and a restrictive and rigid repertoire of behaviors (American Psychiatric Association, 2013).

Many individuals with ASD have problems developing perceptual expertise for familiar faces (Boucher, Lewis, & Collis, 1998; Dalton et al., 2005; Dawson et al., 2002; Langdell, 1978; Wilson, Palermo, Brock, & Burton, 2010; Wilson, Pascalis, & Blades, 2007). For example, children with ASD were less accurate at recognising the faces of adult staff who worked in their school (Boucher et al., 1998; Wilson et al., 2007) and were poorer at recognising familiar peers from cues contained within the upper region of their faces (Langdell, 1978). Similarly, male observers with ASD were worse at recognising familiar faces than matched controls and exhibited less familiarity-induced modulation of activity in their fusiform face area (Dalton et al., 2005). Individuals with ASD are slower to form an implicit average following exposure to faces with different feature configurations (Gastgeb, Rump, Best, Minshew, & Strauss, 2009; Gastgeb, Wilkinson, Minshew, & Strauss, 2011). Moreover, some individuals with ASD do not exhibit the internal feature advantage for familiar faces, suggestive of aberrant face learning; having been trained to recognise a set of faces, observers with ASD were able to match familiarised faces typically when external cues were visible, but were impaired relative to controls when matching was based solely on internal facial features (Wilson et al., 2010).
3.1 Methods

Participants

Twenty adults with a clinical diagnosis of ASD ($M_{age} = 43.2$ years; $SD_{age} = 12.3$ years; 5 females) and twenty age and ability matched typically developing (TD) adults ($M_{age} = 44.0$; $SD_{age} = 13.93$ years; 6 females) participated in the experiment in return for a small honorarium. All participants had normal or corrected-to-normal vision, gave informed consent, and were fully debriefed upon task completion. Ethical clearance was granted by the local ethics committee, and the study was conducted in accordance with the ethical standards laid down in the 6th (2008) Declaration of Helsinki.

For all individuals in the ASD group, clinical records were available to confirm their diagnosis. All members of the ASD group were also assessed with the Autism Diagnostic Observation Schedule (ADOS; Lord et al., 2000) by individuals trained to research reliability standards. Seven members of the ASD group met the criteria for an ADOS classification of ‘Autism’ and eight met the criteria for ‘Autism Spectrum’ classification. The Autism-Spectrum Quotient Questionnaire (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) was administered to all participants and served to screen TD participants for behavioural difficulties that may be commensurate with an ASD diagnosis. Full scale IQ was assessed using the Wechsler Adult Intelligence Scale (WAIS; Wechsler, 1997). The ASD and TD groups did not differ significantly in their age [$t(38) = .193$, $p = .848$], full scale IQ [$t(38) = .457$, $p = .651$], or proportion of females [$\chi^2(1) = .125$, $p = .723$]. However, the ASD group scored significantly higher than the controls on the AQ [$t(38) = 8.212$, $p < .001$], as expected. Further sample details are provided in Table 1.

| Table-1 |

Procedure

Participants completed training and test procedures identical to those employed in the first experiment. Whether participants started the training procedure with a face or handwriting trial was fully counter-balanced within each group.

3.2 Results and discussion
The source estimates from the training phase (see Figure 4) were analyzed using ANOVA with Trial (1:12) and Stimulus (faces, handwriting) as within-subjects factors, and Group (ASD, control) as a between-subjects factor. The analysis revealed a marginally significant main effect of Stimulus \( [F(1,38) = 3.779, \ p = .059, \ \eta^2_{p} = .090] \), indicating that source estimates for facial identities \( (M = 13.95, \ SD = 7.63) \) were again higher than those for handwriting styles \( (M = 11.73, \ SD = 7.08) \). Importantly, the source estimates for facial identities \( [t(39) = 4.925, \ p < .001] \) and handwriting style \( [t(39) = 3.332, \ p = .002] \) exceeded the true number of sources, replicating the over-estimation effects seen in the first experiment. The analysis also revealed a significant linear trend of Trial in the source estimates \( [F(1,38) = 8.367, \ p = .006, \ \eta^2_{p} = .180] \), that varied as a function of Stimulus \( [F(1,38) = 5.154, \ p = .029, \ \eta^2_{p} = .119] \). Whereas facial identity estimates exhibited a linear decline across the training procedure \( [F(1,39) = 10.093, \ p = .003, \ \eta^2_{p} = .206] \), the linear trend for handwriting estimates did not reach significance \( [F(1,39) = 2.271, \ p = .140, \ \eta^2_{p} = .055] \).

