Recognising faces and reading words: investigations into visual perceptual expertise

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Contents

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Abbreviations

DRC: Dual Route Cascaded

FFA: Fusiform face area

FRU: Face recognition unit

PIN: Person identity node

VWFA: Visual word form area

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This thesis is dedicated to my partner Nick Murphy.

Declaration

This thesis is submitted to the University of Warwick in support of my application for the degree of Doctor of Philosophy. It has been composed by myself and has not been submitted in any previous application for any degree.

The work presented (including data generated and data analysis) was carried out by the author except in the cases outlined below:

Study 1: Laura Björnström, an undergraduate placement student, collected data under the author's supervision. She provided input to the first draft with findings from an initial literature review and helpful discussion. Hashim Hanif provided helpful discussion on the first draft. Jason Barton contributed to the conception of the work and provided helpful supervision throughout.

Study 2: Elsa Ahlén, an undergraduate placement student, collected data under the author's supervision. She provided input to the first draft with findings from an initial literature review and helpful discussion. Hashim Hanif provided helpful discussion on the first draft. Cristina Rubino provided technical eye tracking assistance. Noland Germain was contracted to code the training programme to the author's specifications. Jason Barton contributed to the conception of the work and provided helpful supervision throughout.

Study 3: Raika Pancaroglu performed patient neuroimaging assessments and neuropsychological testing (Tables 1-3, Figures 1-3), and assisted in initial data collection. Brad Duchaine assisted in patient recruitment and provided helpful discussion. Jason Barton designed the experimental tests used in previous publications. He wrote the narrative of the many-to-many hypothesis using initial key contents provided by the author and provided helpful supervision throughout.

Study 4: Kali Romano assisted with stimuli creation in Experiment 1. Jodie-Davies Thompson contributed to the conception of the work and supervised the statistical analysis. Jason Barton provided helpful supervision throughout.

PhD by Published Work declaration

The work was performed under the supervision of Professor Jason Barton, Director of the Human Vision and Eye Movement Laboratory, University of British Columbia, where the candidate held the position of Research Assistant.

I, Charlotte Hills, declare that where the work submitted includes work conducted in collaboration with others, I have provided a written statement on the extent of my individual contribution to the material and the conditions and circumstances under which the work was carried out. This statement has been signed by all collaborating parties.

Author signature: [redacted] 9 November 2019
Charlotte Hills

Individual contribution statement

Includes list of publications included in the thesis in Appendix A.

Study 1

Björnström, L. E., **Hills, C.**, Hanif, H., & Barton, J. J. S. (2014). Visual Word Expertise: A Study of Inversion and the Word-Length Effect, with Perceptual Transforms. Perception, 43(5), 438–450. https://doi.org/10.1068/p7698

The candidate contributed to the conception of the work and co-supervised the first author, a visiting undergraduate medical student, through the programming of the experiment, data collection and analysis, and drafting the paper.

Signed

Laura Björnström: [redacted] Date: 23 May 2019

Hashim Hanif: [redacted] Date: 10 May 2019

Jason Barton: [redacted] Date: 3 May 2019

Study 2

Ahlén, E., **Hills, C. S.**, Hanif, H. M., Rubino, C., & Barton, J. J. S. (2014). Learning to read upside-down: a study of perceptual expertise and its acquisition. Experimental Brain Research, 232(3), 1025–1036. https://doi.org/10.1007/s00221-013-3813-9

The candidate contributed to the conception of the work and co-supervised the first author, a visiting undergraduate medical student, through the programming of the experiment, data collection and analysis, and drafting the paper.

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Hashim Hanif: [redacted] Date: 10 May 2019

Cristina Rubino: [redacted] Date: 21 May 2019

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Study 3

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The candidate contributed to the conception of the work, collected and analysed experimental data, and participated in writing. The candidate is co-first author.

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Study 4

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The candidate co-designed and programmed the experiment, conducted data collection and analysis, assisted in statistical analysis and drafted the paper.

Signed

Kali Romano: [redacted] Date: 17 July 2019

Jodie Davies-Thompson: [redacted] Date: 9 May 2019

Jason Barton: [redacted] Date: 3 May 2019

Full bibliography of author

Articles

Ahlén, E., **Hills, C. S**., Hanif, H. M., Rubino, C., & Barton, J. J. S. (2014). Learning to read upside-down: A study of perceptual expertise and its acquisition. Experimental Brain Research, 232(3), 1025–1036. https://doi.org/10.1007/s00221-013-3813-9

Barton, J. J. S., Hanif, H. M., Eklinder Björnström, L., & **Hills, C**. (2014). The word-length effect in reading: A review. Cognitive Neuropsychology, 31(5–6), 378–412. https://doi.org/10.1080/02643294.2014.895314

Björnström, L. E., **Hills, C**., Hanif, H., & Barton, J. J. S. (2014). Visual Word Expertise: A Study of Inversion and the Word-Length Effect, with Perceptual Transforms. Perception, 43(5), 438–450. https://doi.org/10.1068/p7698

Hills, C., Romano, K., Davies-Thompson, J., & Barton, J. J. S. (2014). An adaptation study of internal and external features in facial representations. Vision Research, 100, 18–28. https://doi.org/10.1016/j.visres.2014.04.002

Hills, C. S., Pancaroglu, R., Duchaine, B., & Barton, J. J. S. (2015). Word and text processing in acquired prosopagnosia. Annals of Neurology, 78(2), 258–271. https://doi.org/10.1002/ana.24437

Liu, R. R., Pancaroglu, R., **Hills, C. S**., Duchaine, B., & Barton, J. J. S. (2016). Voice Recognition in Face-Blind Patients. Cerebral Cortex, 26(4), 1473–1487. https://doi.org/10.1093/cercor/bhu240

Pancaroglu, R., **Hills, C. S**., Sekunova, A., Viswanathan, J., Duchaine, B., & Barton, J. J. S. (2016). Seeing the eyes in acquired prosopagnosia. Cortex; a Journal Devoted to the Study of the Nervous System and Behavior, 81, 251–265. https://doi.org/10.1016/j.cortex.2016.04.024

Davies-Thompson, J., Fletcher, K., **Hills, C**., Pancaroglu, R., Corrow, S. L., & Barton, J. J. S. (2017). Perceptual Learning of Faces: A Rehabilitative Study of Acquired Prosopagnosia. Journal of Cognitive Neuroscience, 29(3), 573–591. https://doi.org/10.1162/jocn_a_01063

Corrow, S. L., Davies-Thompson, J., Fletcher, K., **Hills, C**., Corrow, J. C., & Barton, J. J. S. (2019). Training face perception in developmental prosopagnosia through perceptual learning. Neuropsychologia, 134, 107196. https://doi.org/10.1016/j.neuropsychologia.2019.107196

Conference proceedings

Hills, C., Romano, K., Davies-Thompson, J., & Barton, J. J. (2012). An adaptation study of internal and external features in face representations. Journal of Vision, 12(9), 622–622. https://doi.org/10.1167/12.9.62

Hills, C., Pancaroglu, R., Alonso-Prieto, E., Davies-Thompson, J., Oruç, I., Duchaine, B., & Barton, J. J. S. (2013). Functional neuroimaging and behavioural classification of a case of prosopagnosia with classic bilateral occipitotemporal lesions. Journal of Vision, 13(9), 995–995. https://doi.org/10.1167/13.9.995

Choi, D., Hanif, H., **Hills, C**., & Barton, J. J. S. (2013). The components and modality-specificity of word representations in the human visual system: An adaptation study. Journal of Vision, 13(9), 1304–1304. https://doi.org/10.1167/13.9.1304

Hills, C., Rubino, C., Sheldon, C., Pancaroglu, R., Davies-Thompson, J., & Barton, J. (2014). Processing of words and text in prosopagnosia. Journal of Vision, 14(10), 177–177. https://doi.org/10.1167/14.10.177

Rubino, C., Ahlen, E., **Hills, C. S**., Hanif, H. M., & Barton, J. J. S. (2014). Learning to read upside-down: A study of perceptual expertise and acquisition. Journal of Vision, 14(10), 176–176. https://doi.org/10.1167/14.10.176

Corrow, S., Davies-Thompson, J., Fletcher, K., Corrow, J., **Hills, C**., Duchaine, B., & Barton, J. (2017). Perceptual learning of faces: A rehabilitative study of developmental prosopagnosia. Journal of Vision, 17(10), 625–625. https://doi.org/10.1167/17.10.625

Davies-Thompson, J., Fletcher, K., **Hills, C**., Pancaroglu, R., Corrow, S., & Barton, J. (2017). Perceptual learning of faces: A rehabilitative study of acquired prosopagnosia. Journal of Vision, 17(10), 626–626. https://doi.org/10.1167/17.10.626

Abstract

Faces and words are ‘objects of expertise’. Both have many parts, yet are processed by expert mechanisms which emphasise the whole. The following behavioural studies investigated holistic integration in faces, and parallel-letter, lexical processing in words.

People normally only read upright words, so inverting words may reveal markers of perceptual expertise. **Study 1** explored the impact of word inversion on potential markers. The ‘word-length effect’ was found to be most suitable as it was only exacerbated by inversion in normal word formats.

Study 2 inverted paragraphs of text to reveal further markers of perceptual expertise. 15 hours of training in reading inverted novels partially reversed many of the deleterious effects of inversion. We saw a trend to the reduction of the word-length effect, which may reflect increased use of expert mechanisms.

Study 3 investigated whether expert word and expert face perception networks overlap. Subjects with prosopagnosia due to unilateral right lesions showed normal word-length effects, but struggled to differentiate visual text styles. Therefore, the expert face network in the right hemisphere may not overlap with the expert word network, but it may contribute to the perception of visual text style.

Study 4 asked whether internal features contribute more than external features to mental representations of faces. Isolated internal features produced stronger identity aftereffects, supporting this idea. However, when placed in a whole-face context, the contribution of the internal features was weakened. Holistic integration therefore reduces the saliency of the internal features. This occurs in both familiar and unfamiliar faces.

Overall we find that word perceptual expertise is well characterised by the word-length effect and may be acquired relatively quickly. However, it may not be served by the face recognition network in the right hemisphere. We also confirm that internal and external parts of faces, regardless of familiarity, are represented holistically.

Chapter one: Introduction

1.1 The relationship between faces and words

1.1.1 Objects of perceptual expertise

Despite being familiar with thousands of examples, most adults are able to identify faces and read words they know in an apparently effortless fashion. This ability to make fine ‘within-category’ discriminations between highly similar objects requires both high acuity vision and deep perceptual expertise. For this reason, visual words and faces are both ‘objects of expertise’.

Discussion of one particular characteristic of visual expertise dominates the literature: how objects are perceived as ‘wholes’. More specifically the ‘holistic’ processing of faces, and the ‘whole word’, parallel processing of letters. The four behavioural studies forming this thesis have made clear contributions to this debate.

1.1.2. Key differences and similarities between faces and words

Faces and written words intuitively have little in common. Words are two dimensional line drawn objects, while faces are three dimensional, textured objects (Goffaux et al., 2005; Royer et al., 2017). Reading is a recent cultural invention which requires practice to learn. Face recognition is an evolutionary older function and is naturally acquired (Dehaene & Cohen, 2007). Yet, despite these differences, they share striking similarities.

Faces change in many ways including viewpoint, illumination, expression and styling. Similarly, words appear in different fonts, cases and sizes. Mental representations of words and faces therefore need to be image-invariant to allow people to identify them (Barton et al., 2010; Dehaene & Cohen, 2011; Haxby et al., 2000).

Words and faces contain multiple parts, yet experts perceive them as ‘wholes’. Face parts are perceived together as a global visual unit (Tanaka & Gordon, 2011; Tanaka & Simonyi, 2016). Words are first processed not by their global shape but by their local letters (Grainger & Whitney, 2004; Lavidor & Ellis, 2001), which must all be identifiable (Pelli et al., 2003). Letters are then processed in parallel by a whole-word mechanism (Coltheart et al., 2001; McClelland & Rumelhart, 1981; Rumelhart & McClelland, 1982). So whilst faces offer a clear example of holistic processing, words must first be identified by their parts before whole-word effects contribute to their expert perception.

Many objects are normally only encountered upright. It is therefore unsurprising that recognition is poorer when the object is upside-down. However, faces and other objects in which one is an expert are recognised disproportionately worse when they are inverted (Ashworth et al., 2008; Chin et al., 2018; Diamond & Carey, 1986). Such an 'inversion effect', normally in respect to accuracy, is therefore a marker of expertise. Far fewer reports of word inversion effects exist (Kao et al., 2010; Martelli et al., 2005), and it is unclear which measures would best act as markers of expertise. As well as unfamiliar orientations, being unfamiliar with a particular face or word may impact its expert processing. New faces (Bruce & Young, 1986; Megreya & Burton, 2006) and words (Coltheart et al., 2001) may be processed in a less holistic or whole word manner.

Some parts of a face or a word are thought to be more important than others for identity perception. For example, the exact order of the inner letters may be changed while the word remains recognisable (Grainger & Whitney, 2004), whilst the first letter remains particularly crucial (Johnson & Eisler, 2012). In familiar face recognition, the internal features (eyes nose, mouth) are used more than the external features (hair, contour, forehead) (Butler et al., 2010; Ellis et al., 1979).

Faces and words both activate bilateral cortical networks. However, unlike most objects, they are served by specialised fusiform regions: the fusiform face area (FFA) in the right hemisphere (Kanwisher et al., 1997; Kanwisher & Barton, 2011) and the visual word form area (VWFA) in the left (Cohen et al., 2002; McCandliss et al., 2003; Puce et al., 1996). Injury to these areas or their connections may lead to the selective disruption of face perceptual expertise as in prosopagnosia (Barton, 2008), or word perceptual expertise as in pure alexia (Leff et al., 2006; Starrfelt & Shallice, 2014).

The similarities and differences between faces and written words make them attractive candidates to examine expert visual perception. They are brought together in the current literature, particularly in the search for shared (Behrmann & Plaut, 2013) or recycled neuronal resources (Dehaene & Cohen, 2007).

1.1.3 Meanings and measures of holistic processing

1.1.3.1 Holistic processing in faces

Holistic processing is generally defined as the tendency to process objects as wholes, rather than individual parts (J. Richler et al., 2012). Despite disagreements in the literature about the exact definition (Piepers & Robbins, 2012; J. Richler et al., 2012), it is broadly agreed that holistic face processing involves:

1. *Configural processing*, whereby the viewer is sensitive to the precise distances between facial features (known as second-order spatial information). This helps to distinguish between faces as all have two eyes, above a nose, above a mouth (Diamond & Carey, 1986; D. Maurer et al., 2002; Tanaka & Sengco, 1997).

2. Face parts undergo *perceptual integration* where they are perceived together as a 'gestalt' which is greater than the sum of its parts (Tanaka & Farah, 1993; Yovel et al., 2005). This 'fusing' also applies to face regions, such as the internal and external parts (Andrews et al., 2010). Due to this perceptual integration, selectively attending to just one region is difficult (J. J. Richler et al., 2008).

Different tasks operationalise these two aspects of holistic processing. Configural sensitivity is inferred by the inversion task (Yin, 1969). However, this has been criticised for not directly manipulating second-order configuration (Michel et al., 2006; Tanaka & Simonyi, 2016). The part-whole task probes perceptual integration, whereby facial features are better recognised when in a whole face (Tanaka & Farah, 1993; Tanaka & Sengco, 1997). The composite task also reveals perceptual integration as subjects fail to selectively attend to one part – they perceive the top half of a face to have changed when only the bottom half has (Young et al., 1987). Both the part-whole effect and the composite effect are disrupted by inversion. However, the effects from these three tasks are only weakly correlated and may not be driven by the same underlying mechanism (Rezlescu et al., 2017; J. Richler et al., 2012).

1.1.3.2 Holistic processing in words

Expert processing of familiar words is characterised by 'whole word'*, parallel-letter processing* (Coltheart et al., 2001). Letters in a familiar word are processed in parallel across the whole word (Adelman et al., 2010) to activate lexical representations (McClelland & Rumelhart, 1981; Rumelhart & McClelland, 1982). Parallel letter processing may be indicated by the absence of a 'word-length effect'.

This means that as the number of letters increases, the time taken to read the word aloud does not (Barton et al., 2014). A megastudy of lexical decision times (time taken to decide if a word is real or not) showed they become faster as words increase in length from 3 to 5 letters. It then stays equal for words of 5-8 letters, and only becomes slower as words increase from 8-13 letters (New et al., 2006). This highlights the whole word processing of words up to 8 letters. Longer words may only be processed slower as visual acuity starts to drop off (O'Regan & Jacobs, 1992) and so they need additional fixations (Nazir et al., 2004).

Some authors describe parallel letter processing in words as 'holistic' (e.g. Conway, Brady, & Misra, 2017; Koriat & Norman, 1985; A. C.-N. Wong et al., 2011), although it is most common to reserve this term for the two aspects of holistic processing described in faces. Nevertheless, the idea of some holistic perception in words analogous to those in faces has gained empirical support. A part-whole task has revealed a word superiority effect whereby letters are better recognised in the context of a real word (Reicher, 1969; Wheeler, 1970), although this effect is much weaker than in faces (Pelli et al., 2003). Composite effects have been shown in words (Wong et al., 2011, 2012) which appear to involve abstract lexical representations (Ventura et al., 2017). Before Study 1 below, few had investigated the inversion effect in words. Inversion seems to impact the part-whole advantage in both words and faces to a similar degree (Martelli et al., 2005), and makes same-different judgements in Chinese characters harder (Kao et al., 2010). However, it must be noted that whilst words may have some holistic effects analogous to those in faces, it cannot be inferred from this alone that their underlying mechanisms are similar.

Inversion is thought to impair the usage of the second-order relational information in faces (Diamond & Carey, 1986; D. Maurer et al., 2002; McKone & Yovel, 2009) (but see Civile et al., 2014; Murphy & Cook, 2017). However, in alphabetic languages, the precise distances between features or overall shape does not impact a word's identity (Allen et al., 1995; Besner, 1983). Identity is based on the categorical identification of the letters themselves and their first-order configuration (i.e. their order, e.g. POLO vs POOL), or perhaps the order of pairs of letters across the whole word (e.g. S before R in SEVRICE) (Grainger & Whitney, 2004; Schoonbaert & Grainger, 2004). At the time of Study 1 below, in stark contrast to faces, the literature on the point of how configural, second-order information relates to expert word recognition was sparse. It is perhaps more obvious that sensitivity to precise distances in overall shape of words, tilt and aspect ratio of letters is helpful in visual text style identification (Dyson & Stott, 2012; Wong et al., 2019).

In sum, holistic processing in faces is well established and in words it is less so. Indeed, whether the key characteristic of expert word processing, the parallel processing of letters, should be described as 'holistic' is debatable. Whilst important for our understanding of holistic processes in word perception, comparisons with analogous effects in faces must be made with caution. For example, it is not yet clear what exact role configural sensitivity plays in expert word recognition despite this being established as important in face processing.

1.1.4 Holistic processing as a characteristic of expertise

1.1.4.1 Holistic processing modulated by experience

'Holistic' processing is a proposed characteristic of expertise. One way this has been evaluated is with examinations of how word, face and object perception is modulated by experience and ability in neurotypical populations.

Holistic effects in face processing have been associated with superior face recognition (DeGutis et al., 2013; J. J. Richler et al., 2011; Wang et al., 2012), (but see Konar, Bennett, & Sekuler, 2010). Similarly, in words, a failure of selective attention to parts and sensitivity to configural information seem to become more pronounced with experience (Wong et al., 2011, 2019). Interestingly there may be interplay between the two object categories. As individuals learn to read, they become better at selectively attending to regions in a face. This suggests that literacy develops an analytic perceptual strategy which can also be used for faces (Ventura et al., 2013).

In regards to whole-word, parallel letter processing, developing readers process letters in a serial fashion which transitions to a parallel strategy over time (Aghababian & Nazir, 2000; Bijeljac-Babic et al., 2004). Concerted practice decreases the word-length effect until it eventually disappears, at least for words of up to 8 letters (Barton et al., 2014; New et al., 2006).

Objects in which one does not have expertise do not generally elicit holistic effects (Cassia et al., 2009; Robbins & McKone, 2007). For example, inversion effects for common objects which we normally encounter upright is around 0-8% whilst faces elicit effects of 15-25% (Robbins & McKone, 2007). Experts in other categories of objects may process their chosen objects holistically. This was first shown in dog show judges discriminating dogs (Diamond & Carey, 1986). Since then, similar inversion effects (Ashworth et al., 2008; Chin et al., 2018) and composite effects (Bukach et al., 2010; Gauthier et al., 1998; Wong, Palmeri, & Gauthier, 2009) have been found for objects of expertise, although they tend to be smaller and less consistent than those found with faces (DeGutis et al., 2012; Robbins & McKone, 2007). Such holistic processing of objects of expertise other than faces may be served by the FFA (Gauthier et al., 2000; Tarr & Gauthier, 2000; Wong, Palmeri, Rogers, et al., 2009). Although the impact of inversion on faces and objects of expertise has been well studied, in words there is a scarcity of data.

1.1.4.2 Impact of specific impairments on holistic processing

Considerable evidence suggests that holistic face processing is impaired in acquired (Barton, 2009; Farah, 1992; Ramon et al., 2010) and developmental prosopagnosia (Avidan et al., 2011; DeGutis et al., 2012). A laborious feature-based strategy is then used to identify faces (Busigny et al., 2010). Both acquired and developmental prosopagnosics report using aspects which require less holistic processing. These include distinctive facial features, as well as external features such as hair (Levine & Calvanio, 1989; Nunn et al., 2001) and face contour (Barton, 2008).

Those with pure alexia may struggle to perceive individual letters (Arguin & Bub, 1993; Behrmann et al., 1998; Starrfelt & Behrmann, 2011), especially when in the context of a word (Fiset et al., 2005). However, the condition is generally thought to represent a breakdown in ‘whole word’ processing, where each letter is no longer perceived or encoded in parallel (Leff & Starrfelt, 2014). This is well characterised by elevated word-length effects, which probably indicates a serial processing strategy in pure alexia (Barton et al., 2014; Rayner & Johnson, 2005) (but see Fiset et al., 2005). Most pure alexics also lack a word superiority effect (Behrmann et al., 1990; Habekost et al., 2014), which could reflect both the lack of perceptual integration and residual parallel processing (Habekost et al., 2014).

