# FUNCTIONAL SPECIFICITY IN EYE GAZE PROCESSING: EVIDENCE FROM DEVELOPMENTAL PROSOPAGNOSIA

BY

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#### Abstract

The eyes of other people subserve two core functions in human social cognition: gaze perception and face identity recognition. This thesis reports two psychophysical studies that examine the degree of functional specificity between eye gaze processing and face identity processing by testing if various aspects of gaze processing are intact in people with developmental prosopagnosia (DP) – the lifelong inability to recognise face identity. Study 1 investigates spatial integration in eye gaze perception using two tasks. DP and control participants completed one task that measured perception of gaze direction from the two eyes and another that measured the Wollaston illusion (whereby perceived eye gaze is pulled by head rotation; requiring the integration of eye and head direction). Study 2 investigates temporal integration in eye gaze perception using two tasks. The first task measured adaptation effects in eye gaze perception, which reflects sensitivity to gaze direction and its sensory representations. The second task measured serial dependence in gaze perception, which reflects temporal integration of gaze direction and its perceptual stability. Despite their deficits in recognising face identity, DP participants showed normal gaze processing across all studies. These results demonstrate the functional specificity of gaze processing and imply that gaze perception is carried out by dedicated mechanisms not used for processing identity. Our findings align with models of face processing that posit distinct pathways for gaze and identity analysis, and further clarify the selectivity of face processing dysfunctions in developmental prosopagnosia.

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#### **Chapter 1: Introduction**

The eyes make up only a small part of a face, and a smaller part still of the whole person we are interacting with. But as social stimuli, the eyes of other people are vital. We prefer to look at open eyes over closed eyes from birth; we are sensitive to the gaze direction of others from four days old; and we use gaze to form evaluations of objects from just three months old (Batki et al., 2000; Farroni et al., 2002; Hoehl et al., 2008; Reid et al., 2004). The human eye is structurally optimised for social interaction – it has the greatest horizontal elongation and the largest amount of exposed sclera of all primates. These features facilitate the detection of gaze cues and predict social complexity and neocortex ratio in primates (Grossmann, 2017; Kobayashi & Kohshima, 1997; Mayhew & Gómez, 2015). The eyes also serve as windows into the mental lives of other people: providing information to detect their minds, attribute mental states to them, and ultimately interact with them (Baron-Cohen, 1997; Frith, 2001; Grossmann, 2017; Mareschal et al., 2013b; Pelphrey et al., 2005, Tomasello et al., 2007).

Two key functions of eyes as social stimuli are to facilitate gaze perception and identity recognition. Eye gaze is used to form joint attention (orienting to the same object another person is looking at while being aware of each other's attentional states), a cognitive capacity essential for much of human learning and early social development (Frischen et al., 2007). We use gaze cues to understand the intentions and emotions of the people we are interacting with (Mareschal et al., 2013b). Cues conveyed by eye gaze also influence how we behave in certain social settings – for example, whether we will act co-operatively or altruistically (Bateson et al., 2006; Ernest-Jones et al., 2011; Haley & Fessler, 2005). The eyes are also essential for face identity recognition. People tend to use the eye region when recognising faces (Chelnokova & Laeng, 2011; Peterson & Eckstein, 2012; Wu et al., 2011), and experimental manipulation of eyes impacts recognition more than manipulation of other face parts such as nose or mouth (Fisher et al., 2017; Itier et al., 2007; Lewis & Edmonds, 2003; McKelvie, 1976).

Prominent neurocognitive models of face perception suggest that the processing of faces for eye gaze and identity analysis dissociate. In the classic Bruce and Young (1986) model (Figure 1), gaze and identity segregate at an early stage – face identity is encoded with "expression-independent" descriptions, while other aspects of face perception such as expression and facial speech analysis (which is likely to be more related to eye gaze processing) rely on "view-centred" descriptions. Another influential model, Haxby and colleagues' (2000) distributed human neural system for face perception (Figure 2), groups aspects such as expression, eye gaze, and speech-related movements together as *changeable* aspects of the face, while identity and gender are *invariant* face features. The invariant and changeable aspects are associated with different underlying neural pathways: invariant aspects are processed via the lateral fusiform gyrus, while the superior temporal sulcus (STS) is specialised for changeable aspects. However, the interactions between these streams in the core system and the extended system indicate that they can be mediated by one another.