The analysis revealed no main effect of Group \( [F(1,38) = 1.322, \ p = .257, \ \eta^2_{p} = .034] \), and neither the linear trend \( [F(1,38) = 1.091, \ p = .303, \ \eta^2_{p} = .028] \), nor the linear trend × Stimulus interaction \( [F(1,38) = .035, \ p = .853, \ \eta^2_{p} = .001] \) varied significantly as a function of Group. We note, however, that clear linear trends were observed in the controls’ source estimates for facial identity \( [F(1,19) = 6.791, \ p = .017, \ \eta^2_{p} = .263] \) and handwriting style \( [F(1,19) = 8.203, \ p = .010, \ \eta^2_{p} = .302] \), replicating the learning effects seen in the first experiment. In contrast, the ASDs’ source estimates for facial identity \( [F(1,19) = 3.298, \ p = .085, \ \eta^2_{p} = .148] \) and handwriting styles \( [F(1,19) = .091, \ p = .766, \ \eta^2_{p} = .005] \) did not exhibit significant linear decline.

Figure-4

Test performance (see Figure 4) was analyzed using ANOVA with Stimulus (faces, handwriting) as a within-subjects factor, and Group (ASD, control) as a between-subjects factor. The analysis revealed a highly significant main effect of Group \( [F(1,38) = 16.223, \ p < .001, \ \eta^2_{p} = .299] \). The main effect of Stimulus \( [F(1,38) = 3.605, \ p = .065, \ \eta^2_{p} = .087] \) and the Stimulus × Group interaction \( [F(1,38) = 3.853, \ p = .057, \ \eta^2_{p} = .092] \) also approached significance. Simple contrasts revealed that the control group \( (M = 74.7\%, \ SD = 10.9\%) \)
outperformed the ASD group ($M = 62.2\%, SD = 8.6\%$) on the facial identity discrimination task [$t(38) = 4.015, p < .001$]. Similar results were observed for handwriting discrimination [$t(38) = 2.594, p = .013$], where controls ($M = 68.7\%, SD = 7.5\%$) again outperformed the ASDs ($M = 62.3\%, SD = 8.2\%$). Having collapsed across the ASD and TD samples, a significant correlation [$r = .525, p = .001$] was observed between observers’ recognition of the learned handwriting styles and facial identities when (Figure 3). This correlation may partly reflect group difference between the ASD and the typical observers. Despite the loss of statistical power, however, evidence of correlation was also observed when analysis was restricted to the ASD group alone [$r = .508, p = .022$]. A similar trend was observed in the typical group [$r = .324, p = .164$], but this did not reach significance. Interestingly, whilst the controls found the faces task easier [$t(19) = 2.431, p = .025$], the ASD group exhibited very similar performance on the two tasks [$t(19) = .053, p = .958$].

4. Discussion

Considerable research has addressed whether the cognitive and neural representations recruited by faces are similar to those engaged by other types of visual stimulus (McKone et al., 2007; Richler, Wong, & Gauthier, 2011). For example, research has examined the extent to which objects of expertise recruit holistic representation (Diamond & Carey, 1986; Gauthier et al., 1998; Robbins & McKone, 2007) and engage the fusiform face area (Tarr & Gauthier, 2000). Less is known, however, about the domain-specificity of the exemplar pooling processes, thought to underlie the acquisition of facial familiarity. We addressed this question in two experiments comparing the acquisition of familiarity for facial identities and handwriting styles, following exposure to multiple exemplars. In our first experiment, we not only found that typical observers’ ability to learn handwriting styles and facial identities correlated closely, but also observed similar over-estimation effects during training; observers attributed the exemplars to more sources than were present, particularly at the start of the procedure when sources were unfamiliar. In our second experiment, we found that observers with ASD were impaired at learning both facial identities and handwriting styles from multiple exemplars, relative to matched typical controls.

The findings from both experiments suggest that similar exemplar pooling processes are recruited when learning facial identities and handwriting styles. While handwritten words
and faces differ considerably in their topographic form, both learning tasks share a common exemplar pooling component. Reliance on this common process explains why performance on these two very different tasks correlates strongly in the typical and ASD populations. Theoretical accounts of exemplar pooling, including database (Longmore et al., 2008) and averaging (Benson & Perrett, 1993; Burton & Jenkins, 2011; Jenkins & Burton, 2011) models, have been developed to explain how different facial exemplars are combined to form stable representations of familiar identities. In the absence of relevant evidence, however, authors have avoided strong claims about face-specificity (e.g., Burton & Jenkins, 2011). The present results suggest that these models may offer valuable insight into exemplar pooling across a range of domains, extending beyond face learning. Similarly, source overestimation (Jenkins et al., 2011), and its decline with familiarity (Murphy et al., 2015), do not appear to be hallmarks of face-learning per se, but rather examples of wider exemplar pooling phenomena.