1.2 Neural mechanisms of face and word perception

1.2.1 Object recognition: the ventral visual stream

Face and word perception are the products of processing streams that start with low-level analysis of contrast in the striate cortex. Contour and increasingly complex shapes are then analysed in the extrastriate visual cortex and as processing continues further along the ventral stream in the inferior temporal cortex (Avidan et al., 2002; Baars & Gage, 2010). All object recognition begins in this way. However, the extent to which object categories, such as faces and words diverge, and use different neural resources is the topic of lively debate (Barton & Corrow, 2016). The many-to-many hypothesis and the neuronal recycling hypothesis attempt to tackle this issue.

In the occipitotemporal cortex, lateral regions respond to high-resolution foveal shapes, and with increasing image-invariance as one moves in an anterior direction (Dehaene et al., 2005; Dehaene & Cohen, 2007). The fusiform face area in the right fusiform gyrus makes use of these properties and is able to detect minute variations to discriminate and encode facial structure, particularly in relation to identity (Fox et al., 2011; Kanwisher et al., 1997; Kanwisher & Barton, 2011). In the left fusiform gyrus in a slightly more lateral position, the visual word form area is thought to extract pre-lexical information which interacts with abstract representations of letters and words (Cohen et al., 2002; Dehaene et al., 2005; McCandliss et al., 2003; Puce et al., 1996).

The perception of words and faces, up to the level of the occipitotemporal cortex, can be considered a mid-level visual function. The streams then continue on to anterior temporal areas and beyond where semantic, and, in the case of words, phonological information is accessed (Bouhali et al., 2014; Haxby et al., 2000; McCandliss et al., 2003).

1.2.2 The development of face and word expertise

In a relatively recent twist in our understanding of face and word perceptual expertise, the acquisition of literacy and the degree of face processing lateralisation may be causally related.

Due to competition for neural resources for words during reading acquisition (Dehaene & Cohen, 2011), responses to faces are 'pruned' in the left fusiform (Cantlon et al., 2011), having initially been processed more bilaterally (Centanni et al., 2018; Dehaene et al., 2010). As reading proficiency increases, stronger left hemisphere lateralisation of word processing emerges (U. Maurer et al., 2008; McCandliss et al., 2003).

The premise of the neuronal recycling hypothesis (Dehaene & Cohen, 2007) is that this occurs because some, but not all, neurons which are initially face selective are ‘recycled’ to respond to words (Dehaene & Cohen, 2011). This occurs mainly in the left hemisphere as it suits word recognition to keep connections short to language areas (Dehaene et al., 2010).

The neuronal recycling hypothesis suggests a tight developmental link between the neural resources that serve word and face recognition. This link from a functional perspective forms the basis of the many-to-many hypothesis (Behrmann & Plaut, 2013; Plaut & Behrmann, 2011).

1.2.3 Neural networks for face and word perception

The many-to-many hypothesis challenges the textbook knowledge that words and faces rely on highly lateralised, independent mechanisms (Robotham & Starrfelt, 2017). It instead posits that the perception of words and faces, and indeed objects in general, is served by distributed bilateral cortical networks. It reasserts that one object category, such as faces, is processed by *many* areas (Haxby et al., 2000). However, the claim that one region, such as the FFA or VWFA also participates in the graded processing of *many* object categories is more contentious.

The hypothesis was motivated by neuroimaging findings that lateralisation does not appear to be complete for either faces or words (but especially for faces) with minor activations in the non-dominant hemisphere (Cohen et al., 2002; Dien, 2009; Kanwisher et al., 1997). In addition, there are bilateral areas of overlap (Nestor et al., 2013), mostly on the left (Harris et al., 2016), which respond to both object categories.

The many-to-many hypothesis made the key and controversial prediction that with suitably sensitive tests, word recognition problems should be found in patients with prosopagnosia, and face recognition issues in patients with pure alexia (Behrmann & Plaut, 2013).

1.3 Processing objects as parts and wholes

1.3.1 The holistic-analytic continuum

The classic view is that words sit at one extreme of a continuum (Figure 1) as objects which are identified by multiple parts. Faces sit at the other extreme, identified as complex wholes. Common objects fall somewhere in the middle (Farah, 1992). The drivers of this continuum are two distinct capacities: holistic processing served by the right hemisphere and analytic processing by the left. This continuum is based on an early systematic review (Farah, 1991) which found a double dissociation between pure alexia and prosopagnosia, no clear cases of pure visual (object) agnosia without face or word deficits, and no clear cases of co-occurring face and word deficits without visual agnosia. Such a pattern suggests that both words and faces are two special cases of object recognition supported by distinct capacities. If the continuum holds, and words are purely processed by their 'parts' by the left hemisphere, those with prosopagnosia should show no word perception deficits.

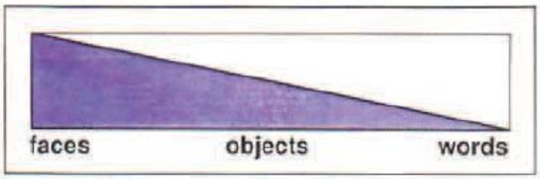

Figure 1. *The holistic-analytic continuum. The shaded area represents the importance of holistic processing. The unshaded area represents the importance of analytic processing. From Farah (1992).*

However, the extreme position of words on the continuum as completely part-based objects is already challenged by the existence of the word composite and word superiority effects (Reicher, 1969; Ventura et al., 2019; Wheeler, 1970; Wong et al., 2011). Analogously, the left hemisphere appears to play a key role in the part-based processing of faces (Hillger & Koenig, 1991; Rossion et al., 2000). This challenges the positioning of faces on the continuum as objects only processed as wholes and by the right hemisphere.

1.3.2 Cognitive models and the impact of familiarity

Even in experts, the familiarity of a word or a face may modulate the nature of its processing, with more whole word or holistic face processing for familiar exemplars.

1.3.2.1 Face recognition

The Bruce and Young (1986) model of face recognition (Figure 2) was the first to propose that a familiar face can access face recognition units (FRUs) which store image-invariant representations of that face. FRUs, later proposed to be in the fusiform gyrus in a neural model (Haxby et al., 2000), activate person identity nodes (PINs), which access semantic information and a sense of familiarity. Whilst Bruce and Young (1986) and a subsequent interactive activation model (Burton et al., 1990) are primarily models of familiar face recognition, they suggest that unfamiliar faces do not have access to FRUs and PINs and so must be distinguished in an image-dependent manner, with the help of directed visual processes to focus on a particular feature. When study and test image are not identical, performance in matching unfamiliar faces is therefore much worse than with familiar faces (Bruce, 1982; Bruce et al., 1999; Jenkins et al., 2011; Longmore et al., 2008).

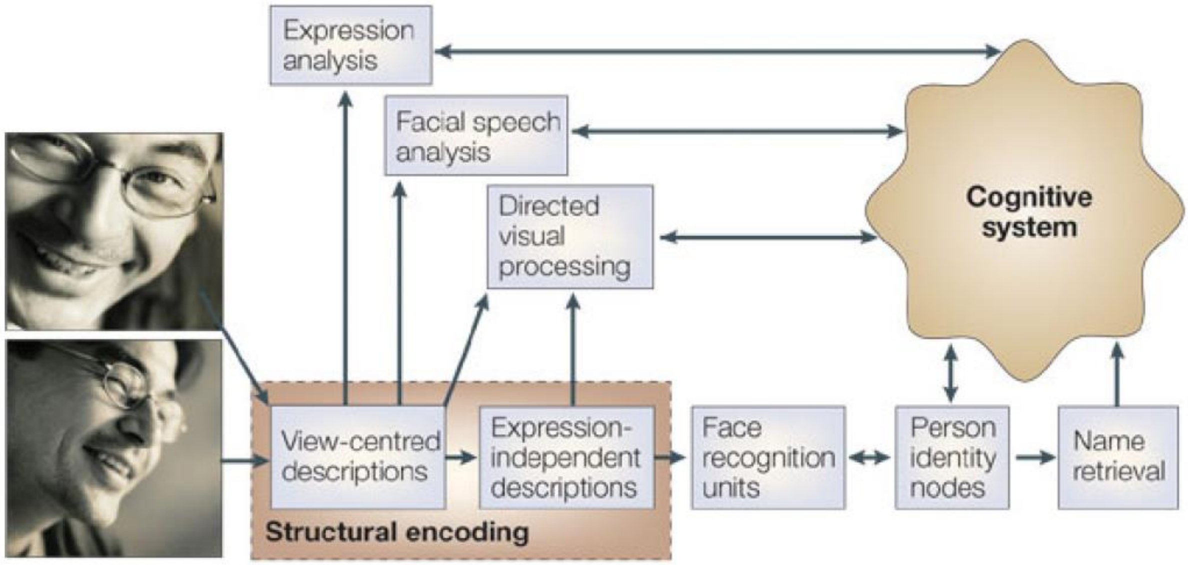

Figure 2. *The functional model of face recognition (Bruce & Young, 1986). Familiar face recognition proceeds via FRUs, whilst unfamiliar face discrimination proceeds via the directed visual processing route. From Calder & Young (2005).*

However, it is debated whether unfamiliar faces are indeed recognised by their parts, as the model suggests. In support, one influential study (Megreya & Burton, 2006) found a high correlation between familiar and unfamiliar face identification performance, but only when the familiar faces were inverted. The authors suggest that upright familiar faces have access to a processing mechanism (assumed to be holistic), which unfamiliar and inverted faces do not. In addition, familiar faces are identified more by their internal features (Ellis et al., 1979), which contain the critical spacing required for configural processing. However, inversion effects (Hancock et al., 2000) and composite effects (Hole, 1994; Young et al., 1987), are shown with unfamiliar faces indicating that they are processed holistically too, albeit less efficiently.

1.3.2.2 Word recognition

Turning to words, the Dual Route Cascaded (DRC) model of reading (Coltheart et al., 2001) (Figure 3) proposes two main routes from text to sound. Familiar words are represented in the orthographic lexicon and may be primarily processed as 'wholes' by the expert, lexical route which employs top-down activation (as well as bottom-up) as specified in the Interactive Activation model (McClelland & Rumelhart, 1981). Pseudowords and novel words without an entry in the orthographic lexicon must be read as 'parts' by a sublexical route which converts graphemes to phonemes, and relies on serial letter processing. Parallel processing via the lexical route results in non-existent, or minimal word-length effects, whilst word-length effects of around 10–30 ms per letter are generated by the sublexical route (Cosky, 1976; Jared & Seidenberg, 1990; Weekes, 1997). The VWFA in the ventral visual stream underlies the parallel processing of letters, with additional selective attentional support required from the dorsal stream for sequential letter processing in sublexical route (Vinckier et al., 2006).

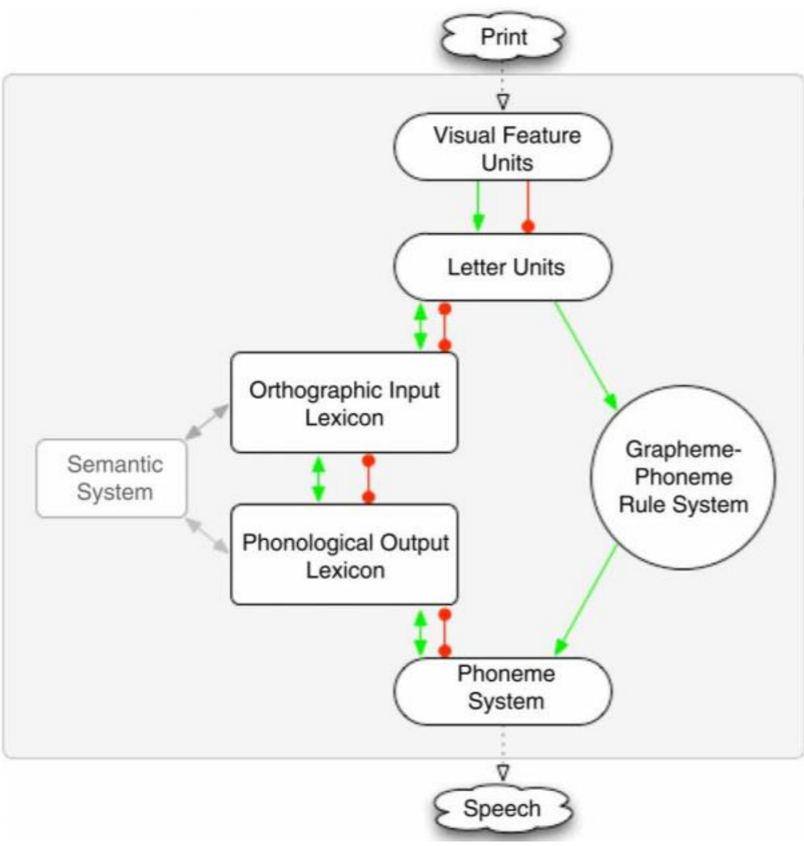

Figure 3. *The Dual Route Cascaded model of reading (Coltheart et al., 2001). Arrows are excitatory connections, circular ends are inhibitory. The lexical route receives top-down feedback, whilst the sublexical route does not. The semantic*

route is not yet computationally simulated, so is greyed out. From Coltheart, Saunders, & Tree (2010).

1.4 Key questions of the thesis

Four behavioural studies examine the expert processing of words in terms of their parallel letter processing, and faces in terms of their holistic perceptual integration.

In **Study 1** we asked “What is the impact of inversion on the expert processing of words?” We used contrasts in reading performance between upright and inverted words to search for markers of expertise, of which the word-length effect was an obvious candidate.

In **Study 2** we explored “What are the markers of perceptual expertise in reading and how are they impacted by training?” Again, we used inversion to reveal further behavioural and oculomotor markers of expertise in paragraph reading. We then used these to examine the acquisition of perceptual expertise as subjects trained to read inverted novels.

Study 3 asked “Do words and faces share expert perceptual mechanisms?” To do so, we investigated whether those with acquired prosopagnosia also showed word perceptual deficits.

Finally, in **Study 4**, we asked “How do parts of a face contribute to its holistic representation?” We specifically explored the contribution of internal and external facial features to whole face representations and whether this is impacted by familiarity.

Chapter two: Study 1: What is the impact of inversion on the expert processing of words?

Title: Visual word expertise: A study of inversion and the word-length effect, with perceptual transforms

2.1 Background

As people normally only encounter words upright, the use of expert mechanisms should be somewhat disrupted by inversion. Contrasts between upright and inverted words can therefore derive markers of perceptual expertise in single word reading. The face inversion effect is well established and shows that holistic processing is disrupted (Rossion et al., 2000; Tanaka & Farah, 1993), but few studies have investigated word inversion (Kao et al., 2010; Martelli et al., 2005). However, one study of lexical decision in Hebrew suggested that letter-by-letter reading occurs with rotations of over 60° (Koriat & Norman, 1985) and that the use of expert 'whole word' processing may be disrupted by inversion.

The word-length effect may index if a word is processed in a whole object fashion. It is therefore an obvious candidate as a marker of perceptual expertise. If it is suitable, the impact of inversion should be specific to normally configured text in which subjects are expert.

We aimed to determine whether inversion only disrupted the word-length effect of normally configured words. In doing so, we asked whether the word-length effect is a suitable index of reading expertise. We also asked if transformed words are read letter-by-letter, and so included comparisons of transforms where letters are preserved with those where they are distorted.

2.2 Methods

We measured response times of 12 healthy subjects reading 3- to 9- letter words matched for frequency. We used these to calculate word-length effects. Words were presented normally or in mirror reflected or backwards spelt transformations, and either upright or inverted as in Figure 4.

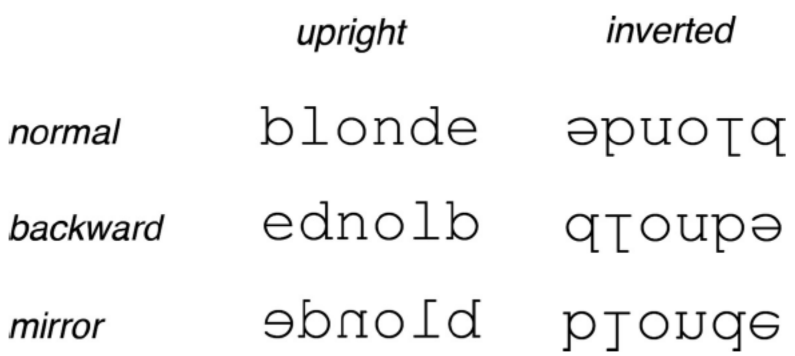

Figure 4. *The three different text transforms (normal, backwards spelt, and mirrored) in two different orientations (upright, inverted).*

2.3 Results

Normal text had smaller word-length effects than backward text, which had smaller word-length effects than mirrored text. Inversion only significantly increased the word-length effect of normal text. However, simple mean response times for normal and mirrored words were significantly increased when inverted, with a trend in this direction for backward spelt words.

2.4 Discussion

Study 1 set out to investigate the impact of inversion on expert word reading, and therefore reveal markers of perceptual expertise. We found that parallel letter processing in normal words was indeed impaired by inversion, as indicated by dramatically elevated word-length effects. This confirmed that the lexical mechanism facilitating parallel letter processing is specific to words in an upright orientation. This finding contributed to the literature by confirming that the word-length effect is a suitable marker of perceptual expertise as it is only impacted by inversion in normal words (in which we are expert). This was not the case for simple mean response time, indicating it is not the best marker of expertise.

We also suggested that transformed words are read letter-by-letter by using a second comparison. In a backwards spelt word, local letters are preserved and so are easier to read, although the global word form is destroyed. The reverse is true for mirrored words, where the letters are mirrored but the overall shape can be restored with just one mental rotation. As the word-length effect for backward words was smaller than for mirrored words, letter-by-letter reading appears to be used for these unfamiliar transforms.

Our work in Study 1 with English words complements similar findings in Hebrew (Koriat & Norman, 1985) which found that parallel letter processing is disrupted by inversion. Indeed, neuroimaging evidence suggests the expert ventral visual system is only tuned to normally formatted words, with the dorsal visual pathway supplementing letter-by-letter reading under perceptual difficulty (Cohen et al., 2008; Sussman et al., 2018). We also complement reports that tough perceptual conditions can induce word-length effects, including reduced contrast (Legge et al., 1997), mIxEd CaSe (Lavidor & Ellis, 2001) and peripheral presentation (Cohen et al., 2008), and high-pass filtering (Fiset et al., 2006).

In sum, we contributed the finding that the word-length is a suitable marker of expertise and that whole-word processing is specific to words in normal formats. Next, we searched for further markers of expertise in paragraph reading.

Chapter three: Study 2: What are the markers of perceptual expertise in reading and how are they impacted by training?

Title: Learning to read upside-down: a study of perceptual expertise and its acquisition

3.1 Background

Reading is an expert visual and oculomotor skill which takes years of practice to acquire. Expertise must be applied to foveal vision, and to further out in the so called 'perceptual span'. Here, useful information such as gross letter features may be extracted from characters in the span (Rayner, 1986; Rayner & McConkie, 1976).

Although perceptual expertise is important, reading is thought to be primarily a linguistic task (Bellocchi et al., 2013; Vellutino et al., 2004). Previous studies of reading acquisition in developing readers had confounded linguistic with perceptual expertise (e.g. Lefton, Nagle, Johnson, & Fisher, 1979; Rayner, 1986; Taylor, 1965). As children learn to read, not only do they perceive words more easily, but their language skills improve too. This had made it difficult to determine the impact of perceptual expertise alone on changes normally observed in improving readers.

Inversion essentially isolates the impact of perceptual expertise (i.e. the words are harder to read, while the linguistic content remains the same). Whilst it had been previously shown that inverted paragraphs take longer to read (Kolers, 1968), how eye movements are affected was unknown.

We aimed to isolate the behavioural and oculomotor markers of perceptual expertise in reading from linguistic expertise. Using these markers we aimed to examine the acquisition of perceptual expertise in reading. To achieve this, we trained subjects to read inverted text.

3.2 Methods

Seven subjects engaged in a ten-week program of 30 x 30-minute sessions of reading inverted novels.

Before and after training, we assessed subjects' reading of upright and inverted single words for response time and word-length effects, as well as their reading of paragraphs for time required, accuracy, and oculomotor parameters using eye tracking.

3.3 Results

Pre-training, we compared performance with upright text to that with inverted text to reveal markers of perceptual expertise. Upright single words were read faster and with smaller word-length effects. Paragraphs were read faster both silently and aloud when upright. Accuracies for both single words and paragraphs remained high even when inverted. Fixations were fewer and shorter with upright text. There were fewer regressive saccades with upright text although the amplitude did not change. There were also longer and fewer forward saccades in upright text.

To examine the impact of training on inverted reading, we compared performance with inverted text pre- and post-training. Additional illustrative analysis which indicated expertise gain is shown in brackets. After training, single words were read faster (37%) with a trend towards a reduction of the word-length effect (32%). Paragraphs were read faster both silently (18%) and aloud (77%) after training. Accuracies for both single words and paragraphs remained high. Fixations were fewer (53%) and with a trend to being shorter (32%) after training. There was also a trend towards fewer regressive (80%) and forward saccades (38%). However, contrary to our expectations, there was no change in forward saccade amplitude after training.

3.4 Discussion

3.4.1 The markers of perceptual expertise

The pre-training results indicate that behavioural markers of perceptual expertise in reading are smaller word-length effects, with faster speeds when reading paragraphs both silently and aloud. Oculomotor markers are fewer and shorter fixations, fewer regressive saccades, and longer and fewer forward saccades.

Our first main contribution to the literature was to isolate perceptual expertise from linguistic expertise which had been confounded in studies of developing readers (e.g. Lefton et al., 1979; Rayner, 1986; Taylor, 1965). Longer fixations and more regressive saccades are characteristics of inefficient processing and have been described as indicators of linguistic difficulty (Reichle et al., 2003) and are seen in poor readers (Lefton et al., 1979; Rayner, 1998). However, with the first published assessment of eye movement in inverted reading, we demonstrated that perceptual difficulty alone may elicit this behaviour.

Study 2 demonstrated that perceptual expertise is crucial for normal reading. When its use is disrupted, reading proficiency and oculomotor behaviour are impacted in ways which may be readily observed in difficult and developing reading.