### Figure 1.





*Note.* Bruce and Young's (1986) functional model suggests that eye gaze processing would diverge from face identity processing at the level of view-centred descriptions. "Directed visual processing" has been left off this diagram for simplicity.

### Figure 2.

Haxby and colleagues' (2000) Distributed Human Neural System for Face Perception.



*Note.* This model (sourced from Haxby et al., 2000) also suggests eye gaze processing deviates early from face identity processing.

Both models point out that gaze information is changeable, while identity information is invariant. They further connect these different types of information to different processing streams. A powerful way to test these models is by looking at whether gaze and identity processing can dissociate in developmental prosopagnosia (DP) – a neurodevelopmental condition marked by the lifelong inability to recognise face identity (McConachie, 1976). Studying the range of face processing impairments in people with DP can allow insight into the degree of functional specificity within face perception. For example, processing of facial expression is largely intact in DP (Bell & Susilo, 2018; Biotti et al., 2016; Duchaine et al., 2003), suggesting that the mechanisms used for processing this changeable face aspect are distinct from the mechanisms used to process face identity.

The aim of this thesis is to examine whether eye gaze processing is intact in DP. This will be done in two psychophysical studies that measure spatial and temporal aspects of gaze processing in DP and control participants. The structure of the thesis is as follows: throughout the rest of Chapter 1, I provide background knowledge on eye gaze processing, the use of eyes in face identity processing, and developmental prosopagnosia. Chapter 2 describes Study 1, which is focused on spatial integration, a core component of eye gaze and identity processing. Study 1 tests gaze-related spatial integration by examining how information being presented independently by either eye is integrated, as well as how eye information is integrated with head information. Chapter 3 describes Study 2, which is focused on temporal integration, as eye gaze and face identity processing both involve the consolidation of information over time. Study 2 tests gaze-related temporal integration by examining the effects of adaptation and serial dependence on perceived eye gaze. Chapter 4 discusses the results of these two studies in terms of what they suggest about the functional specificity of eye gaze and identity processing, how they advance theories on the functions and mechanisms of eye gaze processing, and whether they may elucidate the nature of impairment in DP.

#### **1.1 Eye Gaze Processing**

Correctly perceiving the eye gaze of others allow us to make inferences about their intentions, emotions, and attentional states. This helps to facilitate communication and alert us to socially significant stimuli in our environment (Adams, 2003; Mareschal et al., 2013b). The eyes are also vital in helping us to detect the minds of others, infer the contents of other minds, and collaborate with other minds – core processes of being a social human (Grossmann, 2017). The human visual system is therefore extremely sensitive to eye gaze cues; we are able to detect

changes in eye gaze direction as small as 1.4° from a metre away (Anstis et al., 1969; Cline, 1967).

One aspect of eye gaze processing is interpreting the gaze of another person as being averted from direct. Averted gaze allows us to infer where another person's attention has been placed, and direct our own attention there. This has many benefits. It facilitates joint and shared attention (Frischen et al., 2007), both of which are required in the inference of mental states from others (Pfeiffer et al., 2013). When in conversation with another person, a shift in that person's gaze from direct to averted may signal that something important has caught their attention, perhaps a threat, particularly when coupled with a fearful facial expression (Adams, 2003). Averted gaze can be used in Posner cueing tasks to trigger both overt and covert shifts of attention (Friesen and Kingstone, 1998), suggesting it is an important social cue with the power to automatically direct our attention.

Direct gaze is also a salient social stimulus. Faces with direct gaze are memorised better, and direct gaze speeds up identity and emotional expression recognition. Faces with direct gaze are judged more positively and as more likeable, and they create a higher probability of conversation ensuing (Schilbach, 2015). Newborn infants prefer to look at faces with open eyes over closed eyes (Batki et al., 2000) and direct gaze over averted gaze (Farroni et al., 2002). Direct gaze tends to "pop-out" amongst averted gaze distractors in visual search tasks, meaning it is oriented to easily (von Grünau & Anston, 1995). Additionally, in attentional cueing tasks using eye gaze, direct gaze can have a "sticky effect" – the detection of peripherally presented targets is delayed when the centrally-presented image is direct gaze capture our attention, but it is also difficult to disengage our attention from it. Finally, humans display a "cone of direct gaze" – a tendency to accept a wide range of objectively averted gazes as looking directly at them (Balsdon & Clifford, 2018; Gamer & Hecht, 2007). This cone

widens – more extremely averted gazes begin to appear direct – with increased uncertainty. This assumption that slightly averted eyes are looking directly at you likely functions to ensure that direct gaze, an important social cue, is rarely missed (Mareschal et al., 2013a).