Observers’ ability to recognise familiar faces is related to structural variability in the inferior longitudinal fasciculus (ILF), a white matter tract connecting the occipital and temporal lobes (Gomez et al., 2015; Thomas et al., 2009). Where observed, reduced density and coherence of the ILF may impair information exchange between the occipital and fusiform face regions, thought to play important roles in face encoding (Haxby, Hoffman, & Gobbini, 2000), and regions of the anterior temporal lobe, thought to serve as an interface between face perception and face memory (Collins & Olson, 2014). As a result, observers may take longer to accrue perceptual knowledge for familiar faces, and benefit less from associated top-down contributions to perception (Friston, 2005; Gregory, 1997; Kersten, Mamassian, & Yuille, 2004). Less is known about the neural substrates that mediate the recognition of familiar handwriting styles. However, evidence implicating bilateral regions of fusiform cortex (Barton, Fox, et al. 2010; Barton, Sekunova et al., 2010; Hills et al., 2015), suggests that structural connectivity in occipitotemporal cortex may influence perceptual learning in both domains.

Interestingly, the ILF is known to be atypical in ASD (Koldewyn et al., 2014). Reduced structural integrity of the ILF may therefore be a common source of the face and handwriting learning deficits seen in our second experiment. The finding that observers with ASD exhibit aberrant exemplar pooling may explain why they have problems
recognising familiar faces (Boucher et al., 1998; Dalton et al., 2005; Dawson et al., 2002; Langdell, 1978; Wilson et al., 2010; Wilson et al., 2007), and are disproportionately reliant on external features, such as hairstyle and face shape (Wilson et al., 2010). Aberrant exemplar pooling also accords with previous findings that members of this population have difficulties extracting prototypes (Gastgeb et al., 2009; Gastgeb et al., 2011; Klinger & Dawson, 2001; but see Froehlich et al., 2012; Molesworth, Bowler, & Hampton, 2005).

Some reports of atypical face processing in ASD may reflect delayed developmental trajectories. For example, child and adolescent samples appear to exhibit reduced adaptive coding of faces, inferred from weaker facial aftereffects (e.g., Pellicano, Jeffery, Burr, & Rhodes, 2007). However, by the time observers reach adulthood, individuals with ASD exhibit aftereffects comparable with the typical population (Cook, Brewer, Shah, & Bird, 2014; Walsh et al., 2015). Complex developmental differences are perhaps not surprising given that the neurocognitive mechanisms of face recognition may not reach maturity until observers are in their early thirties (Germaine, Duchaine, & Nakayama, 2011; see also Golarai et al., 2007; Scherf, Behrmann, Humphreys, & Luna, 2007). It is noteworthy that the group differences described here were obtained with adult samples. While complementary studies of face learning in child samples are needed, problems extracting prototypes from exemplar variation may be a relatively stable feature of the ASD phenotype, affecting observers throughout their lives.

The view that impaired exemplar pooling underlies learning deficits seen for handwriting styles and facial identities in ASD, accords with similar suggestions that domain-general deficits can affect the perception of faces in this population. For example, many individuals with ASD exhibit a local processing style, whereby local features are attended to in preference of global form (Dakin & Frith, 2005; Happe & Frith, 2006; Simmons et al., 2009). This processing style might detract from holistic face perception, and thereby detract from recognition (Behrmann, Thomas, & Humphreys, 2006). Similarly, wider deficits of predictive coding (Lawson, Rees, & Friston, 2014; Pellicano & Burr, 2012), visual working memory (Ewing, Pellicano, Rhodes, 2013), emotion processing (Bird & Cook, 2013; Gaigg, 2012), and motion processing (Atkinson, 2009; Pellicano, Gibson, Maybery, Durkin, & Badcock, 2005; Simmons et al., 2009), may all hinder the perception of faces in ASD.
Whereas typical observers showed a clear advantage for facial identities over handwriting styles in their test performance, observers with ASD exhibited virtually identical performance in the two conditions. While the learning of facial identities and handwriting styles may share a common exemplar pooling process, this trend raises the possibility that other aspects of face and handwriting perception may dissociate. One possibility is that face perception benefits from additional domain-specific processing. Such processing may be gated, and accessed only when basic face-like arrangements are detected in the environment (Johnson, 2005; Tsao & Livingstone, 2008). Because handwritten words do not contain a rudimentary ‘faciotopy’ (Henriksson, Mur, & Kriegeskorte, 2015), they may not gain access to this additional processing. Consistent with this suggestion, neuropsychological patients have been described who exhibit typical recognition of handwriting style, despite severe face recognition deficits (Barton, Sekunova et al., 2010). Should individuals with ASD find social stimuli less salient (e.g., Schultz, 2005; but see Shah, Gaule, Bird, & Cook, 2013) or be less motivated to attend to social stimuli (Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012), face-specific neurocognitive mechanisms may develop atypically.