3.4.2 The impact of perceptual learning

30 sessions of perceptual training partially reversed many of the damaging effects of text inversion, with an expertise gain of around 30% on most markers. Particularly impressive gains were made on the number of regressive saccades (80%) and aloud reading speed (77%). Aloud and silent paragraph reading speeds were similar post-training. However, as silent reading was much faster than aloud reading when upright, less impressive gains were made in silent reading (18%). This suggests that speech processes are no longer the limiting factor in aloud reading speed, as is the case in upright reading (Ashby et al., 2012).

Subjects showed a trend towards a reduction in the word-length effect after training. Large reductions in word-length effect have been interpreted as an increase in lexical processing (Zoccolotti et al., 2005). Whether this is a reasonable interpretation in the context of Study 2 is explored in the General Discussion.

Our oculomotor findings post-training closely parallel changes in children as they learn to read. These include reductions in fixation number and duration, and number of regressive saccades (Lefton et al., 1979; Rayner, 1985; Taylor, 1965). However, there was one notable exception. Interestingly, training did not lead to a change in forward saccade amplitude. A potential reason for this is that the perceptual span did not expand. This span is plastic (Pollatsek et al., 1981; Rayner, 1986) but would have had to expand significantly to reach levels in normal reading. This span in skilled readers extends 15 characters to the right, but only 3-4 to the left when reading upright English words (Rayner, 1986) and is asymmetric in the opposite direction in right to left readers of Hebrew (Pollatsek et al., 1981). Additional investigations pre- and post-training using a gaze-contingent moving window technique (McConkie & Rayner, 1975) to specifically examine the extent of the perceptual span would have helped confirm that the perceptual span did not increase.

In summary, we contributed the finding that subjects can regain around 30% on most markers of reading expertise with as little as 15 hours of training. Next we examined whether whole-word, expert processing is dependent on the face processing network in the right hemisphere.

Chapter four: Study 3: Do words and faces share expert perceptual mechanisms?

Title: Word and text processing in acquired prosopagnosia

4.1 Background

The many-to-many hypothesis (Behrmann & Plaut, 2013) states that expert face and word recognition networks overlap. It makes a key prediction that those with apperceptive prosopagnosia should have a mild form of pure alexia, and those with pure alexia should have a mild form of apperceptive prosopagnosia. Such a breakdown in word perceptual expertise would again be indicated by an elevated word-length effect.

A previous study found evidence of mild pure alexia in all three prosopagnosic patients (Behrmann & Plaut, 2014). However, two had previous diagnoses of integrative agnosia (Behrmann & Kimchi, 2003), and so a word deficit is not so surprising given this more general issue is often accompanied by reading deficits (Farah, 1991).

Although much of the many-to-many hypothesis focuses on the occipitotemporal cortex, further anterior temporal regions are part of the extended face recognition network in the right hemisphere. Lesions here result in an associative variant of prosopagnosia, where there is a failure to gain access to face memory (Davies-Thompson et al., 2014). If this area overlaps with the word processing network, reading difficulties may be present in those with associative prosopagnosia.

The many-to-many hypothesis assumes that the right and left inferior temporal cortex make the *same* type of contribution to word processing, and that normal performance requires both (Gerlach et al., 2014; Rubino et al., 2016). However, it is possible that each hemisphere makes a different contribution to the processing of a single multi-dimensional object. Indeed, previous anecdotal reports and smaller studies of prosopagnosia show that whilst the perception of word content is spared, handwriting or font perception may not be (Barton et al., 2010; Campbell et al., 1986; Rentschler et al., 1994).

We aimed to test the predictions of the many-to-many hypothesis with subjects with apperceptive and associative prosopagnosia. We also broadened the search and extended a previous smaller study (Barton et al., 2010) to see if those with right-only lesions struggled to perceive another aspect of visual text – its style.

4.2 Methods

We examined the word-length effect in the aloud reading of single words of 3-9 letters in ten patients with prosopagnosia resulting from a variety of lesions. As some patients had homonymous hemianopia (hemifield blindness), word-length effects were compared to data from 13 control subjects, against the appropriate full field, simulated left or right hemianopia condition.

We then examined text style discrimination in the same patients, with the addition of one other prosopagnosic patient with occipitotemporal lesions. Our 11 patients took part in a card sorting task, first sorting according to word content, then sorting those same cards by handwriting or font style (typeface). Results were compared to the performance of 11 control subjects.

4.3 Results

In comparison to controls, none of the five subjects with right-only lesions had an elevated word-length effect, whereas four out of the five with bilateral lesions did. We found no evidence that unilateral right hemisphere lesions lead to the breakdown of parallel letter processing in words.

No subjects were slow on sorting the words by content. Ten out of 11 subjects were impaired on accuracy for font or handwriting discrimination. Whilst four of six occipitotemporal patients were slower at this task than controls, none of the five with anterior temporal lesions were slow.

4.4 Discussion

Study 3 was an important early evaluation of the many-to-many hypothesis. Prosopagnosics with unilateral right hemisphere lesions did not exhibit elevated word-length effects which would have indicated mild pure alexia. The right inferior temporal cortex therefore made no detectable contribution to the expert perception of word identity. This suggested that word and face identification uses at least partially distinct expert perceptual mechanisms. This meant we could not support the many-to-many hypothesis in its most restrictive form.

However, all but one subject showed impairments in font or handwriting style discrimination. This suggested that the right inferior temporal cortex made a crucial contribution to the perception of visual text style. Our results could support a broader position in the hypothesis in which neural resources for face perception and visual text style discrimination are at least partially shared. Next, further implications of Study 3 as revealed by subsequent related studies are discussed.

4.4.1 Visual text style discrimination

It is also possible that another network in close proximity to the face network is responsible for visual text style perception, and was simply damaged by ‘messy’ lesions in our prosopagnosics. A later study of developmental prosopagnosia found no issues with text style perception (Rubino et al., 2016). This weakens the case for overlapping perceptual resources. However developmental prosopagnosics are less likely to struggle with ‘within-category object’ discriminations – such as with different tools and cars (Barton et al., 2019). Such ability requires configural processing (Barton, 2009), which is also crucial for handwriting style perception (Barnhart & Goldinger, 2013; Dyson & Stott, 2012), and so it may not be surprising that acquired prosopagnosics are disproportionately impaired.

4.4.2 Word identification

Our findings contradicted an earlier study which found mild pure alexia in prosopagnosia (Behrmann & Plaut, 2014). However, our results were later supported by three other investigations which found no significant word recognition deficits in acquired (Susilo et al., 2015) or developmental prosopagnosia (Burns et al., 2017; Starrfelt et al., 2018). These three studies valuably extended the findings of Study 3 by specifically examining the impact on linguistic processing in individual words (Burns et al., 2017; Susilo et al., 2015), and on paragraph reading (Starrfelt et al., 2018). All failed to find broader reading deficits in prosopagnosia. This means the studies could not support the many-to-many hypothesis, even when moving beyond the perceptual level, which is the current focus of the hypothesis.

4.4.3 Evidence on the many-to-many hypothesis from alexia

The many-to-many hypothesis received recent support with findings of subtle face recognition deficits in pure alexia (Albonico & Barton, 2017; Behrmann & Plaut, 2014; Roberts et al., 2015) and developmental dyslexia (Gabay et al., 2017; Sigurdardottir et al., 2015, 2018). Evidence of associations between face and word deficits is more robust in alexia than it is in prosopagnosia (Asperud et al., 2019;

Robotham & Starrfelt, 2017). This may indicate that these neural resources are closer together, or overlap more in the left than in the right hemisphere (Asperud et al., 2019; Rubino et al., 2016). This aligns with the neural recycling hypothesis, where competition for these neural resources mainly occurs in the left hemisphere (Dehaene et al., 2010; Dundas et al., 2013). Study 3 supports this view in that it does not appear that resources which underpin face discrimination in the right hemisphere are recycled to support word discrimination.

4.4.4 Improvements and further considerations

We derived the word-length effect from word naming time, as is most common in the diagnosis of pure alexia (Leff & Starrfelt, 2014). As naming time probes individual level identification and lexical decision probes a more general familiarity (Balota & Chumbley, 1984) both have been assessed in subsequent studies (Burns et al., 2017; Starrfelt et al., 2018; Susilo et al., 2015), although this did not reveal reading issues in prosopagnosia.

Some argue that letter confusability (how visually similar a letter is with others in the alphabet) underlies the word-length effect in pure alexia, and must be carefully controlled (Burns et al., 2017; Fiset et al., 2005). Others view the calculation of summed confusability scores for whole words as problematic (Starrfelt et al., 2015) or simply as a more sophisticated measure of the effect of word-length (Barton et al., 2014). We did not choose to control confusability in our word stimuli, but it may have been pragmatic to do so as it may play a role in impaired reading.

In sum, Study 3 found that the right hemisphere face network does not measurably support expert word reading. However, it may support the discrimination of visual text style. Whilst we cannot support the many-to-many hypothesis in its most restrictive form, it currently enjoys further support in studies of alexia.

Chapter five: Study 4: How do parts of a face contribute to its holistic representation?

Title: An adaptation study of internal and external features in facial representations

5.1 Background

Internal facial features (eyes, nose and mouth) are thought to be more important than external features (forehead, external contour and hair) to identify faces (Butler et al., 2010; Fletcher et al., 2008). However, this contribution is affected by familiarity, with the external features being equally helpful in unfamiliar face matching (Ellis et al., 1979; Young et al., 1985). How the internal and external face parts contribute to their mental representation was not known. Such representation may be probed using identity adaptation. Adapting to one face, e.g. 'Matt', makes one more likely to identify a 50:50 morph of Ben and Matt as 'Ben'.

We aimed to determine the relative contributions of the internal and external features to the mental representations of faces. We wanted to examine this when parts were presented in isolation or in a 'whole face' context, for both familiar and unfamiliar faces.

5.2 Methods

In a first experiment with 14 subjects, we used identity adaptation for famous and unfamiliar faces. The adapting stimuli were whole faces, isolated internal and isolated external features. The magnitude of the identity aftereffect was the dependent variable.

In a second experiment with 12 different subjects, we used the same faces and protocol, but the adapting internal and external features were shown in a neutral whole face context (Figure 5).

Figure 5. *Example adaptors used in both experiments. Experiment 1 adaptors were whole faces, isolated internal components or isolated external components. Experiment 2 adaptors were a 100% whole face, 100% internal with a 50:50 morph external, 100% external with a 50:50 morph internal, or a 50:50 morph whole face. Yellow shading is shown here only to highlight the morphed areas.*

5.3 Results

Isolated internal features elicited aftereffects which were not significantly different to whole faces. These were stronger than those from isolated external features. However, when the features were not isolated, but placed in a whole-face context, this pattern changed. The aftereffects for the internal features were significantly weaker than those from whole faces, and were equivalent to those from external features. No difference in this pattern was found in either experiment for familiarity.

5.4 Discussion

In this study we used aftereffects to probe the mental representations of faces. The aftereffects indicated that, when presented alone, isolated internal features contributed more to face representations than external features. But, strikingly, when placed in a whole-face context, both parts contributed equally. In both experiments, the contribution of internal and external features seem to combine in an additive manner to equal that of the whole face. This was the case for both familiar and unfamiliar faces. This indicated that holistic integration had occurred between the two regions in the mental representation of a whole face, and that it occurs regardless of familiarity with the face. Study 4 therefore provided the first behavioural parallel of a previous neuroimaging finding that perceptual integration reduces the regional saliency of isolated internal features, regardless of familiarity (Andrews et al., 2010).

In contrast to our results, previous studies found internal features were more important in the perception of familiar faces than unfamiliar ones (Clutterbuck &

Johnston, 2002; Ellis et al., 1979; Young et al., 1985). However, unlike these studies, we showed the unfamiliar faces repeatedly. Whilst no difference could be found between the first and second half of experiment 2, it could be that *image* familiarity occurs rapidly which is perhaps all that is required to initiate the internal feature advantage. Indeed, the internal feature advantage has been induced by repeatedly showing the same image of an unfamiliar face (Clutterbuck & Johnston, 2005), in as little as 3 minutes (Osborne & Stevenage, 2008).

Study 4 may shed light on the results of a more recent training study (Longmore et al., 2015). When participants learnt new faces by training with isolated internal features, they recognised the target across new viewpoints better than when training with whole faces. The authors explained that participants had focused attention on internal features which contained more 'useful' identity information. Study 4 suggests that the influence of these 'useful' internal features to face representations is enhanced by isolation. This enhancement may underlie some of the positive training effect in Longmore et al. (2015).

In addition, in natural settings one sees internal facial features in the context of a whole face. Indeed this context is important as the internal features combine with the external to create an overall representation (Andrews & Thompson, 2010; Sinha & Poggio, 1996). Study 4 suggested that if isolated, internal features influence identity judgements more than if shown in a natural whole-face context. A subsequent study (Royer et al., 2017) found that removing external contour decreased reliance on low spatial frequencies, and so changed the perceptual strategy used. These studies further highlighted the importance of considering the ecological value of using isolated face parts.

In sum, in this final study, we found that internal and external parts of faces influence each other to create an overall mental representation which balances the contribution of both parts.

Chapter six: General discussion

6.1 Summary of findings

Most adults are experts at identifying familiar written words and faces. The four behavioural studies in this thesis contributed to our understanding of this perceptual expertise. To summarise, in answer to our **key questions**, we found the following.

We first asked **'What is the impact of inversion on the expert processing of words?'** We confirmed that as with face expertise, single word perceptual expertise is not generalised to inverted words. Inversion dramatically increased word-length effects only for normal words, and not for mirrored or backward controls in which we are not experts. This indicated that the word-length effect is a suitable marker of expertise.

We then used inverted single words and paragraphs to ask a broader question '**What are the markers of perceptual expertise in reading and how are they impacted by training?**' We found these behavioural markers to be very rapid reading times with minimal word-length effects. The oculomotor markers were few and very brief fixations with few and large forward saccades and few regressive saccades. Using these markers, we showed it is possible to gain about 30% on most parameters after only 15 hours of training on inverted text. A trend to the reduction of the word-length effect was observed.

We then asked **'Do words and faces share expert perceptual mechanisms?'** Our subjects with prosopagnosia following unilateral right lesions showed no impairment in the perception of word identity. This indicated that the expert networks for word and face perception are partially distinct or not shared at all. However, nearly all patients struggled to perceive the handwriting or font style of the text. Therefore the right hemisphere makes a non-redundant contribution to the perception of visual text style.

We finally asked **'How do parts of a face contribute to its holistic representation?'** We found that when presented in isolation, internal features produced stronger aftereffects than external features. This indicated that they contributed more to the mental representation of the face. However, when presented in a whole-face context, this saliency of the internal features was reduced. This modulation suggested that both parts were integrated together as a whole in both familiar and unfamiliar faces.

6.2 Theoretical implications

6.2.1 The holistic-analytic continuum: where do words sit?

Words are often described as objects lateralised to the left hemisphere during recognition. Indeed, Study 3 supported this account in respect to word identity. However, we also proposed that the right hemisphere is crucial in recognising a word's visual style, a task which requires configural processing (Barnhart & Goldinger, 2013; Dyson & Stott, 2012). This is broadly analogous to a finding in faces that whilst the left hemisphere processes parts, the right processes wholes (Ramon & Rossion, 2012; Rhodes, 1993; Rossion et al., 2000).

In short, we suggest that it is not categories of stimuli which are lateralised, but the cognitive operation one performs on them. This somewhat challenges Farah's (1992) holistic-analytic continuum (Figure 1) if style recognition, rather than simply word identity is considered in its interpretation. This continuum places words at one extreme as objects recognised *entirely* as parts by the left hemisphere. Faces sit at the other end as objects recognised *entirely* as wholes by the right hemisphere.

A fundamental challenge to even restrictive interpretations of the continuum comes from the studies which found subtle face processing difficulties in alexia following left hemisphere lesions (Albonico & Barton, 2017; Behrmann & Plaut, 2014; Roberts et al., 2015). This suggests that the left hemisphere is involved in the recognition of faces. These studies also found that the face recognition difficulties were in line with characteristics ascribed to the left hemisphere. These include difficulties in processing faces *analytically* in dyslexia (Gabay et al., 2017; Sigurdardottir et al., 2015) and in pure alexia (Behrmann & Plaut, 2014), (but see Roberts et al., 2015). Four pure alexics also struggled with a *linguistic* aspect of face processing – lip reading (although these subjects also had surface dysgraphia – a linguistic issue). They also performed worse with line drawn faces (Albonico & Barton, 2017). This aligns with the idea that pure alexics may find processing *high spatial frequencies* difficult (Fiset et al., 2005; Starrfelt & Shallice, 2014), a left lateralised function (Sergent, 1983).

Further challenge to the continuum comes from evidence of other holistic processes in word identification. These include configural sensitivity (Wong et al., 2019), and perceptual integration in the composite word effect (Ventura et al., 2017, 2019; Wong et al., 2011), which was also lateralised to the right hemisphere (Ventura et al., 2018). Being right hemisphere functions, these holistic processes in words may well have been disrupted in the prosopagnosic subjects in Study 3. Interestingly, the use of both types of holistic processing are disrupted by inversion (Ventura et al., 2019; Wong et al., 2019) as is parallel letter processing (Study 1 and 2), suggesting a possible link between the processes (Ventura et al., 2019).

6.2.2 DRC model: did training increase the use of the lexical route?

Before they can read words using a rapid whole-word strategy, developing readers rely on a part-based strategy to convert letters into sounds (Castles et al., 2018; Nation & Castles, 2017). Studies 1 and 2 showed that accomplished readers also resort to part-based processing to read words in unfamiliar formats, such as upside down. But it remains unclear as to what strategy subjects used after 15 hours of training with upside down words in Study 2.

The DRC model of reading (Coltheart et al., 2001) proposes that only the lexical route can process letters in parallel, leading to no word-length effects. As the sublexical route uses serial letter processing, it generates word-length effects of 10-30 ms/letter (Cosky, 1976; Jared & Seidenberg, 1990; Weekes, 1997). Study 1 confirmed that the word-length effect is indeed a good marker of expertise, and aligned with previous suggestions that only words in formats in which one is expert may access the lexical route (Cohen et al., 2008). For these reasons, the lexical route may be viewed as an expert reading pathway.

It seems clear that as one develops perceptual expertise in upside down words, the lexical route should be reengaged. So did our trainees in Study 2 begin to accomplish this? The word-length effect showed a trend to a reduction from 158 to 113 ms/letter after training. Similar declines in word-length effects in developing readers have previously been interpreted as transitioning to an expert lexical strategy (Zoccolotti et al., 2005). However, this conclusion must be viewed cautiously. As the faster serial processing of each letter may also lead to reduced word-length effects, our trainees in Study 2 may have simply become better at this using the sublexical route.

However, the results from Study 1 indicate that inversion impairs word processing, rather than letter processing. Backwards spelt words contain normal letters, just in the wrong order. If inversion mainly impaired letter perceptual expertise, backwards spelt words should be just as impacted by inversion as normal words. However, Study 1 indicated that this was not the case. Consequently, the impairment (due to inversion), and therefore the basis for improvement in Study 2, is probably at the word level. As the lexical pathway emphasises the whole word, it is likely that training did increase use of this expert route.

Although this is a tentative conclusion, future studies could use word frequency effects as a marker of lexical reading to strengthen this claim. If the expert lexical route were indeed relied on by our subjects, a stronger word frequency effect would be found post-training than pre-training. In this effect, high-frequency words would be identified faster in lexical decision tasks than low-frequency words (Burani et al., 2002; Martens & de Jong, 2006).

6.2.3 The Bruce and Young (1986) model of face recognition

The Bruce and Young model (Figure 2) proposes that familiar and unfamiliar faces are processed differently. However, the results from Study 4 may challenge this idea. The model states that familiar faces are represented holistically in special units called FRUs. Unfamiliar faces are not granted access to these units, so are processed in a distinct channel in a part-based manner. However, we found the same pattern of aftereffects and holistic integration, regardless of familiarity. This supports the claim that they may be processed in similar ways, at least eventually (Hole, 1994; Young et al., 1987). However, there are a couple of ways of interpreting our results according to the model.

The first interpretation is that unfamiliar faces are able to access mechanisms similar to the FRUs and that adaptation occurs here. The proposed neuroanatomic location of the FRUs is the fusiform face area (Haxby et al., 2000), an area which adapts to face identity (Winston et al., 2004), and is involved in the perception of unfamiliar faces (Andrews et al., 2010; Kanwisher et al., 1997). The level of the FRUs are therefore a reasonable candidate for adaptation. However, one issue is that the FRUs in the model represent faces in an image-invariant manner. Our unfamiliar faces were only shown in one view, and so would not have had exposure to the variety of images needed to construct an image-invariant representation (Kramer et al., 2018; Longmore et al., 2008).

The second interpretation which is less problematic for the model is that adaptation occurs at an earlier level common to both familiar and unfamiliar faces, during image-dependent structural encoding. This would need to be at the expression-independent stage, as the identity aftereffect is not impacted by different expressions in adaptor and test faces, regardless of familiarity (Fox et al., 2008).

6.3 Practical implications: Markers of perceptual expertise in reading

Our finding that the word-length effect is a suitable marker of expertise will particularly interest those who assess reading acquisition or disorder. Indeed, the word-length effect is routinely used in the diagnosis of pure alexia (Leff & Starrfelt, 2014; Starrfelt & Shallice, 2014), with nearly every report including an assessment of the effect (Barton et al., 2014). A recent investigation into developmental dyslexia found single word reading times of dyslexics were more impacted by word length than those of controls, but the opposite was true for inversion. This suggests developmental dyslexics' holistic or expert parallel letter processing is impaired (Conway et al., 2017). We used the word-length effect marker ourselves in Study 3 to ask whether reading expertise is impacted by cortical damage to the face recognition network.

In Study 2, both words and paragraphs were read with a high degree of accuracy in both orientations. This suggests that accuracy may not be a sensitive marker of word perceptual expertise. This is in line with other work which showed minimal (Albonico et al., 2018) or no word inversion effects (Sussman et al., 2018) with accuracy-based measures, and the finding that patients with mild to moderate pure alexia tend to make few reading errors (Behrmann et al., 2001; Leff & Starrfelt, 2014).