## 1.2 The Role of the Eyes in Face Identity Processing

The eye region is essential for identity processing. Eye colour, eye shape, and interocular and interpupillary distances are specific to each individual (Itier & Batty, 2009), meaning the eye region contains an abundance of diagnostic information. Eye tracking studies show that using this information by looking at the eye region is optimal for multiple aspects of face recognition, particularly identity recognition (Peterson & Eckstein, 2012). The eyes tend to be fixated on for longer periods of time than other regions of the face during identity recognition tasks (Chelnokova & Laeng, 2011; Wu et al., 2011). Changing the eyes of a face can dramatically alter the perceived similarity of two otherwise highly similar faces, and people use the eyes more often when making judgements about face similarity (Abudarham et al., 2019; Abudarham & Yovel, 2016). Masking the eyes of a face hinders both detection and recognition, while masking the mouth or nose has little effect (Lewis & Edmonds, 2003; McKelvie, 1976). When the eyes are shown in apertures of sharper relief than the rest of the face, recognition accuracy is higher than when these apertures are located over other features (Royer et al., 2018; Vinette et al., 2004). Overall, use of the eye region can explain 20% of individual differences in face recognition abilities (Royer et al., 2018).

Neural data also show that the eye region is important for identity processing. In the fusiform face area (FFA), fMRI responses to the isolated the eye region are stronger than those to non-face objects (Baron-Cohen et al., 2001; Tong et al., 2000). Single cell recordings from monkeys show that the same cells that respond preferentially to eyes do so to whole faces also, and that some face-selective cells respond to isolated eyes (Issa & DiCarlo, 2012; Perrett et al., 1992; Perrett et al., 1985). EEG studies of the N170 event-related potential

(ERP), thought to reflect the structural encoding of faces (Bentin et al., 1996), have also found similar selectivity to the eye region and to the whole face (Itier et al., 2007; Itier et al., 2006; Itier et al., 2011; Nemrodov et al., 2014).

Some populations with markedly poor face recognition abilities are linked with atypical processing of the eyes. Children with autism spectrum disorder (ASD) show impaired face recognition (Weigelt et al., 2012) and decreased eye contact (Senju & Johnson, 2009). The amount of displeasure or discomfort displayed in response to direct eye contact negatively predicts face recognition abilities in children with ASD but not typically-developing children (Joseph et al., 2008; Kylliäinen & Hietanen, 2006). People with developmental prosopagnosia pay less attention to the eye region than people with typical or above-average face recognition skills (Bobak et al., 2017). Patients with acquired prosopagnosia, that which arises due to brain injury, tend to fixate more often and for longer on the lower half of the face (Lee et al., 2019; de Xivry et al., 2008), are poor at recognising or discriminating between the eyes of faces (Pancaroglu et al., 2016; Rossion et al., 2009), and may show generally chaotic patterns of fixations compared to controls (Lee et al., 2019; Barton et al., 2007).

Crucially, identity recognition depends not only on the use of the eyes, but also on the integration of the eye region with the rest of the face. This spatial integration is the focus of Study 1 and will be described in more detail in Chapter 2.

### **1.3 Developmental Prosopagnosia**

Developmental prosopagnosia (DP) is a neurodevelopmental condition characterised by the lifelong inability to recognise faces (McConachie, 1976). DP occurs despite no apparent brain injury, intact general sensory abilities, normal intelligence, and a typical developmental environment with ample opportunity to acquire face expertise (Behrmann & Avidan, 2005). DP is thought to occur in up to 2% of the population (Kennerknecht et al., 2006). DP is commonly diagnosed based on poor performance on objective tests of face recognition as well as self-reports of face recognition problems in everyday life (Barton & Corrow, 2016).