In summary, our findings suggest that similar exemplar pooling processes are recruited when learning facial identities and handwriting styles. Models of exemplar pooling originally developed to explain face learning, may therefore offer valuable insights into exemplar pooling across a range of domains, extending beyond face learning. Aberrant exemplar pooling, possibly resulting from structural differences in the ILF, may underlie difficulties recognising familiar faces often experienced by individuals with ASD, and leave observers overly reliant on local details present in particular exemplars.
Footnotes

1. Previous research has addressed whether individuation expertise for newly acquired non-face object categories resembles face recognition expertise in typical observers (e.g., Gauthier et al., 1998) and in individuals with prosopagnosia (e.g., Duchaine, Dingle, Butterworth, & Nakayama, 2004; Rezlescu, Barton, Pitcher, & Duchaine, 2014). However, these studies address learning through the repetition of a single exemplar, and not exemplar pooling (i.e., the learning of identity through exposure to exemplar variation).

2. Face and handwriting training trials were interleaved to minimise carry-over effects. Crucially, i) the training task requires participants to identify the number of source identities represented in the array, and ii) participants are unaware there are always eight sources present. In a blocked procedure, knowledge about the number of sources present in the first condition, inferred through learning, may affect performance in the second condition. For example, participants may be inclined to over-estimate the number of source identities present in the first condition, but not in the second.
References


### Tables

*Table 1:* Mean age, gender, Autism-Spectrum Quotient (AQ) and IQ scores for the ASD group and the matched TD group. Total Autism Diagnostic Schedule (ADOS) score, and scores for the Communication and Reciprocal Social Interaction (RSI) subscales, for the ASD group.

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<td><strong>Gender</strong></td>
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<td>43.2 ($SD = 12.28$)</td>
<td>44 ($SD = 13.93$)</td>
<td>$p = .848$</td>
</tr>
<tr>
<td><strong>Mean Full Scale IQ</strong></td>
<td>108.7 ($SD = 15.20$)</td>
<td>110.8 ($SD = 13.86$)</td>
<td>$p = .651$</td>
</tr>
<tr>
<td><strong>Mean AQ</strong></td>
<td>32.05 ($SD = 7.16$)</td>
<td>15.15 ($SD = 5.78$)</td>
<td>$p &lt; .001$</td>
</tr>
<tr>
<td><strong>ADOS (Communication)</strong></td>
<td>2.60 (range: 0-5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ADOS (RSI)</strong></td>
<td>6.15 (range: 1-12)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ADOS Total</strong></td>
<td>8.85 (range: 5-17)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Note on interpretation.* AQ scores reflect the presence of self-assessed autistic traits. Individuals scoring 32 or higher have clinically significant levels of autistic traits. ADOS scores are derived from a diagnostic algorithm with a higher score representing a greater number of autistic symptoms. Individuals receive a classification of ‘autism’ if they receive a score of 3 or more on the communication subscale, a score of 6 or more on the social interaction subscale, providing the sum of their communication and social interaction scores is 10 or higher. Individuals are classified as ‘autism spectrum’ if they receive a communication score of at least 3, a social interaction score of at least 4, and a total score of at least 7. If at least one of the criteria for autism spectrum is not met, individuals are classified as ‘non-spectrum’.
Figures

Figure 1

Figure 1: Examples of the face and handwriting stimuli used during the training (left) and test (right) procedures.
Figure 2: The left panel shows the decline in source estimates (i.e., how many identities / styles observers believed to be present within each array) across the training procedure in Experiment 1. Unbeknown to participants there were always eight sources present in each training array. The right panel shows the test performance observed for facial identities and handwriting styles in Experiment 1.
Figure 3: Correlations observed between observers’ discrimination of the handwriting styles and facial identities in the first (left) and second (right) experiment.
Figure 4: The training and test performance observed for the facial identities (top panels) and handwriting styles (bottom panels) in the second experiment.