We found that subjects can gain around 30% on most markers of reading expertise with as little as 15 hours of training with inverted text. Information on the markers and time course of expertise acquisition may be of interest to those involved in neuro-rehabilitation and perceptual learning. In addition, learning to read upside down has been suggested as potential compensatory rehabilitation for those with right homonymous hemianopia (loss of the right visual field in both eyes), as inverting the text places upcoming words in the intact left visual field (Rodriguez & Barton, 2015).

7 Conclusion

Most adults are experts at identifying written words and faces with which they are familiar. To accomplish this, they perceive words as ‘wholes’ by all their letters in parallel, and faces as an indivisible gestalt.

In respect to word perceptual expertise, the word-length effect is an appropriate marker. This marker shows that readers can only apply expert ‘whole-word’ processing to text in familiar formats. As soon as words are manipulated by a transformation such as inversion, this whole-word strategy is destroyed. However, it is likely that this lexical strategy can be partially generalised by training on inverted text over a matter of weeks.

Contrary to the many-to-many hypothesis, expert parallel-letter word mechanisms are at least partially distinct from those for faces in the right hemisphere. However, there appears to be shared mechanisms used to discriminate both faces and the style of visual text. Both of these tasks require the use of configural processing. Each hemisphere appears to process different dimensions of the word, with the left dealing with language content, i.e. the identity of the word, and the right with its stylistic properties, i.e. the font or handwriting.

With respect to faces, the internal features interact with the external features in the processing of whole faces. This interaction is served by holistic mechanisms which act across the whole face to reduce the saliency of the internal features. This is the case for both familiar and unfamiliar faces, potentially challenging the idea that familiar and unfamiliar faces are processed in different ways.

8 References

Adelman, J. S., Marquis, S. J., & Sabatos-DeVito, M. G. (2010). Letters in Words Are Read Simultaneously, Not in Left-to-Right Sequence. *Psychological Science*, *21*(12), 1799–1801. https://doi.org/10.1177/0956797610387442

Aghababian, V., & Nazir, T. A. (2000). Developing normal reading skills: Aspects of the visual processes underlying word recognition. *Journal of Experimental Child Psychology*, *76*(2), 123–150. https://doi.org/10.1006/jecp.1999.2540

Albonico, A., & Barton, J. J. S. (2017). Face perception in pure alexia: Complementary contributions of the left fusiform gyrus to facial identity and facial speech processing. *Cortex*, *96*, 59–72. https://doi.org/10.1016/j.cortex.2017.08.029

Albonico, A., Furubacke, A., Barton, J. J. S., & Oruc, I. (2018). Perceptual efficiency and the inversion effect for faces, words and houses. *Vision Research*, *153*, 91–97. https://doi.org/10.1016/j.visres.2018.10.008

Allen, P. A., Wallace, B., & Weber, T. A. (1995). Influence of case type, word frequency, and exposure duration on visual word recognition. *Journal of Experimental Psychology. Human Perception and Performance*, *21*(4), 914–934.

Andrews, T. J., Davies-Thompson, J., Kingstone, A., & Young, A. W. (2010). Internal and External Features of the Face Are Represented Holistically in Face-Selective Regions of Visual Cortex. *Journal of Neuroscience*, *30*(9), 3544–3552. https://doi.org/10.1523/JNEUROSCI.4863-09.2010

Andrews, T. J., & Thompson, P. (2010). Face-to-Face Coalition. *I-Perception*, *1*(1), 28–30. https://doi.org/10.1068/i0402

Arguin, M., & Bub, D. N. (1993). Single-character processing in a case of pure alexia. *Neuropsychologia*, *31*(5), 435–458. https://doi.org/10.1016/0028-3932(93)90059-9

Ashby, J., Yang, J., Evans, K. H. C., & Rayner, K. (2012). Eye movements and the perceptual span in silent and oral reading. *Attention, Perception, & Psychophysics*, *74*(4), 634–640. https://doi.org/10.3758/s13414-012-0277-0

Ashworth, A. R. S., Vuong, Q. C., Rossion, B., & Tarr, M. J. (2008). Recognizing rotated faces and Greebles: What properties drive the face inversion effect? *Visual Cognition*, *16*(6), 754–784. https://doi.org/10.1080/13506280701381741

Asperud, J., Kühn, C. D., Gerlach, C., Delfi, T. S., & Starrfelt, R. (2019). Word recognition and face recognition following posterior cerebral artery stroke: Overlapping networks and selective contributions. *Visual Cognition*. https://www.tandfonline.com/doi/abs/10.1080/13506285.2019.1599481

Avidan, G., Harel, M., Hendler, T., Ben-Bashat, D., Zohary, E., & Malach, R. (2002). Contrast sensitivity in human visual areas and its relationship to object recognition. *Journal of Neurophysiology*, *87*(6), 3102–3116. https://doi.org/10.1152/jn.2002.87.6.3102

Avidan, G., Tanzer, M., & Behrmann, M. (2011). Impaired holistic processing in congenital prosopagnosia. *Neuropsychologia*, *49*(9), 2541–2552. https://doi.org/10.1016/j.neuropsychologia.2011.05.002

Baars, B. J., & Gage, N. M. (2010). *Cognition, Brain, and Consciousness*. Elsevier. https://doi.org/10.1016/C2009-0-01556-6

Balota, D. A., & Chumbley, J. I. (1984). Are lexical decisions a good measure of lexical access? The role of word frequency in the neglected decision stage. *Journal of Experimental Psychology. Human Perception and Performance*, *10*(3), 340–357. https://doi.org/10.1037//0096-1523.10.3.340

Barnhart, A. S., & Goldinger, S. D. (2013). Rotation reveals the importance of configural cues in handwritten word perception. *Psychonomic Bulletin & Review*, *20*(6), 1319–1326. https://doi.org/10.3758/s13423-013-0435-y

Barton, J. J. S. (2008). Structure and function in acquired prosopagnosia: Lessons from a series of 10 patients with brain damage. *Journal of Neuropsychology*, *2*(Pt 1), 197–225.

Barton, J. J. S. (2009). What is meant by impaired configural processing in acquired prosopagnosia? *Perception*, *38*(2), 242–260. https://doi.org/10.1068/p6099

Barton, J. J. S., Albonico, A., Susilo, T., Duchaine, B., & Corrow, S. L. (2019). Object recognition in acquired and developmental prosopagnosia. *Cognitive Neuropsychology*, *36*(1–2), 54–84. https://doi.org/10.1080/02643294.2019.1593821

Barton, J. J. S., & Corrow, S. L. (2016). Selectivity in acquired prosopagnosia: The segregation of divergent and convergent operations. *Neuropsychologia*, *83*, 76–87. https://doi.org/10.1016/j.neuropsychologia.2015.09.015

Barton, J. J. S., Hanif, H. M., Eklinder Björnström, L., & Hills, C. (2014). The word-length effect in reading: A review. *Cognitive Neuropsychology*, *31*(5–6), 378–412. https://doi.org/10.1080/02643294.2014.895314

Barton, J. J. S., Sekunova, A., Sheldon, C., Johnston, S., Iaria, G., & Scheel, M. (2010). Reading words, seeing style: The neuropsychology of word, font and handwriting perception. *Neuropsychologia*, *48*(13), 3868–3877. https://doi.org/10.1016/j.neuropsychologia.2010.09.012

Behrmann, M., Black, S. E., & Bub, D. (1990). The evolution of pure alexia: A longitudinal study of recovery. *Brain and Language*, *39*(3), 405–427. https://doi.org/10.1016/0093-934X(90)90148-A

Behrmann, M., & Kimchi, R. (2003). What does visual agnosia tell us about perceptual organization and its relationship to object perception? *Journal of Experimental Psychology. Human Perception and Performance*, *29*(1), 19–42.

Behrmann, M., & Plaut, D. (2014). Bilateral Hemispheric Processing of Words and Faces: Evidence from Word Impairments in Prosopagnosia and Face

Impairments in Pure Alexia. *Cerebral Cortex*, *24*(4), 1102–1118. https://doi.org/10.1093/cercor/bhs390

Behrmann, M., & Plaut, D. C. (2013). Distributed circuits, not circumscribed centers, mediate visual recognition. *Trends in Cognitive Sciences*, *17*(5), 210–219. https://doi.org/10.1016/j.tics.2013.03.007

Behrmann, M., Plaut, D. C., & Nelson, J. (1998). A literature review and new data supporting an interactive account of letter-by-letter reading. *Cognitive Neuropsychology*, *15*(1–2), 7–51. https://doi.org/10.1080/026432998381212

Behrmann, M., Shomstein, S. S., Black, S. E., & Barton, J. J. (2001). The eye movements of pure alexic patients during reading and nonreading tasks. *Neuropsychologia*, *39*(9), 983–1002.

Bellocchi, S., Muneaux, M., Bastien-Toniazzo, M., & Ducrot, S. (2013). I can read it in your eyes: What eye movements tell us about visuo-attentional processes in developmental dyslexia. *Research in Developmental Disabilities*, *34*(1), 452–460. https://doi.org/10.1016/j.ridd.2012.09.002

Besner, D. (1983). Basic decoding components in reading: Two dissociable feature extraction processes. *Canadian Journal of Psychology/Revue Canadienne de Psychologie*, *37*(3), 429–438. https://doi.org/10.1037/h0080739

Bijeljac-Babic, R., Millogo, V., Farioli, F., & Grainger, J. (2004). A developmental investigation of word length effects in reading using a new on-line word identification paradigm. *Reading and Writing*, *17*(4), 411–431. https://doi.org/10.1023/B:READ.0000032664.20755.af

Bouhali, F., Schotten, M. T. de, Pinel, P., Poupon, C., Mangin, J.-F., Dehaene, S., & Cohen, L. (2014). Anatomical Connections of the Visual Word Form Area. *Journal of Neuroscience*, *34*(46), 15402–15414. https://doi.org/10.1523/JNEUROSCI.4918-13.2014

Bruce, V. (1982). Changing faces: Visual and non-visual coding processes in face recognition. *British Journal of Psychology*, *73*(1), 105–116. https://doi.org/10.1111/j.2044-8295.1982.tb01795.x

Bruce, V., Henderson, Z., Greenwood, K., Hancock, P. J. B., Burton, A. M., & Miller, P. (1999). Verification of face identities from images captured on video. *Journal of Experimental Psychology: Applied*, *5*(4), 339–360. https://doi.org/10.1037/1076-898X.5.4.339

Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology (London, England: 1953)*, *77 (Pt 3)*, 305–327.

Bukach, C. M., Phillips, W. S., & Gauthier, I. (2010). Limits of generalization between categories and implications for theories of category specificity. *Attention, Perception & Psychophysics*, *72*(7), 1865–1874. https://doi.org/10.3758/APP.72.7.1865

Burani, C., Marcolini, S., & Stella, G. (2002). How Early Does Morpholexical Reading Develop in Readers of a Shallow Orthography? *Brain and Language*, *81*(1), 568–586. https://doi.org/10.1006/brln.2001.2548

Burns, E. J., Bennetts, R. J., Bate, S., Wright, V. C., Weidemann, C. T., & Tree, J. J. (2017). Intact word processing in developmental prosopagnosia. *Scientific Reports*, *7*. https://doi.org/10.1038/s41598-017-01917-8

Burton, A. M., Bruce, V., & Johnston, R. A. (1990). Understanding face recognition with an interactive activation model. *British Journal of Psychology*, *81*(3), 361–380. https://doi.org/10.1111/j.2044-8295.1990.tb02367.x

Busigny, T., Joubert, S., Felician, O., Ceccaldi, M., & Rossion, B. (2010). Holistic perception of the individual face is specific and necessary: Evidence from an extensive case study of acquired prosopagnosia. *Neuropsychologia*, *48*(14), 4057–4092. https://doi.org/10.1016/j.neuropsychologia.2010.09.017

Butler, S., Blais, C., Gosselin, F., Bub, D., & Fiset, D. (2010). Recognizing famous people. *Attention, Perception, & Psychophysics*, *72*(6), 1444–1449. https://doi.org/10.3758/APP.72.6.1444

Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nature Reviews. Neuroscience*, *6*(8), 641–651. https://doi.org/10.1038/nrn1724

Campbell, R., Landis, T., & Regard, M. (1986). Face recognition and lipreading. A neurological dissociation. *Brain*, *109*(3), 509–521. https://doi.org/10.1093/brain/109.3.509

Cantlon, J. F., Pinel, P., Dehaene, S., & Pelphrey, K. A. (2011). Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cerebral Cortex (New York, N.Y.: 1991)*, *21*(1), 191–199. https://doi.org/10.1093/cercor/bhq078

Cassia, V. M., Picozzi, M., Kuefner, D., Bricolo, E., & Turati, C. (2009). Holistic processing for faces and cars in preschool-aged children and adults: Evidence from the composite effect. *Developmental Science*, *12*(2), 236–248. https://doi.org/10.1111/j.1467-7687.2008.00765.x

Castles, A., Rastle, K., & Nation, K. (2018). Ending the Reading Wars: Reading Acquisition From Novice to Expert. *Psychological Science in the Public Interest*, *19*(1), 5–51. https://doi.org/10.1177/1529100618772271

Centanni, T. M., Norton, E. S., Park, A., Beach, S. D., Halverson, K., Ozernov-Palchik, O., Gaab, N., & Gabrieli, J. D. (2018). Early Development of Letter Specialization in Left Fusiform is Associated with Better Word Reading and Smaller Fusiform Face Area. *Developmental Science*, *21*(5), e12658. https://doi.org/10.1111/desc.12658

Chin, M. D., Evans, K. K., Wolfe, J. M., Bowen, J., & Tanaka, J. W. (2018). Inversion effects in the expert classification of mammograms and faces.

Cognitive Research: Principles and Implications, *3*. https://doi.org/10.1186/s41235-018-0123-6

Civile, C., McLaren, R. P., & McLaren, I. P. L. (2014). The face inversion effect--parts and wholes: Individual features and their configuration. *Quarterly Journal of Experimental Psychology (2006)*, *67*(4), 728–746. https://doi.org/10.1080/17470218.2013.828315

Clutterbuck, R., & Johnston, R. A. (2002). Exploring levels of face familiarity by using an indirect face-matching measure. *Perception*, *31*(8), 985–994. https://doi.org/10.1068/p3335

Clutterbuck, R., & Johnston, R. A. (2005). Demonstrating how unfamiliar faces become familiar using a face matching task. *European Journal of Cognitive Psychology*, *17*(1), 97–116. https://doi.org/10.1080/09541440340000439

Cohen, L., Dehaene, S., Vinckier, F., Jobert, A., & Montavont, A. (2008). Reading normal and degraded words: Contribution of the dorsal and ventral visual pathways. *NeuroImage*, *40*(1), 353–366. https://doi.org/10.1016/j.neuroimage.2007.11.036

Cohen, L., Lehéricy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area. *Brain: A Journal of Neurology*, *125*(Pt 5), 1054–1069.

Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review*, *108*(1), 204–256.

Coltheart, M., Saunders, S. J., & Tree, J. J. (2010). Computational modelling of the effects of semantic dementia on visual word recognition. *Cognitive Neuropsychology*, *27*(2), 101–114. https://doi.org/10.1080/02643294.2010.502887

Conway, A., Brady, N., & Misra, K. (2017). Holistic word processing in dyslexia. *PloS One*, *12*(11), e0187326. https://doi.org/10.1371/journal.pone.0187326

Cosky, M. J. (1976). The role of letter recognition in word recognition. *Memory & Cognition*, *4*(2), 207–214. https://doi.org/10.3758/BF03213165

Davies-Thompson, J., Pancaroglu, R., & Barton, J. (2014). Acquired prosopagnosia: Structural basis and processing impairments. *Frontiers in Bioscience (Elite Edition)*, *6*, 159–174.

DeGutis, J., Cohan, S., Mercado, R. J., Wilmer, J., & Nakayama, K. (2012). Holistic processing of the mouth but not the eyes in developmental prosopagnosia. *Cognitive Neuropsychology*, *29*(5–6), 419–446. https://doi.org/10.1080/02643294.2012.754745

DeGutis, J., Wilmer, J., Mercado, R. J., & Cohan, S. (2013). Using regression to measure holistic face processing reveals a strong link with face recognition ability. *Cognition*, *126*(1), 87–100. https://doi.org/10.1016/j.cognition.2012.09.004

Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, *56*(2), 384–398. https://doi.org/10.1016/j.neuron.2007.10.004

Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences*, *15*(6), 254–262. https://doi.org/10.1016/j.tics.2011.04.003

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, *9*(7), 335–341. https://doi.org/10.1016/j.tics.2005.05.004

Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Filho, G. N., Jobert, A., Dehaene-Lambertz, G., Kolinsky, R., Morais, J., & Cohen, L. (2010). How Learning to Read Changes the Cortical Networks for Vision and Language. *Science*, *330*(6009), 1359–1364. https://doi.org/10.1126/science.1194140

Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology. General*, *115*(2), 107–117.

Dien, J. (2009). A tale of two recognition systems: Implications of the fusiform face area and the visual word form area for lateralized object recognition models. *Neuropsychologia*, *47*(1), 1–16. https://doi.org/10.1016/j.neuropsychologia.2008.08.024

Dundas, E. M., Plaut, D. C., & Behrmann, M. (2013). The joint development of hemispheric lateralization for words and faces. *Journal of Experimental Psychology. General*, *142*(2), 348–358. https://doi.org/10.1037/a0029503

Dyson, M. C., & Stott, C. (2012). Characterizing typographic expertise: Do we process typefaces like faces? *Visual Cognition*, *20*(9), 1082–1094. https://doi.org/10.1080/13506285.2012.722568

Ellis, H. D., Shepherd, J. W., & Davies, G. M. (1979). Identification of familiar and unfamiliar faces from internal and external features: Some implications for theories of face recognition. *Perception*, *8*(4), 431–439. https://doi.org/10.1068/p080431

Farah, M. J. (1991). Cognitive Neuropsychology: Patterns of Co-occurrence Among the Associative Agnosias: Implications for Visual Object Representation. *Cognitive Neuropsychology*, *8*(1), 1–19. https://doi.org/10.1080/02643299108253364

Farah, M. J. (1992). Is an Object an Object an Object? Cognitive and Neuropsychological Investigations of Domain Specificity in Visual Object Recognition. *Current Directions in Psychological Science*, *1*(5), 164–169.

Fiset, D., Arguin, M., Bub, D., Humphreys, G. W., & Riddoch, M. J. (2005). How to make the word-length effect disappear in letter-by-letter dyslexia: Implications for an account of the disorder. *Psychological Science*, *16*(7), 535–541. https://doi.org/10.1111/j.0956-7976.2005.01571.x

Fiset, D., Gosselin, F., Blais, C., & Arguin, M. (2006). Inducing Letter-by-letter Dyslexia in Normal Readers. *Journal of Cognitive Neuroscience*, *18*(9), 1466–1476. https://doi.org/10.1162/jocn.2006.18.9.1466

Fletcher, K. I., Butavicius, M. A., & Lee, M. D. (2008). Attention to internal face features in unfamiliar face matching. *British Journal of Psychology (London, England: 1953)*, *99*(Pt 3), 379–394. https://doi.org/10.1348/000712607X235872

Fox, C. J., Hanif, H. M., Iaria, G., Duchaine, B. C., & Barton, J. J. S. (2011). Perceptual and anatomic patterns of selective deficits in facial identity and expression processing. *Neuropsychologia*, *49*(12), 3188–3200. https://doi.org/10.1016/j.neuropsychologia.2011.07.018

Fox, C. J., Oruç, I., & Barton, J. J. S. (2008). It doesn't matter how you feel. The facial identity aftereffect is invariant to changes in facial expression. *Journal of Vision*, *8*(3), 11–11. https://doi.org/10.1167/8.3.11

Gabay, Y., Dundas, E., Plaut, D., & Behrmann, M. (2017). Atypical perceptual processing of faces in developmental dyslexia. *Brain and Language*, *173*, 41–51. https://doi.org/10.1016/j.bandl.2017.06.004

Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*(2), 191–197. https://doi.org/10.1038/72140

Gauthier, I., Williams, P., Tarr, M. J., & Tanaka, J. (1998). Training 'greeble' experts: A framework for studying expert object recognition processes. *Vision Research*, *38*(15–16), 2401–2428. https://doi.org/10.1016/s0042-6989(97)00442-2

Gerlach, C., Marstrand, L., Starrfelt, R., & Gade, A. (2014). No strong evidence for lateralisation of word reading and face recognition deficits following posterior brain injury. *Journal of Cognitive Psychology*, *26*(5), 550–558. https://doi.org/10.1080/20445911.2014.928713

Goffaux, V., Hault, B., Michel, C., Vuong, Q. C., & Rossion, B. (2005). The respective role of low and high spatial frequencies in supporting configural and featural processing of faces. *Perception*, *34*(1), 77–86. https://doi.org/10.1068/p5370

Grainger, J., & Whitney, C. (2004). Does the huamn mnid raed wrods as a wlohe? *Trends in Cognitive Sciences*, *8*(2), 58–59. https://doi.org/10.1016/j.tics.2003.11.006

Habekost, T., Petersen, A., Behrmann, M., & Starrfelt, R. (2014). From word superiority to word inferiority: Visual processing of letters and words in pure alexia. *Cognitive Neuropsychology*, *31*(5–6), 413–436. https://doi.org/10.1080/02643294.2014.906398

Hancock, P. J. B., Bruce, V., & Burton, A. M. (2000). Recognition of unfamiliar faces. *Trends in Cognitive Sciences*, *4*(9), 330–337. https://doi.org/10.1016/S1364-6613(00)01519-9

Harris, R. J., Rice, G. E., Young, A. W., & Andrews, T. J. (2016). Distinct but Overlapping Patterns of Response to Words and Faces in the Fusiform Gyrus. *Cerebral Cortex*, *26*(7), 3161–3168. https://doi.org/10.1093/cercor/bhv147

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*(6), 223–233. https://doi.org/10.1016/S1364-6613(00)01482-0

Hillger, L. A., & Koenig, O. (1991). Separable mechanisms in face processing: Evidence from hemispheric specialization. *Journal of Cognitive Neuroscience*, *3*(1), 42–58. https://doi.org/10.1162/jocn.1991.3.1.42

Hole, G. J. (1994). Configurational Factors in the Perception of Unfamiliar Faces. *Perception*, *23*(1), 65–74. https://doi.org/10.1068/p230065

Jared, D., & Seidenberg, M. S. (1990). Naming multisyllabic words. *Journal of Experimental Psychology. Human Perception and Performance*, *16*(1), 92–105.

Jenkins, R., White, D., Van Montfort, X., & Mike Burton, A. (2011). Variability in photos of the same face. *Cognition*, *121*(3), 313–323. https://doi.org/10.1016/j.cognition.2011.08.001

Johnson, R. L., & Eisler, M. E. (2012). The importance of the first and last letter in words during sentence reading. *Acta Psychologica*, *141*(3), 336–351. https://doi.org/10.1016/j.actpsy.2012.09.013

Kanwisher, N., & Barton, J. J. S. (2011). The Functional Architecture of the Face System: Integrating Evidence from fMRI and Patient Studies. *Oxford Handbook of Face Perception*. https://doi.org/10.1093/oxfordhb/9780199559053.013.0007

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The Fusiform Face Area: A Module in Human Extrastriate Cortex Specialized for Face Perception. *Journal of Neuroscience*, *17*(11), 4302–4311. https://doi.org/10.1523/JNEUROSCI.17-11-04302.1997

Kao, C.-H., Chen, D.-Y., & Chen, C.-C. (2010). The inversion effect in visual word form processing. *Cortex*, *46*(2), 217–230. https://doi.org/10.1016/j.cortex.2009.04.003

Kolers, P. A. (1968). The recognition of geometrically transformed text. *Perception & Psychophysics*, *3*(1), 57–64. https://doi.org/10.3758/BF03212713

Konar, Y., Bennett, P. J., & Sekuler, A. B. (2010). Holistic processing is not correlated with face-identification accuracy. *Psychological Science*, *21*(1), 38–43. https://doi.org/10.1177/0956797609356508

Koriat, A., & Norman, J. (1985). Reading rotated words. *Journal of Experimental Psychology. Human Perception and Performance*, *11*(4), 490–508.

Kramer, R. S. S., Young, A. W., & Burton, A. M. (2018). Understanding face familiarity. *Cognition*, *172*, 46–58. https://doi.org/10.1016/j.cognition.2017.12.005

Lavidor, M., & Ellis, A. W. (2001). Mixed-case effects in lateralized word recognition. *Brain and Cognition*, *46*(1), 192–195. https://doi.org/10.1016/S0278-2626(01)80063-4

Leff, A., Spitsyna, G., Plant, G. T., & Wise, R. J. S. (2006). Structural anatomy of pure and hemianopic alexia. *Journal of Neurology, Neurosurgery & Psychiatry*, *77*(9), 1004–1007. https://doi.org/10.1136/jnnp.2005.086983

Leff, A., & Starrfelt, R. (2014). *Alexia: Diagnosis, Treatment and Theory*. Springer-Verlag. https://www.springer.com/gp/book/9781447155287

Lefton, L. A., Nagle, R. J., Johnson, G., & Fisher, D. F. (1979). Eye Movement Dynamics of Good and Poor Readers: Then and Now. *Journal of Reading Behavior*, *11*(4), 319–328. https://doi.org/10.1080/10862967909547338

Legge, G. E., Ahn, S. J., Klitz, T. S., & Luebker, A. (1997). Psychophysics of reading—XVI. The visual span in normal and low vision. *Vision Research*, *37*(14), 1999–2010.

Levine, D. N., & Calvanio, R. (1989). Prosopagnosia: A defect in visual configural processing. *Brain and Cognition*, *10*(2), 149–170. https://doi.org/10.1016/0278-2626(89)90051-1

Longmore, C. A., Liu, C. H., & Young, A. W. (2008). Learning faces from photographs. *Journal of Experimental Psychology. Human Perception and Performance*, *34*(1), 77–100. https://doi.org/10.1037/0096-1523.34.1.77

Longmore, C. A., Liu, C. H., & Young, A. W. (2015). The importance of internal facial features in learning new faces. *Quarterly Journal of Experimental Psychology*, *68*(2), 249–260. https://doi.org/10.1080/17470218.2014.939666

Martelli, M., Majaj, N. J., & Pelli, D. G. (2005). Are faces processed like words? A diagnostic test for recognition by parts. *Journal of Vision*, *5*(1), 58–70. https://doi.org/10.1167/5.1.6

Martens, V. E. G., & de Jong, P. F. (2006). The effect of word length on lexical decision in dyslexic and normal reading children. *Brain and Language*, *98*(2), 140–149. https://doi.org/10.1016/j.bandl.2006.04.003

Maurer, D., Grand, R. L., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, *6*(6), 255–260. https://doi.org/10.1016/S1364-6613(02)01903-4

Maurer, U., Rossion, B., & McCandliss, B. D. (2008). Category specificity in early perception: Face and word N170 responses differ in both lateralization and habituation properties. *Frontiers in Human Neuroscience*, *2*. https://doi.org/10.3389/neuro.09.018.2008

McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, *7*(7), 293–299.

McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: I. An account of basic findings. *Psychological Review*, *88*(5), 375–407. https://doi.org/10.1037/0033-295X.88.5.375

McConkie, G. W., & Rayner, K. (1975). The span of the effective stimulus during a fixation in reading. *Perception & Psychophysics*, *17*(6), 578–586. https://doi.org/10.3758/BF03203972

McKone, E., & Yovel, G. (2009). Why does picture-plane inversion sometimes dissociate perception of features and spacing in faces, and sometimes not? Toward a new theory of holistic processing. *Psychonomic Bulletin & Review*, *16*(5), 778–797. https://doi.org/10.3758/PBR.16.5.778

Megreya, A. M., & Burton, A. M. (2006). Unfamiliar faces are not faces: Evidence from a matching task. *Memory & Cognition*, *34*(4), 865–876. https://doi.org/10.3758/BF03193433

Michel, C., Rossion, B., Han, J., Chung, C.-S., & Caldara, R. (2006). Holistic processing is finely tuned for faces of one's own race. *Psychological Science*, *17*(7), 608–615. https://doi.org/10.1111/j.1467-9280.2006.01752.x

Murphy, J., & Cook, R. (2017). Revealing the mechanisms of human face perception using dynamic apertures. *Cognition*, *169*, 25–35. https://doi.org/10.1016/j.cognition.2017.08.001

Nation, K., & Castles, A. (2017). Putting the learning into orthographic learning. *Theories of Reading Development*, 147–168. https://doi.org/10.1075/swll.15.09nat

Nazir, T. A., Ben-Boutayab, N., Decoppet, N., Deutsch, A., & Frost, R. (2004). Reading habits, perceptual learning, and recognition of printed words. *Brain and Language*, *88*(3), 294–311. https://doi.org/10.1016/S0093-934X(03)00168-8

Nestor, A., Behrmann, M., & Plaut, D. C. (2013). The neural basis of visual word form processing: A multivariate investigation. *Cerebral Cortex (New York, N.Y.: 1991)*, *23*(7), 1673–1684. https://doi.org/10.1093/cercor/bhs158

New, B., Ferrand, L., Pallier, C., & Brysbaert, M. (2006). Reexamining the word length effect in visual word recognition: New evidence from the English Lexicon Project. *Psychonomic Bulletin & Review*, *13*(1), 45–52. https://doi.org/10.3758/BF03193811

Nunn, J. A., Postma, P., & Pearson, R. (2001). Developmental prosopagnosia: Should it be taken at face value? *Neurocase*, *7*(1), 15–27. https://doi.org/10.1093/neucas/7.1.15

O'Regan, J. K., & Jacobs, A. M. (1992). Optimal viewing position effect in word recognition: A challenge to current theory. *Journal of Experimental*

Psychology: Human Perception and Performance, *18*(1), 185–197. https://doi.org/10.1037/0096-1523.18.1.185

Osborne, C. D., & Stevenage, D. S. V. (2008). Internal feature saliency as a marker of familiarity and configural processing. *Visual Cognition*, *16*(1), 23–43. https://doi.org/10.1080/13506280701238073

Pelli, D. G., Farell, B., & Moore, D. C. (2003). The remarkable inefficiency of word recognition. *Nature*, *423*(6941), 752. https://doi.org/10.1038/nature01516

Piepers, D., & Robbins, R. (2012). A Review and Clarification of the Terms "holistic," "configural," and "relational" in the Face Perception Literature. *Frontiers in Psychology*, *3*. https://doi.org/10.3389/fpsyg.2012.00559

Plaut, D. C., & Behrmann, M. (2011). Complementary neural representations for faces and words: A computational exploration. *Cognitive Neuropsychology*, *28*(3–4), 251–275. https://doi.org/10.1080/02643294.2011.609812

Pollatsek, A., Bolozky, S., Well, A. D., & Rayner, K. (1981). Asymmetries in the perceptual span for Israeli readers. *Brain and Language*, *14*(1), 174–180. https://doi.org/10.1016/0093-934X(81)90073-0

Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance imaging study. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *16*(16), 5205–5215.

Ramon, M., Busigny, T., & Rossion, B. (2010). Impaired holistic processing of unfamiliar individual faces in acquired prosopagnosia. *Neuropsychologia*, *48*(4), 933–944. https://doi.org/10.1016/j.neuropsychologia.2009.11.014

Ramon, M., & Rossion, B. (2012). Hemisphere-dependent holistic processing of familiar faces. *Brain and Cognition*, *78*(1), 7–13. https://doi.org/10.1016/j.bandc.2011.10.009

Rayner, K. (1985). The Role of Eye Movements in Learning to Read and Reading Disability. *Remedial and Special Education*, *6*(6), 53–60. https://doi.org/10.1177/074193258500600609

Rayner, K. (1986). Eye movements and the perceptual span in beginning and skilled readers. *Journal of Experimental Child Psychology*, *41*(2), 211–236. https://doi.org/10.1016/0022-0965(86)90037-8

Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, *124*(3), 372–422. https://doi.org/10.1037/0033-2909.124.3.372

Rayner, K., & Johnson, R. L. (2005). Letter-by-Letter Acquired Dyslexia Is Due to the Serial Encoding of Letters. *Psychological Science*, *16*(7), 530–534. https://doi.org/10.1111/j.0956-7976.2005.01570.x

Rayner, K., & McConkie, G. W. (1976). What guides a reader's eye movements? *Vision Research*, *16*(8), 829–837. https://doi.org/10.1016/0042-6989(76)90143-7

Reicher, G. M. (1969). Perceptual recognition as a function of meaningfulness of stimulus material. *Journal of Experimental Psychology*, *81*(2), 275–280. https://doi.org/10.1037/h0027768

Reichle, E. D., Rayner, K., & Pollatsek, A. (2003). The E-Z reader model of eye-movement control in reading: Comparisons to other models. *The Behavioral and Brain Sciences*, *26*(4), 445–476; discussion 477-526.

Rentschler, I., Treutwein, B., & Landis, T. (1994). Dissociation of local and global processing in visual agnosia. *Vision Research*, *34*(7), 963–971. https://doi.org/10.1016/0042-6989(94)90045-0

Rezlescu, C., Susilo, T., Wilmer, J. B., & Caramazza, A. (2017). The inversion, part-whole, and composite effects reflect distinct perceptual mechanisms with varied relationships to face recognition. *Journal of Experimental Psychology.*

Human Perception and Performance, *43*(12), 1961–1973. https://doi.org/10.1037/xhp0000400

Rhodes, G. (1993). Configural Coding, Expertise, and the Right Hemisphere Advantage for Face Recognition. *Brain and Cognition*, *22*(1), 19–41. https://doi.org/10.1006/brcg.1993.1022

Richler, J. J., Cheung, O. S., & Gauthier, I. (2011). Holistic Processing Predicts Face Recognition. *Psychological Science*, *22*(4), 464–471. https://doi.org/10.1177/0956797611401753

Richler, J. J., Tanaka, J. W., Brown, D. D., & Gauthier, I. (2008). Why does selective attention to parts fail in face processing? *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *34*(6), 1356–1368. https://doi.org/10.1037/a0013080

Richler, J., Palmeri, T. J., & Gauthier, I. (2012). Meanings, Mechanisms, and Measures of Holistic Processing. *Frontiers in Psychology*, *3*. https://doi.org/10.3389/fpsyg.2012.00553

Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, *103*(1), 34–79. https://doi.org/10.1016/j.cognition.2006.02.008

Roberts, D. J., Lambon Ralph, M. A., Kim, E., Tainturier, M.-J., Beeson, P. M., Rapcsak, S. Z., & Woollams, A. M. (2015). Processing deficits for familiar and novel faces in patients with left posterior fusiform lesions. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *72*, 79–96. https://doi.org/10.1016/j.cortex.2015.02.003

Robotham, R. J., & Starrfelt, R. (2017). Face and Word Recognition Can Be Selectively Affected by Brain Injury or Developmental Disorders. *Frontiers in Psychology*, *8*. https://doi.org/10.3389/fpsyg.2017.01547

Rodriguez, A. R., & Barton, J. J. S. (2015). The 20/20 patient who can't read. *Canadian Journal of Ophthalmology*, *50*(4), 257–264. https://doi.org/10.1016/j.jcjo.2015.05.013

Rossion, B., Dricot, L., Devolder, A., Bodart, J. M., Crommelinck, M., De Gelder, B., & Zoontjes, R. (2000). Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *12*(5), 793–802.

Royer, J., Willenbockel, V., Blais, C., Gosselin, F., Lafortune, S., Leclerc, J., & Fiset, D. (2017). The influence of natural contour and face size on the spatial frequency tuning for identifying upright and inverted faces. *Psychological Research*, *81*(1), 13–23. https://doi.org/10.1007/s00426-015-0740-3

Rubino, C., Corrow, S. L., Corrow, J. C., Duchaine, B., & Barton, J. J. S. (2016). Word and text processing in developmental prosopagnosia. *Cognitive Neuropsychology*, *33*(5–6), 315–328. https://doi.org/10.1080/02643294.2016.1204281

Rumelhart, D. E., & McClelland, J. L. (1982). An interactive activation model of context effects in letter perception: Part 2. The contextual enhancement effect and some tests and extensions of the model. *Psychological Review*, *89*(1), 60–94.

Schoonbaert, S., & Grainger, J. (2004). Letter position coding in printed word perception. *Cerebral Cortex - CEREB CORTEX*, *19*. https://doi.org/10.1080/01690960344000198

Sergent, J. (1983). Role of the input in visual hemispheric asymmetries. *Psychological Bulletin*, *93*(3), 481–512. https://doi.org/10.1037/0033-2909.93.3.481

Sigurdardottir, H. M., Fridriksdottir, L. E., Gudjonsdottir, S., & Kristjánsson, Á. (2018). Specific problems in visual cognition of dyslexic readers: Face discrimination deficits predict dyslexia over and above discrimination of scrambled faces and novel objects. *Cognition*, *175*, 157–168. https://doi.org/10.1016/j.cognition.2018.02.017

Sigurdardottir, H. M., Ívarsson, E., Kristinsdóttir, K., & Kristjánsson, Á. (2015). Impaired recognition of faces and objects in dyslexia: Evidence for ventral stream dysfunction? *Neuropsychology*, *29*(5), 739–750. https://doi.org/10.1037/neu0000188

Sinha, P., & Poggio, T. (1996). I think I know that face... *Nature*, *384*(6608), 404–404. https://doi.org/10.1038/384404a0

Starrfelt, R., & Behrmann, M. (2011). Number reading in pure alexia—A review. *Neuropsychologia*, *49*(9), 2283–2298. https://doi.org/10.1016/j.neuropsychologia.2011.04.028

Starrfelt, R., Klargaard, S. K., Petersen, A., & Gerlach, C. (2018). Reading in developmental prosopagnosia: Evidence for a dissociation between word and face recognition. *Neuropsychology*, *32*(2), 138–147. https://doi.org/10.1037/neu0000428

Starrfelt, R., Lindegaard, M., & Bundesen, C. (2015). Confusing confusability: On the problems of using psychophysical measures of letter confusability in neuropsychological research. *Cognitive Neuropsychology*, *32*(5), 314–320. https://doi.org/10.1080/02643294.2015.1061488

Starrfelt, R., & Shallice, T. (2014). What's in a name? The characterization of pure alexia. *Cognitive Neuropsychology*, *31*(5–6), 367–377. https://doi.org/10.1080/02643294.2014.924226

Susilo, T., Wright, V., Tree, J. J., & Duchaine, B. (2015). Acquired prosopagnosia without word recognition deficits. *Cognitive Neuropsychology*, *32*(6), 321–339. https://doi.org/10.1080/02643294.2015.1081882

Sussman, B., Reddigari, S., & Newman, S. (2018). The impact of inverted text on visual word processing: An fMRI study. *Brain and Cognition*, *123*. https://doi.org/10.1016/j.bandc.2018.02.004

Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, *46*(2), 225–245.

Tanaka, J. W., & Gordon, I. (2011). Features, Configuration, and Holistic Face Processing. *Oxford Handbook of Face Perception*. https://doi.org/10.1093/oxfordhb/9780199559053.013.0010

Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory & Cognition*, *25*(5), 583–592. https://doi.org/10.3758/BF03211301

Tanaka, J. W., & Simonyi, D. (2016). The "parts and wholes" of face recognition: A review of the literature. *Quarterly Journal of Experimental Psychology (2006)*, *69*(10), 1876–1889. https://doi.org/10.1080/17470218.2016.1146780

Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience*, *3*(8), 764–769. https://doi.org/10.1038/77666

Taylor, S. E. (1965). Eye Movements in Reading: Facts and Fallacies. *American Educational Research Journal*, *2*(4), 187–202. JSTOR. https://doi.org/10.2307/1161646

Vellutino, F. R., Fletcher, J. M., Snowling, M. J., & Scanlon, D. M. (2004). Specific reading disability (dyslexia): What have we learned in the past four decades? *Journal of Child Psychology and Psychiatry, and Allied Disciplines*, *45*(1), 2–40. https://doi.org/10.1046/j.0021-9630.2003.00305.x

Ventura, P., Delgado, J., Ferreira, M., Farinha-Fernandes, A., Guerreiro, J. C., Faustino, B., Leite, I., & Wong, A. C.-N. (2018). Hemispheric asymmetry in holistic processing of words. *Laterality: Asymmetries of Body, Brain and Cognition*, *0*(0), 1–15. https://doi.org/10.1080/1357650X.2018.1475483

Ventura, P., Domingues, M., Ferreira, I., Madeira, M., Martins, A., Neto, M. L., & Pereira, M. (2019). *Holistic Word Processing Is Involved in Fast Parallel Reading*.

Ventura, P., Fernandes, T., Cohen, L., Morais, J., Kolinsky, R., & Dehaene, S. (2013). Literacy acquisition reduces the influence of automatic holistic processing of faces and houses. *Neuroscience Letters*, *554*, 105–109. https://doi.org/10.1016/j.neulet.2013.08.068

Ventura, P., Fernandes, T., Leite, I., Almeida, V. B., Casqueiro, I., & Wong, A. C.-N. (2017). The Word Composite Effect Depends on Abstract Lexical Representations But Not Surface Features Like Case and Font. *Frontiers in Psychology*, *8*. https://doi.org/10.3389/fpsyg.2017.01036

Vinckier, F., Naccache, L., Papeix, C., Forget, J., Hahn-Barma, V., Dehaene, S., & Cohen, L. (2006). “What” and “Where” in Word Reading: Ventral Coding of Written Words Revealed by Parietal Atrophy. *Journal of Cognitive Neuroscience*, *18*(12), 1998–2012. https://doi.org/10.1162/jocn.2006.18.12.1998

Wang, R., Li, J., Fang, H., Tian, M., & Liu, J. (2012). Individual differences in holistic processing predict face recognition ability. *Psychological Science*, *23*(2), 169–177. https://doi.org/10.1177/0956797611420575

Weekes, B. S. (1997). Differential Effects of Number of Letters on Word and Nonword Naming Latency. *The Quarterly Journal of Experimental Psychology Section A*, *50*(2), 439–456. https://doi.org/10.1080/713755710

Wheeler, D. D. (1970). Processes in word recognition. *Cognitive Psychology*, *1*(1), 59–85. https://doi.org/10.1016/0010-0285(70)90005-8

Winston, J. S., Henson, R. n. a., Fine-Goulden, M. R., & Dolan, R. J. (2004). FMRI-Adaptation Reveals Dissociable Neural Representations of Identity and Expression in Face Perception. *Journal of Neurophysiology*, *92*(3), 1830–1839. https://doi.org/10.1152/jn.00155.2004

Wong, A. C.-N., Bukach, C. M., Hsiao, J., Greenspon, E., Ahern, E., Duan, Y., & Lui, K. F. H. (2012). Holistic processing as a hallmark of perceptual expertise for nonface categories including Chinese characters. *Journal of Vision*, *12*(13), 7. https://doi.org/10.1167/12.13.7

Wong, A. C.-N., Bukach, C. M., Yuen, C., Yang, L., Leung, S., & Greenspon, E. (2011). Holistic Processing of Words Modulated by Reading Experience. *PLoS ONE*, *6*(6). https://doi.org/10.1371/journal.pone.0020753

Wong, A. C.-N., Palmeri, T. J., & Gauthier, I. (2009). Conditions for facelike expertise with objects: Becoming a Ziggerin expert--but which type? *Psychological Science*, *20*(9), 1108–1117. https://doi.org/10.1111/j.1467-9280.2009.02430.x

Wong, A. C.-N., Palmeri, T. J., Rogers, B. P., Gore, J. C., & Gauthier, I. (2009). Beyond Shape: How You Learn about Objects Affects How They Are Represented in Visual Cortex. *PLOS ONE*, *4*(12), e8405. https://doi.org/10.1371/journal.pone.0008405

Wong, A. C.-N., Wong, Y. K., Lui, K. F. H., Ng, T. Y. K., & Ngan, V. S. H. (2019). Sensitivity to configural information and expertise in visual word recognition. *Journal of Experimental Psychology. Human Perception and Performance*, *45*(1), 82–99. https://doi.org/10.1037/xhp0000590

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*(1), 141–145. https://doi.org/10.1037/h0027474

Young, A. W., Hay, D. C., McWeeny, K. H., Flude, B. M., & Ellis, A. W. (1985). Matching familiar and unfamiliar faces on internal and external features. *Perception*, *14*(6), 737–746. https://doi.org/10.1068/p140737

Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational Information in Face Perception. *Perception*, *16*(6), 747–759. https://doi.org/10.1068/p160747

Yovel, G., Paller, K. A., & Levy, J. (2005). A whole face is more than the sum of its halves: Interactive processing in face perception. *Visual Cognition*, *12*(2), 337–352. https://doi.org/10.1080/13506280444000210

Zoccolotti, P., De Luca, M., Di Pace, E., Gasperini, F., Judica, A., & Spinelli, D. (2005). Word length effect in early reading and in developmental dyslexia. *Brain and Language*, *93*(3), 369–373. https://doi.org/10.1016/j.bandl.2004.10.010

Appendix A: Copies of publications included in the thesis

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An adaptation study of internal and external features in facial representations

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Face processing

ABSTRACT

Prior work suggests that internal features contribute more than external features to face processing. Whether this asymmetry is also true of the mental representations of faces is not known. We used face adaptation to determine whether the internal and external features of faces contribute differently to the representation of facial identity, whether this was affected by familiarity, and whether the results differed if the features were presented in isolation or as part of a whole face. In a first experiment, subjects performed a study of identity adaptation for famous and novel faces, in which the adapting stimuli were whole faces, the internal features alone, or the external features alone. In a second experiment, the same faces were used, but the adapting internal and external features were superimposed on whole faces that were ambiguous to identity. The first experiment showed larger aftereffects for unfamiliar faces, and greater aftereffects from internal than from external features, and the latter was true for both familiar and unfamiliar faces. When internal and external features were presented in a whole-face context in the second experiment, aftereffects from either internal or external features was less than that from the whole face, and did not differ from each other. While we reproduce the greater importance of internal features when presented in isolation, we find this is equally true for familiar and unfamiliar faces. The dominant influence of internal features is reduced when integrated into a whole-face context, suggesting another facet of expert face processing.

1. Introducton

Although a number of observations suggest that faces are processed holistically (Farah et al., 1998; Maurer, Le Grand, & Mondloch, 2002), there is also evidence that certain parts of the face may contribute more than others to face processing (Shepherd, Davies, & Ellis, 1981). For frontally viewed faces, one distinction is between the internal features such as the eyes, nose and mouth, and the external features, such as forehead, contour and hair. In particular, mechanisms for identifying faces are thought to analyse primarily the internal features of faces (Butler et al., 2010; Ellis, Shepherd, & Davies, 1979; Fletcher, Butavicius, & Lee, 2008; Stacey, Walker, & Underwood, 2005). A greater dependence of identification on internal features may be advantageous, in that these internal features are less likely to change through the aging process, alterations in hairstyle or facial hair, or occlusion by objects like hats (Young, 1984). In addition, the internal features likely receive disproportionate attention as they are central to social communication, and because of this may develop more prominence in mental representations of faces (Ellis, Shepherd, & Davies, 1979). Others have also argued that internal features may be more useful for creating viewpoint-invariance in facial recognition, an important property for natural encounters (Campbell, Walker, & Baroncohen, 1995).

Neuropsychological studies also support the importance of internal features for normal face identification. Patients with prosopagnosia, the inability to recognise faces, have particular difficulty processing the eyes and rely more on the mouth and external contour (Barton, 2008; Caldara et al., 2005). These patients sometimes report that they use the external features of a face such as hair to recognise others (Nunn, Postma, & Pearson, 2001). On the other hand, a patient with object agnosia but not prosopagnosia could recognise faces by their internal features but not by their external aspects (Moscovitch, Wincour, & Behrmann, 1997). While these types of observations support a proposed dominance of internal features in face recognition, they should not be taken as implying that external features do not contribute at all to face recognition. Even the earliest studies showed that, though less accurate, recognition of people from their

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external features is still possible (Ellis, Shepherd, & Davies, 1979), and changing hairstyle or disguising the external contours can impede face recognition (Chan & Ryan, 2012; Patterson & Baddeley, 1977). Furthermore, healthy observers perceive identical inner faces as different when they are surrounded by two different sets of external features (Sinha & Poggio, 1996), particularly if external features are distinctive (Andrews & Thompson, 2010). Functional imaging studies also show that the fusiform face area shows adaptation effects generated by external features (Axelrod & Yovel, 2010).

Another intriguing prior observation is that the relative importance of internal features over external ones may vary with the familiarity of the face. A number of reports have argued that there are differences in the way that familiar and unfamiliar faces are processed and perceived (Dubois et al., 1999; Megreya & Burton, 2006; Young et al., 1986), An early distinction that was drawn was between pictorial codes to represent an image, and a more abstract structural code that represents the complex three-dimensional shape of real-life objects such as faces (Bruce & Young, 1986). Structural codes are expected to be sparse for novel faces, particularly if there has been little experience with variations in viewpoint and expression. Others suggest that, as a result, this may lead to greater dependence of the processing of unfamiliar faces on pictorial codes, or 'low-level image descriptions', which do not support recognition very well when lighting direction or viewpoint are changed.

Most of the previous work on internal and external features has focused on perceptual processing of faces. However, the contribution of internal and external facial features has not yet been assessed using behavioural adaptation techniques. Such adaptation can be used to probe the neural representations of faces in the human visual system that are accessed during perceptual processing (Webster & MacLeod, 2011). Although classically used for low-level visual properties such as contrast, orientation, hue and motion, adaptation techniques have recently been applied to high-level visual representations, in particular for faces. This has been used to investigate the representations of many different facial attributes including ethnicity and gender (Oruç, Guo, & Barton, 2009; Webster et al., 2004), expression (Fox & Barton, 2007; Webster et al., 2004), attractiveness (Rhodes et al., 2003), age (Lai, Oruc, & Barton, 2012, 2013), and identity (Fox, Oruc, & Barton, 2008; Leopold et al., 2001). Even isolated aspects of faces such as silhouettes are sufficient to elicit strong aftereffects (Davidenko, Witthoft, & Winawer, 2008). Also, by using careful manipulations of stimuli, it has been possible to use adaptation to clarify the relative contributions of specific facial properties to these attributes, such as the role of texture versus shape in facial age and identity (Lai, Oruc, & Barton, 2013; O'Neil & Webster, 2011), the contributions of features versus their spatial relations (Pichler et al., 2012), and of shape versus reflectance (Jiang, Blanz, & O'Toole, 2006). Familiarity has also previously been shown to modulate both adaptation strength and transfer across viewpoints (Jiang, Blanz, & O'Toole, 2007).

In the first experiment of this study, we pursued a similar strategy to reveal the relative contributions of internal versus external features of the face to identity judgments. We first explored the hypothesis that internal features are also emphasised over external facial components in the neural representations of faces. If so, this should be reflected in greater aftereffects from internal features than from external features. Second, if this difference is particularly characteristic of representations of familiar faces, we should find that this asymmetry between internal and external aftereffects should be more for familiar than for unfamiliar faces. Hence the results should show an interaction between the facial component being adapted and the familiarity of the face.

In the second experiment, we explored a third issue, the role of the whole facial context in these asymmetries. There is a substantial body of data that faces are processed as a whole rather than simply a collection of features (Maurer, Le Grand, & Mondloch, 2002), and that this may be particularly true of the processing of familiar faces (Megreya & Burton, 2006). Thus the spatial relationships between features may be as important as the features themselves, and there is evidence that perception of one feature or portion of the face is influenced by other portions of the face (Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987), and that perception of spatial relations in one facial part are integrated with that in another (Barton, Zhao, & Keenan, 2003). Likewise, neuroimaging studies suggest that internal features and external features may be represented independently but also influence the processing of each other (Andrews & Thompson, 2010; Betts & Wilson, 2010) (Axelrod & Yovel, 2010). However, despite the current emphasis on holistic processing (Schiltz & Rossion, 2006), behavioural studies of the processing of internal and external features have typically presented these components as isolated facial fragments (Clutterbuck & Johnston, 2002, 2005; Ellis, Shepherd, & Davies, 1979; Young et al., 1985). In the concluding experiment, we examined whether the asymmetry in internal versus external aftereffects is found when these components are integrated in a whole-face representation more typical of natural facial encounters.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

14 participants took part in the Experiment 1 (10 females; mean age 28, range 21–42). All participants were right handed, had normal to corrected-to-normal vision. Only participants who could correctly identify the famous faces from an array of familiar and unfamiliar faces were used in this study. The institutional review boards of Vancouver General Hospital and the University of British Columbia approved the protocol, all subjects gave informed consent and the experiment was conducted in accordance with the principles of the Declaration of Helsinki.

2.1.2. Apparatus and stimuli

A HP Compaq 6730b Notebook with 15.4″ screen displayed stimuli at 1280×786 pixels resolution and a 60 Hz refresh rate. The screen was viewed from a distance of approximately 57 cm under consistent lighting conditions. The protocol was designed and conducted with SuperLab 4.0 (www.superlab.com).

Unfamiliar frontal face images of anonymous people were obtained from the HVEM-FIVE face database, while familiar faces were frontal face images of celebrities collected from a variety of internet sources (Fig. 1). Hair that fell below the jawline and any distinguishing marks were removed using Adobe Photoshop CS2 (www.adobe.com). The face images were first converted to grey scale and superimposed on a black background. They were then re-sized so that the two members of a pair were as close in size as possible, to optimise the morphing process below. This was done by first making each image the same height, then aligning the pupils of the two images on top of each other, and equating the inter-pupillary distance of the two images, with a final minor adjustment. This last adjustment resulted in slight variation in image height between the members of a pair, the largest difference being 0.4° (1.6% of image height).

2.1.2.1. Adaptors. The border between internal and external components of each face was demarcated by an oval. The size of this

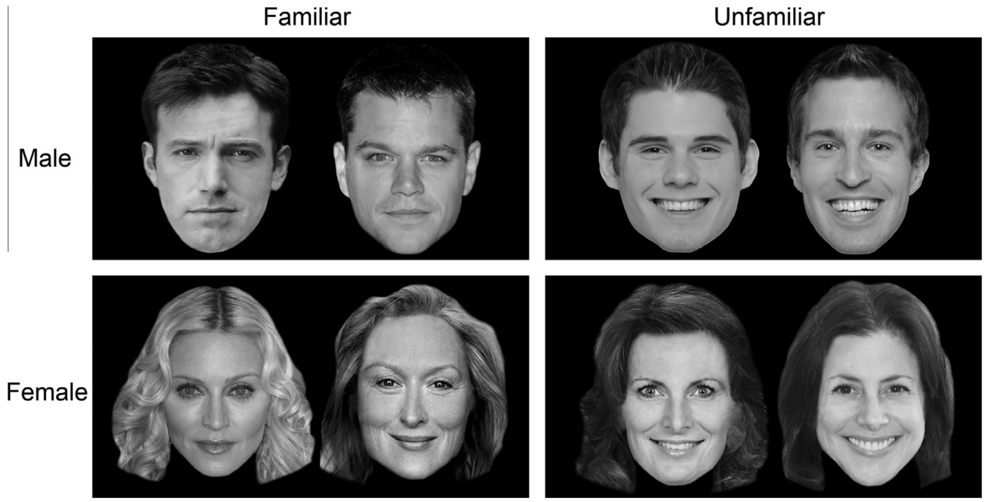

Fig. 1. The pairs of face identities used in both experiments. In both experiments, images were aligned using inter-pupillary distance and height.

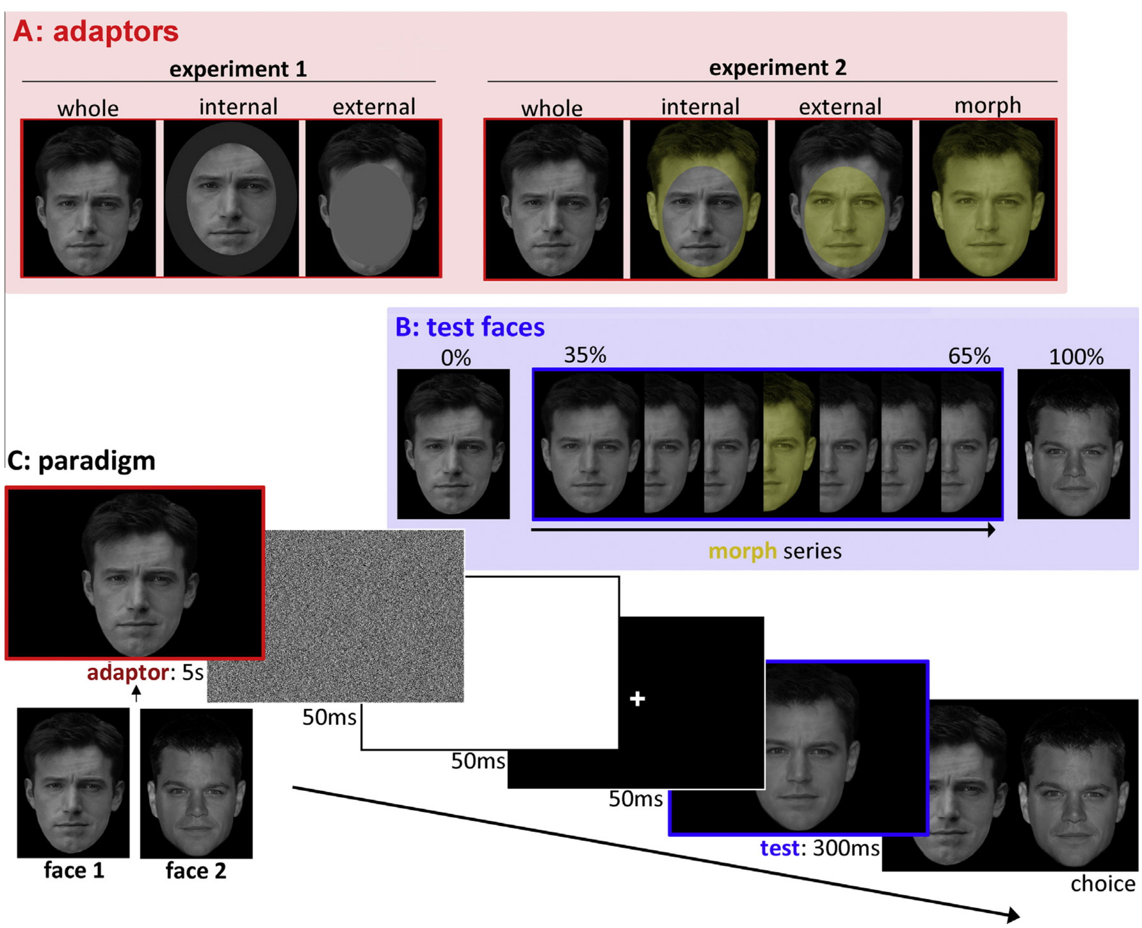

Fig. 2. Methods and example stimuli used in both experiments. (A) Adaptors. In Experiment 1, adaptors were either whole faces, internal components with a grey external oval or, the external component with a grey internal oval. In Experiment 2, adaptors were either a 100% whole face, 100% internal with a 50:50 morph external, or 100% external with a 50:50 morph internal, or a 50:50 morph whole face. Yellow shading is shown here only to highlight the morphed areas. (B) Test images were created using a morph series of a face pair, using increments of 2.5%. 13 morph images from between 35% and 65% were used. (C) Paradigm. An adaptor was shown for 5 s, followed by a Gaussian white noise mask, a blank screen and a fixation cross each for 50 ms. The test stimulus of a morphed face was then presented for 300 ms. A choice screen was used to capture which of the two faces the test stimuli most resembled with a key press. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

oval was the same for male and female faces, so that the ‘internal face’ occupied the same area for all. This oval was sized so that there were approximately equal numbers of pixels for the internal and external features of male faces. However, because women had more hair, it was inevitable that their external component would be larger than the internal component, as we wished to maintain

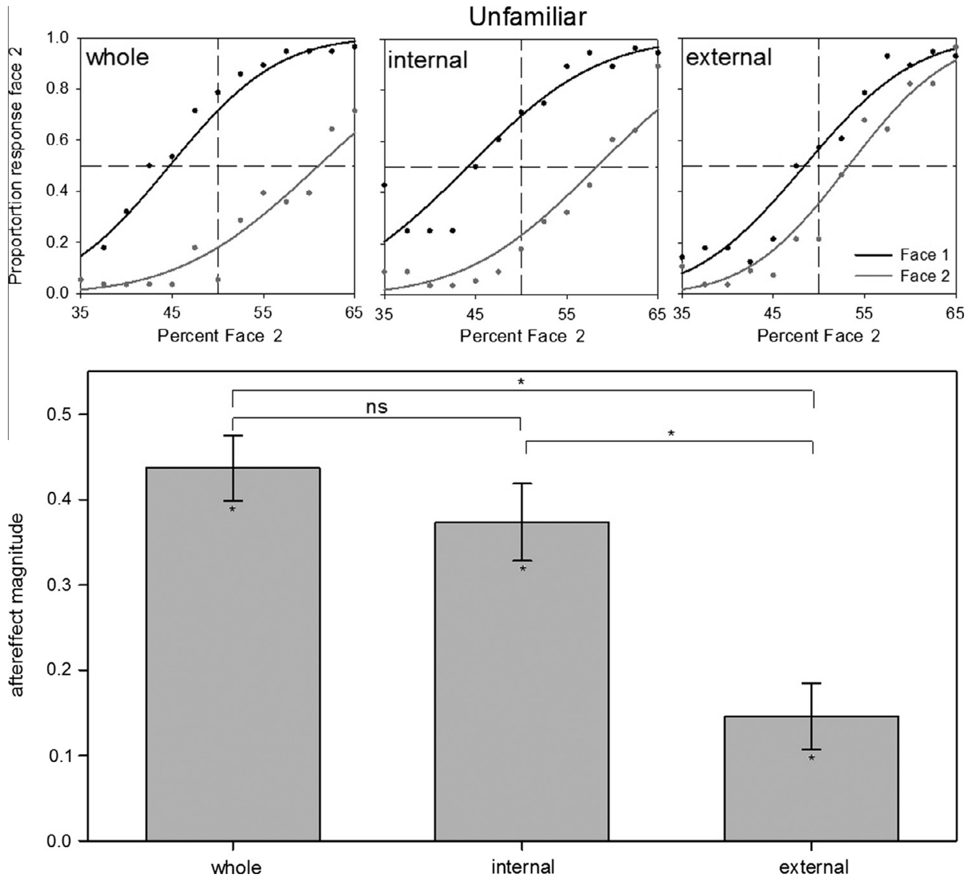

Fig. 3. Experiment 1 results: adaptation aftereffects for unfamiliar faces. Top row: Response functions for Face 1 and Face 2 collapsed across both pairs of faces. The percent of face 1 in the morph image test is plotted on the *x*-axis, with the proportion of Face 2 responses plotted on the *y*-axis. Bottom row: Aftereffect magnitudes. There were significant aftereffects from all conditions. However, the aftereffect from external features alone were reduced compared to those from the whole face or internal features. Aftereffects did not differ between the whole face and internal features alone. Error bars represent ±1 standard error. $^{*}P < 0.05$; ns = non-significant. Horizontal lines indicate significance of pair-wise contrasts.

the natural external face and hair contours in our images. We created three sets of adaptors (Fig. 2A). For whole-face adaptors, no alteration was made to these stimuli. For internal-face adaptors, the area of the face outside the oval was replaced by a homogenous grey shade which equalled the mean grey shade of the external features it was replacing. For external face adaptors, the area of the face inside the oval was replaced by a grey shade equal to the mean grey of the replaced internal features. All adaptors were approximately 700 pixels in height (17° visual angle) with variable width.

2.1.2.2. Test stimuli. Fantamorph 5 was used to create test stimuli by generating a series of morphs between a pair of two original whole faces in steps of 2.5%, (Fig. 2B). The 13 morph images from 35% face A/65% face B to 65% face A/35% face B were used. To reduce the contribution from low-level retinotopic aftereffects, test images varied in size from the adaptors, with a height of approximately 600 pixels in height (14.5° visual angle) and variable width.

2.1.2.3. Choice screen. These screens were created for each pair showing the two whole, un-morphed choice faces at approximately 500 pixels in height (12° visual angle) and variable width. For each face pair there were two choice screens, one with face A on the left and face B on the right, and one with face B on the left and face A on the right.

2.1.3. Protocol

Participants completed four blocks in a counterbalanced block design. Two blocks had familiar face pairs (one male block, one female block), and two blocks had unfamiliar face pairs (one male block, one female block). This 13 morph conditions resulting in a total of 78 trials, meant that there were two test images per block. For example, only Matt Damon and Ben Affleck were presented and tested together in one block. Each block was preceded by four practice trials to familiarise participants with the task. Participants took a rest break after each block.

Within a single trial, participants were first presented with an adapting image (whole, internal or external features) for 5 s, followed by a 50 ms Gaussian white noise mask, a 50 ms blank screen and a 50 ms fixation cross (Fig. 2C). The test stimulus was then presented for 400 ms before a forced-choice screen appeared in which subjects were asked to indicate with a keyboard response which of the two faces the test stimuli most resembled. Each of the 13 morph test images was presented once with each of the 3 types of adaptors with each of the 2 identities used to create the morphs, resulting in 78 trials per block. The entire experiment contained 4 blocks (one for each face pair) and thus 312 trials in total.

2.1.4. Statistical analysis

Within a face pair, each face was arbitrarily categorised as either ‘face 1’ or ‘face 2’, and the proportion of ‘face 2’ responses for all the 13 test images were calculated. For example, in the pairing of Ben Affleck and Matt Damon in the familiar male pair, the frequency of responses that ambiguous test images resembled Ben Affleck (face 2) was counted for the entire block. This was compared between trials in which the adapting image was of Matt Damon (face 1) and those in which the adapting image was of Ben Affleck (face 2). If the frequency of ‘face 2’ responses was greater after adapting to face 1 than to face 2, this would indicate a presence of a repulsive aftereffect. Hence the proportion of 'face 2' responses after adapting to face 1 minus the proportion of "face 2" responses after adapting to face 2 is the "magnitude of aftereffect". These magnitudes of aftereffects were our dependent variables, and were entered into one-sample *t*-tests to determine first if significant repulsive aftereffects were present for the different conditions. We then used a repeated-measures ANOVA with main factors of Familiarity (familiar, unfamiliar) and Adaptor type (whole, internal, external), and subjects as a random effect, with linear contrasts used to explore significant effects.

2.2. Results

Aftereffects were found from whole faces (Figs. 3 and 4) (unfamiliar: magnitude of aftereffect = 43.7%; $t(13) = 11.45$, $p < 0.001$; familiar: magnitude of aftereffect = 25.3%; $t(13) = 8.63$, $p < 0.001$), and from internal features (unfamiliar: magnitude of aftereffect = 37.4%; $t(13) = 8.26$, $p < 0.001$; familiar: magnitude of aftereffect = 14.6%; $t(13) = 3.70$, $p = 0.0015$). External features also generated aftereffects for unfamiliar faces (magnitude of aftereffect = 14.6%; $t(13) = 3.75$, $p = 0.001$), but not for familiar faces (magnitude of aftereffect = 3.0%; $t(13) = 0.96$, $p = 0.178$).

Repeated-measures ANOVA showed a main effect for both Familiarity ($F(1,13) = 19.39$, $P < 0.001$), with larger aftereffects for unfamiliar faces, and Adaptor Type ($F(2,26) = 39.80$, $P < 0.001$). However, there was no interaction between Familiarity and Adaptor Type ($F(2,26) = 2.27$, $P = 0.12$). Paired-sampled *t*-tests (Bonferroni corrected, critical $p = 0.014$) did not find a difference in the aftereffect between whole face adaptors and internal feature adaptors, for either unfamiliar ($t(13) = 1.82$, $p = 0.09$) or familiar ($t(13) = 2.41$, $p = 0.031$) faces. However, the aftereffect generated by external features was smaller than the aftereffect from whole faces (unfamiliar: $t(13) = 7.59$, $P < 0.001$; familiar: $t(13) = 5.49$, $P < 0.001$) or that from internal features (unfamiliar ($t(13) = 5.68$, $P < 0.001$; familiar: $t(13) = 2.85$, $P = 0.014$).

2.2.1. Comment

These results show that, when presented in isolation, the internal features generate face aftereffects similar to those from whole faces, whereas the external features generate weaker adaptation of facial representations. This is despite the fact that for the female faces, the external features accounted for a larger fraction of the pixels in the facial image than the internal features. Of note, while aftereffects were stronger in general for familiar faces, the asymmetry between internal and external effects did not differ between familiar and unfamiliar faces, suggesting that the representations of these particular familiar and unfamiliar faces did not differ much in their emphasis on internal over external features.

Does this internal/external asymmetry persist if the parts are seen in the context of a whole face? On the one hand, while subjects have only the internal or the external features to which to

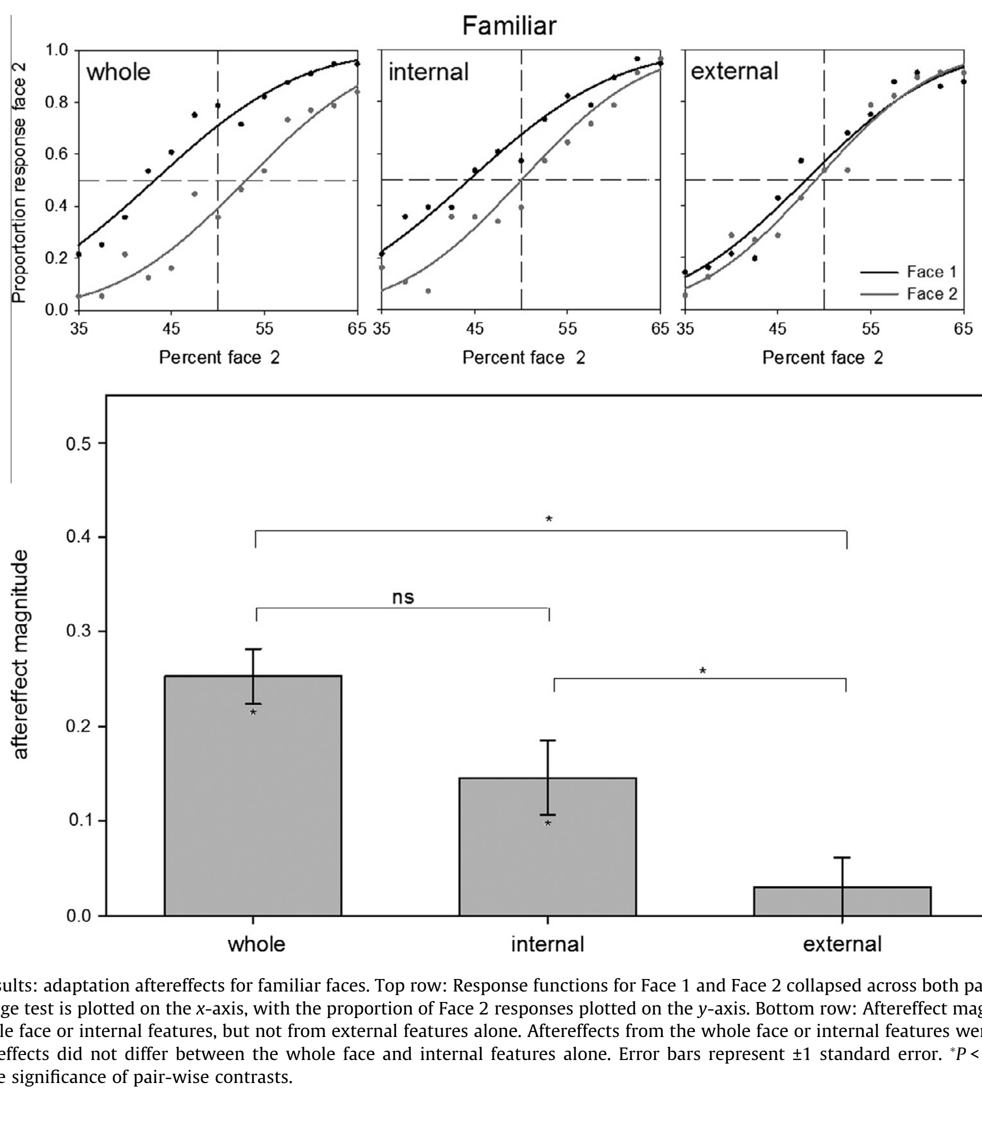

Fig. 4. Experiment 1 results: adaptation aftereffects for familiar faces. Top row: Response functions for Face 1 and Face 2 collapsed across both pairs of faces. The percent of face 1 in the morph image test is plotted on the *x*-axis, with the proportion of Face 2 responses plotted on the *y*-axis. Bottom row: Aftereffect magnitudes. Aftereffects were produced from the whole face or internal features, but not from external features alone. Aftereffects from the whole face or internal features were greater than those from external features. Aftereffects did not differ between the whole face and internal features alone. Error bars represent ±1 standard error. *$P < 0.05$; ns = non-significant. Horizontal lines indicate significance of pair-wise contrasts.

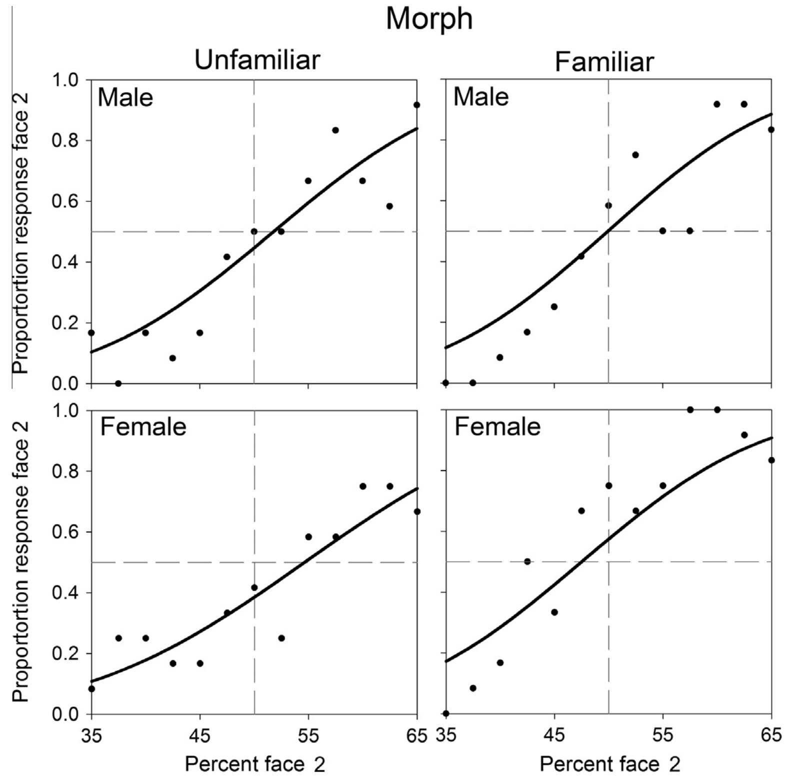

Fig. 5. Responses using the 50:50 morph as an adaptor stimuli in Experiment 2, shown for each of the four pairs of faces (two familiar, two unfamiliar). The percent of face 2 in the morph image test is plotted on the *x*-axis, with the proportion of Face 2 responses plotted on the *y*-axis. The point of equivalence (where proportion of Face 2 responses equals the proportion of Face 1 responses = 0.50, indicated by where the solid curve intersects the horizontal dashed line) is near where the percent of face 1 and face 2 in the test morph image are equal, indicated by the vertical dashed line.

attend when these are presented in isolation, there is evidence that they attend mainly to internal features when viewing whole faces (Barton et al., 2006; Stacey, Walker, & Underwood, 2005). Thus, if anything, the effects of attention may exacerbate the internal/external asymmetry when whole faces are used as adapting stimuli. However, an alternate view is that holistic processing, by treating the face as an indivisible whole, may mitigate against regional disparities, so that all parts contribute approximately equally to the final facial gestalt. To explore this issue, we repeated the experiment but using adaptors that presented the internal features and external features superimposed on a neutral morph image that was a whole face. This neutral image contained 50% of face 1 and 50% of face 2. As the magnitude of aftereffect is calculated by deducting the number of responses following adaptation to face 2 from face 1, the contribution of the components from the neutral image do not impact the magnitude of aftereffect. Since both face 1 and face 2 have the same neutral components, any influence they have would cancel out in the subtraction used to calculate the magnitude of aftereffect.

3. Experiment 2

3.1. Methods

3.1.1. Subjects

12 different participants took part in Experiment 2 (8 females; mean age 25, range 20–51), all right-handed and with normal corrected vision. All subjects were able to identify the famous faces from an array of familiar and unfamiliar faces, and all were able to name the famous faces.

3.1.2. Apparatus and stimuli

The same apparati were used as in Experiment 1. We also used the same faces to create the adaptors and test stimuli. Morphed test images were identical to those of Experiment 1, as were the choice screens. Where Experiment 2 differed from Experiment 1 was in the adapting stimuli. While the whole-face adaptors were identical to those of Experiment 1, the internal-feature and external-feature adaptors were different. The same grey ovals were used to divide internal and external features. For the internal-feature condition, instead of a uniform grey colour replacing the external features, we substituted the external features from the 50:50 morph image from the series of test morph images (Fig. 2A). For the external-feature condition the internal features were likewise replaced by the 50:50 morph image's internal features. We also added a fourth condition, where both the external and internal features were from a 50:50 morph image, to allow us to measure the amount of adaptation generated by this ambiguous image.

3.1.3. Protocol

The sequence of events in single trials was identical to that of Experiment 1. Again, there were four blocks, one each for a male familiar, female familiar, male unfamiliar and female unfamiliar pair of faces. Each block had seven different adaptor conditions instead of six (two each for whole-face, internal-feature, and external feature), because of the addition of the 50:50 morph as an adaptor. As a result, Experiment 2 contained a total of 364 trials.

3.2. Results

First the results show that after adapting to the 50:50 morph test image, in each of the four blocks, subjects were not significantly more likely to respond 'face2' than 'face1' over the entire block (Fig. 5). The mean frequency of 'face 2' responses for the unfamiliar male pair were 0.44, s.d. 0.19 ($t(11) = -1.17$, $p = 0.27$), for the unfamiliar female pair 0.40, s.d. 0.19 ($t(11) = 1.71$, $p = 0.12$), for the familiar male pair 0.46, s.d. 0.12 ($t(11) = 1.25$, $p = 0.24$) and for the familiar female pair 0.59, s.d. 0.17 ($t(11) = 1.85$, $p = 0.09$). Hence, it is unlikely that the components of these hybrid faces derived from the 50:50 morph bias perception significantly. However, we also note that any slight skewing of the responses with adaptation to the 50:50 morph in favour of one face over another would not influence the aftereffect magnitudes measured from internal or external features in this experiment. In the example of internal features, aftereffect magnitude is measured as the difference between adapting to the image with internal features of face 1 and adapting to the image with internal features of face 2. Since both of these adapting images have the same external features of the 50:50 morph, any effect of the latter is cancelled by the subtraction.

For unfamiliar faces (Fig. 6), aftereffects were obtained from the whole face (magnitude of aftereffect = 34.3%; $t(11) = 6.68$, $p < 0.001$), the internal features (magnitude of aftereffect = 11.9% ($t(11) = 2.36$, $p = 0.019$) and external features (magnitude of aftereffect = 10.6%; $t(11) = 2.02$, $p = 0.034$). For familiar faces (Fig. 7), aftereffects were also obtained from the whole face (magnitude of aftereffect = 34.6%; $t(11) = 8.44$, $p < 0.001$), internal features (magnitude of aftereffect = 15.7%; $t(11) = 5.74$, $p < 0.001$) and external features (magnitude of aftereffect = 15.4%; $t(11) = 5.93$, $p < 0.001$).

Repeated-measures ANOVA showed a main effect for Adaptor type ($F(2,22) = 20.71$, $P < 0.001$), but not for Familiarity ($F(1,11) = 0.48$, $P = 0.50$), and no interaction between Familiarity and Adaptor type ($F(2,22) = 0.35$, $P = 0.71$). Paired-sampled t-tests (Bonferroni corrected, critical $p = 0.014$) found larger aftereffects from whole faces than from internal features for both familiar ($t(11) = 4.60$, $p = 0.001$) and unfamiliar faces ($t(11) = 3.87$, $p = 0.003$). Likewise, aftereffects from whole faces were greater than those from external features, again for both familiar ($t(11) = 4.46$, $p = 0.001$) and unfamiliar faces ($t(11) = 3.77$, $p = 0.003$). There was no difference in the aftereffect from internal versus external features (familiar: $t(11) = 0.11$, $P = 0.92$; unfamiliar: $t(11) = 0.32$, $P = 0.75$).

The lack of an effect of familiarity is of interest. One possibility is that subjects became familiar with the anonymous faces through repeated presentation of their images during the course of the experiment. However, this seems unlikely to explain the lack of familiarity effect, as we did find such effects in experiment 1, which followed a very similar protocol. Nevertheless we also conducted a split-half analysis, to see if the magnitude of aftereffects changed for familiar and unfamiliar faces as the experiment progressed. We found no difference in aftereffect magnitude between the first and second halves of the experiment for either the whole face (familiar: $t(22) = 0.11$, $p = 0.91$; unfamiliar: $t(22) = 0.79$, $p = 0.44$), isolated internal features (familiar: $t(22) = 0.58$,

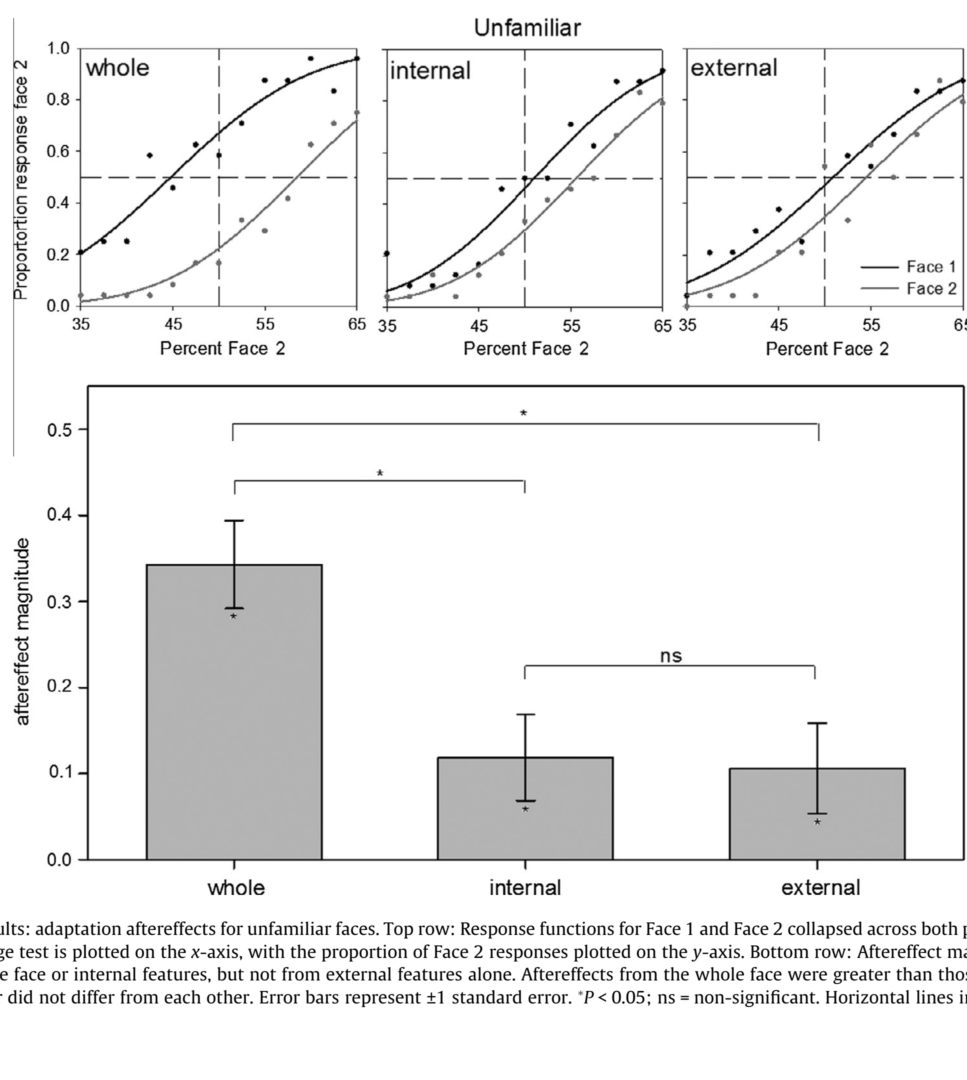

Fig. 6. Experiment 2 results: adaptation aftereffects for unfamiliar faces. Top row: Response functions for Face 1 and Face 2 collapsed across both pairs of faces. The percent of face 1 in the morph image test is plotted on the x-axis, with the proportion of Face 2 responses plotted on the y-axis. Bottom row: Aftereffect magnitudes. Aftereffects were produced from the whole face or internal features, but not from external features alone. Aftereffects from the whole face were greater than those from internal or external features alone: the latter did not differ from each other. Error bars represent ±1 standard error. $^*P < 0.05$; ns = non-significant. Horizontal lines indicate significance of pairwise contrasts.

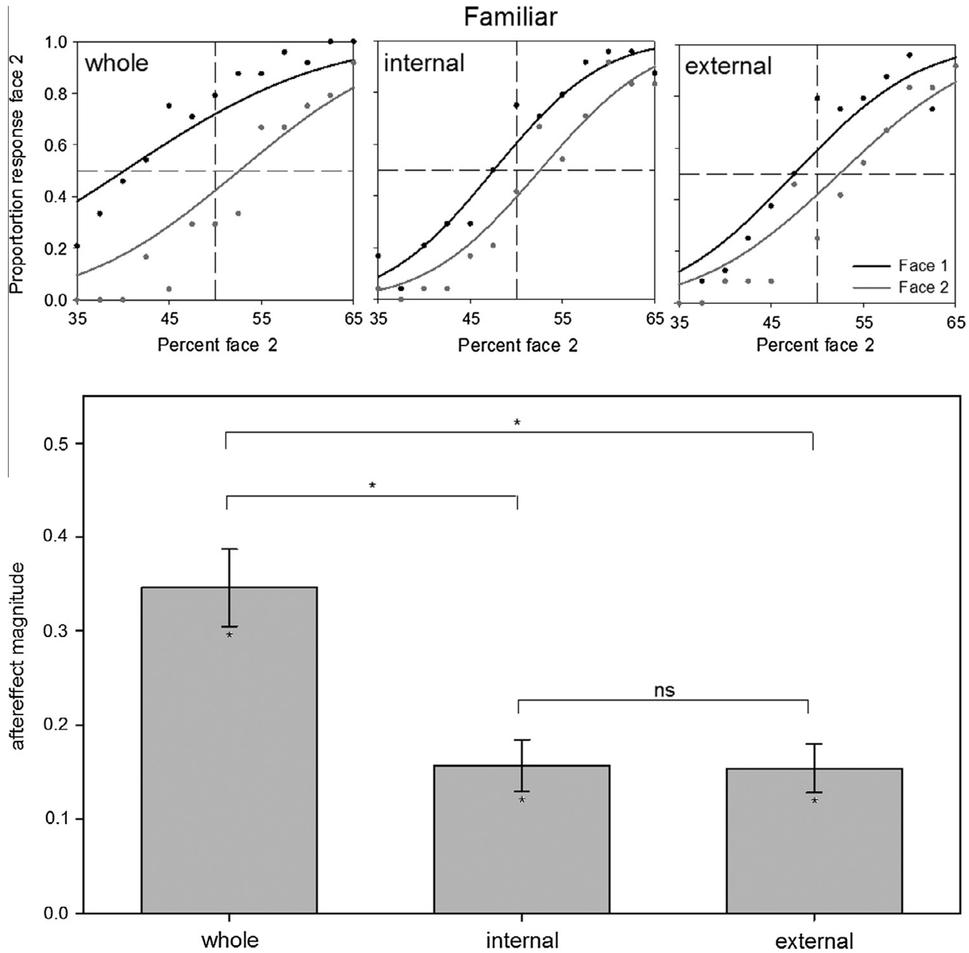

Fig. 7. Experiment 2 results: adaptation aftereffects for familiar faces. Top row: Response functions for Face 1 and Face 2 collapsed across both pairs of faces. The percent of face 1 in the morph image test is plotted on the *x*-axis, with the proportion of Face 2 responses plotted on the *y*-axis. Bottom row: Aftereffect magnitudes. Aftereffects were produced in all three conditions. Aftereffects from the whole face were greater than those from internal or external features alone: the latter did not differ from each other. Error bars represent ±1 standard error. $^{*}P < 0.05$; ns = non-significant. Horizontal lines indicate significance of pair-wise contrasts.

$p = 0.57$; unfamiliar: $t(22) = 0.66$, $p = 0.52$), or isolated external features (familiar: $t(22) = 0.99$, $p = 0.33$; unfamiliar: $t(22) = 0.28$, $p = 0.79$).

4. Low level effects

In order to ensure that the low-level image properties were not driving the relative aftereffect levels, luminance was measured for all RGB values individually using a photometer. These values were then best-fitted with an exponential curve, which was used to interpolate all RGB values within each image. Average luminance, contrast and energy were examined using MATLAB 2011a (www.mathworks.com) (see Supplementary Fig. 1). A $2 \times 2 \times 3$ ANOVA (Experiment, Familiarity, Condition) for *luminance* showed no significant effects for Experiment ($F(1,36) = 2.43$, $P = 0.13$), Familiarity ($F(1,36) = 0.60$, $P = 0.44$), or Condition ($F(2,36) = 0.94$, $P = 0.91$). For *contrast*, there were no significant effects for Experiment ($F(1,36) = 0.08$, $P = 0.78$) or Condition ($F(1,36) = 2.55$, $P = 0.09$), though the contrast for unfamiliar faces were significantly greater than familiar faces ($F(1,36) = 7.80$, $P = 0.01$). Crucially, however, there were no significant interactions between Familiarity × Experiment ($F(1,36) = 0.03$, $P = 0.87$) or Familiarity × Condition ($F(2,36) = 1.27$, $P = 0.29$), suggesting that this difference was similar for both experiments and all conditions. Finally, *energy* showed a similar pattern, with no significant effects for Experiment ($F(1,36) = 0.08$, $P = 0.78$) or Condition ($F(1,36) = 1.95$, $P = 0.16$), but a greater contrast for unfamiliar as compared to familiar faces ($F(1,36) = 5.51$, $P = 0.03$). Again, there were no significant interactions between Familiarity × Experiment ($F(1,36) = 0.07$, $P = 0.79$) or Familiarity × Condition ($F(2,36) = 1.32$, $P = 0.28$). In sum, this analysis showed that, although there were differences in the contrast and energy levels of the familiar and unfamiliar face images, these low-level image properties could not explain the patterns of aftereffect observed.

5. Discussion

Our results show that when presented in isolation, the internal features of faces generate larger aftereffects than do the external features. The whole face condition produced aftereffects roughly that of the sum of the internal and external parts, in both experiments. This may indicate that the internal and external features combine in whole-face processing in an additive or linear manner. Furthermore, even though aftereffects were larger in general for unfamiliar faces in Experiment 1 (but not in Experiment 2, for reasons that are not certain), the asymmetry between internal and external aftereffects was equally true for both familiar and unfamiliar faces. Hence an emphasis on internal features is present for both newly acquired facial representations as well as more longstanding representations of familiar faces. However, this asymmetry is not found when internal and external features are presented in a whole-face context, and again this is true for both unfamiliar and familiar faces. This suggests that whole-face processing tends to reduce regional disparities in the contribution of local facial parts, perhaps indicating another facet of face-expert processing mechanisms.

5.1. Internal versus external features

Increasing dependence on internal features may be one of the markers of acquisition of perceptual expertise with faces, with studies suggesting an emphasis on internal features becoming apparent at around aged 9 years (Campbell, Walker, & Baroncohen, 1995; Want et al., 2003), and in adults, the degree of attention and fixation on internal features is correlated with the ability to recognise faces (Fletcher, Butavicius, & Lee, 2008). Evidence for superiority of internal over external features comes from a variety of approaches. Identification and short-term memory for known faces was superior from viewing isolated internal features than external ones (Ellis, Shepherd, & Davies, 1979), and subjects place more fixations on internal than external features during memory and matching tasks (Stacey, Walker, & Underwood, 2005). On the other hand, some of these same studies report that internal and external features have equivalent effects when unfamiliar faces are used (Ellis, Shepherd, & Davies, 1979), with others even reporting a superiority of external features (Haig, 1986; Nachson, Moscovitch, & Umilta, 1995). One study even reported better matching for external features regardless of familiarity (Davidenko, Witthoft, & Winawer, 2008). Another report found that internal features dominated recognition when high spatial frequencies were present, as when viewing near faces, but external features were more useful when only low spatial frequencies were available, as when viewing from afar (Jarudi & Sinha, 2003). The results of our Experiment 1, also using isolated features, are also consistent with an emphasis on internal features for the mental representation of faces. As the adapting images are larger than the test, this creates unequal overlap between the internal and external components of these images, with less overlap in the external. It could be argued that the increased aftereffects for the external components in Experiment 2 may be partly retinotopic and driven by the low-level image properties contained within this larger overlapping area. Even a weak bias in sampling or spatial selectivity could potentially drive the effect. However, given the small scale of retinotopic receptive fields and size of the features in the internal face, significant overlap of features between adaptor and probe is unlikely.

5.2. Familiarity effects

It has long been speculated that familiar and unfamiliar faces may differ in not only the strength but also the nature of their representations, with the structural encoding of unfamiliar faces being heavily dependent upon the nature of initial exposure, and recognition depending on the pictorial code, or ‘low-level image descriptions’ with a predicted vulnerability of such recognition to changes in lighting and viewpoint (Bruce & Young, 1986) (Hancock, Bruce, & Burton, 2000). In support, one behavioural study demonstrated that familiar faces can generate stronger aftereffects and enhanced transferability across viewpoint changes (Jiang, Blanz, & O'Toole, 2007), while an fMRI-adaptation study showed adaptation to identity is viewpoint-invariant for familiar faces but not for unfamiliar faces (Jiang, Blanz, & O'Toole, 2006). Others show that performance on matching of upright unfamiliar faces is correlated with performance on matching inverted familiar faces, but not with matching upright familiar faces (Megreya & Burton, 2006) – a hall-marker of expert face-processing mechanisms (Farah, Tanaka, & Drain, 1995; Rossion, 2008; Valentine, 1988) suggesting a qualitative difference in processing of upright familiar and unfamiliar faces.

On the other hand, there is also evidence that similar mechanisms may operate on both familiar and unfamiliar faces. In the composite face effect, changes in one half of a face affect discrimination or recognition of the second half, indicating holistic processing, or integration of information across the whole face: this effect is similar for both familiar and unfamiliar faces (Hole, 1994; Young, Hellawell, & Hay, 1987). Likewise, the effects of blurring, inversion and scrambling on recognition are no different for familiar versus unfamiliar faces, suggesting that they share the same processing strategies and dependencies on featural and configural processing (Burness, Morris, & Bruce, 1994). Finally, somewhat problematic for the proposal that unfamiliar faces depend more on pictorial coding while familiar faces do not are observations from three adaptation studies. Two fMRI studies contrasted adaptation when same or different images were used, with one of these studies finding image-invariance for both familiar and unfamiliar faces in the fusiform face and occipital face areas (Davies-Thompson, Newling, & Andrews, 2013), while another found image-dependent representation for both familiar and unfamiliar faces (Davies-Thompson, Gouws, & Andrews, 2009). Second, a behavioural study found that identity adaptation was completely invariant across changes in facial expression regardless of the degree of familiarity (Fox, Oruc, & Barton, 2008). Although this previous study demonstrated that difference in any expression is unlikely to impact the magnitude of the identity aftereffects elicited in our current study, it should be noted that the unfamiliar face set show broader smiles.

5.3. Interactions between familiarity and internal/external feature processing

Studies on internal and external feature processing have contributed significantly to the familiarity debate. Early reports on internal/external contrasts observed that the superiority of internal features in recognition and short-term memory was found only for familiar faces, with equivalent performance for internal versus external features when unfamiliar faces were shown (Ellis, Shepherd, & Davies, 1979). In another study, when subjects performed a matching task of different images of the same person, they showed similar reaction times with internal or external features for familiar faces, but were slower using internal features than external features for unfamiliar faces (Young et al., 1985). Similar results were obtained when images differed in expression or view, but there was not effect of familiarity if identical images were used in the matching task, suggesting that the enhanced use of internal features by familiar faces was found when stimulus conditions promoted structural rather than pictorial codes. This led Bruce and Young (Bruce & Young, 1986) to conclude that the structural code that was dominant for familiar faces would “emphasize the more informative and less changeable (cf. hairstyles) regions of the face.” (p. 308).

More recent studies have reproduced the advantage in reaction time for familiar faces over unfamiliar ones in matching internal but not external features, and even showed a gradient for the speed of matching internal features between unfamiliar, moderately familiar and highly familiar faces (Clutterbuck & Johnston, 2002, 2005). Further support has come from studies of subjects as they became familiar with a set of new faces: matching internal features but not external ones improved reaction time (Clutterbuck & Johnston, 2005), and accuracy (Bonner, Burton, & Bruce, 2003). A functional imaging study found greater adaptation in the fusiform face area from internal features of familiar faces, but similar effects from internal and external features of unfamiliar faces (Andrews et al., 2010). Data from studies of fixations have been less consistent. One study found that subjects made more fixations on internal features: this was slightly more so for familiar faces (95% versus 90% for unfamiliar faces) when subjects matched faces across viewpoint changes, but there was no familiarity effect during recognition and memory tasks (Stacey, Walker, & Underwood, 2005). Another report found the opposite: during a memory task, subjects placed a greater proportion of fixations on internal features when viewing unfamiliar faces than with familiar ones (Althoff & Cohen, 1999). The authors speculated that this might reflect more efficient processing of internal features with familiar faces, so that subjects needed to sample this region less than they did with unfamiliar faces.

Our study produced consistent results between Experiments 1 and 2, in that the familiarity of the face did not influence the pattern of results for internal versus external adaptation. There were larger aftereffects from internal features viewed in isolation, but similar aftereffects from internal and external features when these were incorporated into a whole face. This is consistent with similar representations being accessed and created for familiar and unfamiliar faces, and complements the evidence above that similar types of processing are *eventually* involved in the perception of familiar and unfamiliar faces (Burness, Morris, & Bruce, 1994; Hole, 1994; Young, Hellawell, & Hay, 1987). The discrepancy between this and prior studies that did show a dependence of the balance of internal versus external feature processing on familiarity may stem from the fact that the unfamiliar faces in those prior studies were seen only once (Clutterbuck & Johnston, 2002, 2005; Ellis, Shepherd, & Davies, 1979; Young et al., 1985): hence they are not only unfamiliar (in the sense of lacking semantic or episodic memories from previous contact) but also novel or unexposed, and therefore lacking in any prior stimulus representation. Indeed, one previous study found short exposure to the same image of faces may be adequate to increase the emphasis on internal features (Clutterbuck & Johnston, 2005). Hence, while entirely novel faces may show reduced coding of internal features, unfamiliar faces quickly acquire the internal emphasis seen with familiar faces, consistent with rapid convergence of both unfamiliar and familiar faces on the utilisation of face-expert mechanisms, with similar composite face effects (Hole, 1994; Young, Hellawell, & Hay, 1987), inversion effects (Burness, Morris, & Bruce, 1994), image-invariance (Bruce, 1994), and expression-invariance (Fox, Oruc, & Barton, 2008).

5.4. Effects from whole faces versus isolated features

There have been few reports contrasting the effects of the internal and external features presented in isolation with their effects when seen as part of a whole face. In a functional imaging study, while familiar faces showed more adaptation in the fusiform face from internal than from external features, equivalent effects from these parts were found when they were viewed as part of a whole face (Andrews et al., 2010). Our results provide a behavioural parallel to this neuroimaging observation. Both of these findings indicate that the perceptual context of the features is important in determining the pattern of aftereffects seen.

It is unlikely that the change in effects between isolated and whole-face presentations is attributable to the effects of focal attention. When external features are presented in isolation, they are not subject to competition for such attention; however, when present in a full face, the tendency for subjects to focus on the internal features (Stacey, Walker, & Underwood, 2005) should reduce the attention given to external features. If anything, this should enhance rather than reduce the imbalance in aftereffects favouring internal over external features. Rather, the results suggest that a more even distribution of either attention or perceptual processing takes place when parts are viewed as integrated in a whole face. This suggests that one consequence of whole-face processing is a reduction in the effects of regional saliency documented by others (Shepherd, Davies, & Ellis, 1981). Thus, in addition to confirming a relative importance of internal over external features in the neural or mental representations of faces, our study and the prior neuroimaging report (Andrews et al., 2010) also provide evidence of another facet of whole-face processing.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2014.04.002.

References

Althoff, R., & Cohen, N. (1999). Eye-movement-based memory effect: A reprocessing effect in face perception. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 25*(4), 997–1010.

Andrews, T. J., Davies-Thompson, J., Kingstone, A., & Young, A. W. (2010). Internal and external features of the face are represented holistically in face-selective regions of visual cortex. *The Journal of Neuroscience, 30*(9), 3544–3552.

Andrews, T. J., & Thompson, P. (2010). Face-to-face coalition. *i-Perception, 1*(1), 28–30.

Axelrod, V., & Yovel, G. (2010). External facial features modify the representation of internal facial features in the fusiform face area. *NeuroImage, 52*(2), 720–725.

Barton, J. (2008). Structure and function in acquired prosospagnosia: Lessons from a series of ten patients with brain damage. *Journal of Neuropsychology, 2*, 197–225.

Barton, J. J., Radcliffe, N., Cherkasova, M. V., Edelman, J., & Intriligator, J. M. (2006). Information processing during face recognition: The effects of familiarity, inversion, and morphing on scanning fixations. *Perception, 35*(8), 1089–1105.

Barton, J., Zhao, J., & Keenan, J. (2003). Perception of global facial geometry in the inversion effect and prosopagnosia. *Neuropsychologia, 41*, 1703–1711.

Betts, L. R., & Wilson, H. R. (2010). Heterogeneous structure in face-selective human occipito-temporal cortex. *Journal of Cognitive Neuroscience, 22*(10), 2276–2288.

Bonner, L., Burton, A. M., & Bruce, V. (2003). Getting to know you: How we learn new faces. *Visual Cognition, 10*(5), 527–536.

Bruce, V. (1994). Stability from variation – The case of face recognition. *Quarterly Journal of Experimental Psychology Section A—Human Experimental Psychology, 47*(1), 5–28.

Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology, 77*, 305–327.

Burness, G. P., Morris, R. D., & Bruce, J. P. (1994). Seasonal and annual variation in brood attendance, prey type delivered to chicks, and foraging patterns of male Common Terns (Sterna-Hirundo). *Canadian Journal of Zoology-Revue Canadienne De Zoologie, 72*(7), 1243–1251.

Butler, S., Blais, C., Gosselin, F., Bub, D., & Fiset, D. (2010). Recognizing famous people. *Attention Perception & Psychophysics, 72*(6), 1444–1449.

Caldara, R., Schyns, P., Mayer, E., Smith, M. L., Gosselin, F., & Rossion, B. (2005). Does prosopagnosia take the eyes out of face representations? Evidence for a defect in representing diagnostic facial information following brain damage. *Journal of Cognitive Neuroscience, 17*(10), 1652–1666.

Campbell, R., Walker, J., & Baroncohen, S. (1995). The development of differential use of inner and outer face features in familiar face identification. *Journal of Experimental Child Psychology, 59*(2), 196–210.

Chan, J. P., & Ryan, J. D. (2012). Holistic representations of internal and external face features are used to support recognition. *Frontiers in Psychology, 3*, 87.

Clutterbuck, R., & Johnston, R. A. (2002). Exploring levels of face familiarity by using an indirect face-matching measure. *Perception, 31*(8), 985–994.

Clutterbuck, R., & Johnston, R. A. (2005). Demonstrating how unfamiliar faces become familiar using a face matching task. *European Journal of Cognitive Psychology, 17*(1), 97–116.

Davidenko, N., Witthoft, N., & Winawer, J. (2008). Gender aftereffects in face silhouettes reveal face-specific mechanisms. *Visual Cognition, 16*(1), 99–103.

Davies-Thompson, J., Gouws, A., & Andrews, T. J. (2009). An image-dependent representation of familiar and unfamiliar faces in the human ventral stream. *Neuropsychologia, 47*(6), 1627–1635.

Davies-Thompson, J., Newling, K., & Andrews, T. J. (2013). Image-invariant responses in face-selective regions do not explain the perceptual advantage for familiar face recognition. *Cerebral Cortex, 23*(2), 370–377.

Dubois, S., Rossion, B., Schiltz, C., Bodart, J. M., Michel, C., Bruyer, R., et al. (1999). Effect of familiarity on the processing of human faces. *NeuroImage, 9*(3), 278–289.

Ellis, H. D., Shepherd, J. W., & Davies, G. M. (1979). Identification of familiar and unfamiliar faces from internal and external features: Some implications for theories of face recognition. *Perception, 8*(4), 431–439.
Farah, M., Tanaka, J., & Drain, H. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human perception and performance, 21*(3), 628–634.
Farah, M., Wilson, K., Drain, M., & Tanaka, J. (1998). What is "special" about face perception? *Psychological Review, 105*, 482–498.
Fletcher, K. I., Butavicius, M. A., & Lee, M. D. (2008). Attention to internal face features in unfamiliar face matching. *British Journal of Psychology, 99*(Pt 3), 379–394.
Fox, C. J., & Barton, J. J. S. (2007). What is adapted in face adaptation? The neural representations of expression in the human visual system. *Brain Research, 1127*, 80–89.
Fox, C. J., Oruc, I., & Barton, J. J. (2008). It doesn't matter how you feel. The facial identity aftereffect is invariant to changes in facial expression. *Journal of Vision, 8*(3), 11, 11–13.
Haig, N. (1986). Exploring recognition with interchanged facial features. *Perception, 15*, 235–247.
Hancock, P. J. B., Bruce, V., & Burton, A. M. (2000). Recognition of unfamiliar faces. *Trends in Cognitive Sciences, 4*, 330–337.
Hole, G. J. (1994). Configurational factors in the perception of unfamiliar faces. *Perception, 23*, 65–74.
Jarudi, I. N., & Sinha, P. (2003). *Relative contributions of internal and external features to face recognition*. Cambridge: Massachusetts Institute of Technology.
Jiang, F., Blanz, V., & O'Toole, A. J. (2006). Probing the visual representation of faces with adaptation – A view from the other side of the mean. *Psychological Science, 17*(6), 493–500.
Jiang, F., Blanz, V., & O'Toole, A. J. (2007). The role of familiarity in three-dimensional view-transferability of face identity adaptation. *Vision Research, 47*(4), 525–531.
Lai, M., Oruc, I., & Barton, J. J. (2012). Facial age after-effects show partial identity invariance and transfer from hands to faces. *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior, 48*(4), 477–486.
Lai, M., Oruc, I., & Barton, J. J. (2013). The role of skin texture and facial shape in representations of age and identity. *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior, 49*(1), 252–265.
Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience, 4*(1), 89–94.
Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences, 6*(6), 255–260.
Megreya, A. M., & Burton, A. M. (2006). Unfamiliar faces are not faces: Evidence from a matching task. *Memory & Cognition, 34*(4), 865–876.
Moscovitch, M., Wincour, G., & Behrmann, M. (1997). What is special about face recognition ? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience, 9*(5), 555–604.
Nachson, I., Moscovitch, M., & Umilta, C. (1995). The contribution of external and internal features to the matching of unfamiliar faces. *Psychological Research Psychologische Forschung, 58*(1), 31–37.
Nunn, J. A., Postma, P., & Pearson, R. (2001). Developmental prosopagnosia: Should it be taken at face value? *Neurocase, 7*(1), 15–27.
O'Neil, S. F., & Webster, M. A. (2011). Adaptation and the perception of facial age. *Visual Cognition, 19*(4), 534–550.
Oruç, I., Guo, M., & Barton, J. J. S. (2009). A contrast-based adaptation study of the contribution of gender to face representations. *Journal of Vision, 9*(8), 455.
Patterson, K. E., & Baddeley, A. D. (1977). When face recognition fails. *Journal of Experimental Psychology: Human Learning and Memory, 3*(4), 406–417.
Pichler, P., Dosani, M., Oruc, I., & Barton, J. J. (2012). The nature of upright and inverted face representations: An adaptation-transfer study of configuration. *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior, 48*(6), 725–736.
Rhodes, G., Jeffery, L., Watson, T. L., Clifford, C. W., & Nakayama, K. (2003). Fitting the mind to the world: Face adaptation and attractiveness aftereffects. *Psychological Science, 14*(6), 558–566.
Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychologica, 128*(2), 274–289.
Schiltz, C., & Rossion, B. (2006). Faces are represented holistically in the human occipito-temporal cortex. *NeuroImage, 32*(3), 1385–1394.
Shepherd, J., Davies, G., & Ellis, H. (1981). Studies of cue saliency. In G. Davies, H. Ellis, & J. Shepherd (Eds.), *Perceiving and remembering faces* (pp. 105–131). London: Academic Press.
Sinha, P., & Poggio, T. (1996). I think I know that face. . .. *Nature, 384*, 404.
Stacey, P., Walker, S., & Underwood, J. (2005). Face processing and familiarity: Evidence from eye-movement data. *British Journal of Psychology, 96*, 407–422.
Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology Section A—Human Experimental Psychology, 46*(2), 225–245.
Valentine, T. (1988). Upside-down faces: A review of the effect of inversion upon face recognition. *British Journal of Psychology, 79*, 471–491.
Want, S. C., Pascalis, O., Coleman, M., & Blades, M. (2003). Recognising people from the inner or outer parts of their faces: Developmental data concerning 'unfamiliar' faces. *British Journal of Psychology, 21*, 125–135.
Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature, 428*(6982), 557–561.
Webster, M. A., & MacLeod, D. I. (2011). Visual adaptation and face perception. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences, 366*(1571), 1702–1725.
Young, A. (1984). Right cerebral hemispheric superiority for recognizing the internal and external features of famous faces. *British Journal of Psychology, 75*, 161–169.
Young, A. W., Hay, D. C., McWeeny, K. H., Flude, B. M., & Ellis, A. W. (1985). Matching familiar and unfamiliar faces on internal and external features. *Perception, 14*(6), 737–746.
Young, A., Hellawell, D., & Hay, D. (1987). Configurational information in face perception. *Perception, 16*, 747–759.
Young, A. W., McWeeny, K. H., Hay, D. C., & Ellis, A. W. (1986). Matching familiar and unfamiliar faces on identity and expression. *Psychological Research Psychologische Forschung, 48*(2), 63–68.