DP is defined by the inability to recognise face identity, but whether other aspects of face processing are intact in DP is uncertain. While many studies show that people with DP have impairments restricted to face identity (e.g., Barton et al., 2019; Bell & Susilo, 2018; Carbon et al., 2010; Chatterjee & Nakayama, 2012; DeGutis et al., 2012; Duchaine & Nakayama, 2006; Duchaine et al., 2003; LeGrand et al., 2006; Rezlescu et al., 2013; Todorov & Duchaine, 2008), some people with DP can have trouble recognising facial expressions (Biotti & Cook, 2016) and facial gender (Marsh et al., 2019), or making judgements about facial attractiveness (LeGrand et al., 2006) and facial trustworthiness (Todorov & Duchaine, 2008). Others may show impaired perception of bodies (Biotti et al., 2017) and other non-face objects (Barton et al., 2019; Duchaine & Nakayama, 2006). This variability suggests that DP is likely a heterogenous disorder, presenting with multiple comorbidities (Susilo & Duchaine, 2013).

Very little is known about eye gaze perception in DP. One study has looked at this issue and found typical eye gaze processing, but this study has limited generalisability since it only tested 7 DP participants (Duchaine et al., 2009). Another study of a DP individual found impairment at discriminating direct from averted gaze, but this single case study again lacks generalisability (Campbell et al., 1990). The aforementioned heterogeneity of DP means that large samples may be especially important to overcome individual-level variation in people with DP.

It is conceivable that eye gaze processing could be intact or impaired in DP. Given the important role of eye region in identity processing (e.g., Bobak et al., 2017; Caldara et al., 2005; Itier et al., 2007; Royer et al., 2018; Tong et al., 2000), aberrant processing of the eye region could give rise to both eye gaze and identity recognition deficits. On the other hand, eye

gaze and identity processing differ in important ways. Identity is an invariant feature while eye gaze is a changeable feature, and these different types of information are thought to be processed through different pathways (Bernstein et al., 2018; Bruce & Young, 1986; Haxby et al., 2000; Pitcher et al., 2011). Identity and gaze also differ in terms of processing time course. ERP studies show that identity is processed around 170-200 ms after stimulus onset (Bentin et al., 1996), while gaze may be encoded around 250-300 ms after stimulus onset (Nummenmaa & Calder, 2008; Schweinberger et al., 2007). Lastly, identity and gaze processing rely on different visual structures – identity processing uses mainly horizontal structures contained in the face, while cues to eye gaze are contained in vertical structures (Goffaux, 2019).

The processing of the eyes is intrinsically involved in the processing of face identity. Whether that means that the mechanisms involved in eye gaze processing and face identity processing are shared or functionally specific remains to be seen. To begin answering this question, it should be established whether eye gaze processing can be intact when face identity processing is impaired. Studying eye gaze processing in people with DP, a condition defined by a lifelong inability to recognise faces, will help us to understand this.

#### Chapter 2: Study 1

### **2.1 Spatial Integration**

Gaze perception involves the spatial integration of low-level local cues alongside global information. Figure 3 shows the dual-route model of eye gaze perception (Otsuka et al 2014). The local cues are eye deviation, and the global information is head orientation.

#### Figure 3.

Dual-route Model of Gaze Perception.



Note. Sourced from Otsuka and colleagues (2014).

Gaze perception is determined by the physical cues to gaze deviation conveyed by the eyes. The visual system is sensitive to such physical cues, particularly low-level surface luminance variations occurring at different scales and orientations within the eye region. For example, the eyebrows contain coarse and horizontally-oriented information, while the eyelashes contain fine-grained and vertically-oriented information (Fisher et al., 2017; Goffaux, 2019). Filtering face images to include only horizontal or vertical information then asking participants to categorise eye gaze as left, direct, or right reveals that people have a vertically-tuned sensitivity to eye gaze direction (Goffaux, 2019). Surface luminance also plays a large role; for example, the difference in contrast luminance between the two parts of the

sclera on either side of the iris can be suggestive of the angle of rotation of the eyeball (Langton et al., 2000; Watt, 1999). This information is processed largely in the anterior STS, which contains channels of neurons that respond specifically to left, right, or direct gaze (Calder et al., 2008; Calder et al., 2007; Carlin & Calder, 2013; Carlin et al., 2012; Perrett et al., 1985; Perrett et al., 1992), and encodes eye gaze independently of head orientation (Carlin et al., 2011).

Gaze perception is also influenced by head orientation. This can happen in two opposing ways. The influence of head orientation can be repulsive (i.e., perceived gaze is biased against head orientation, Gibson & Pick, 1963) or attractive (i.e., perceived gaze is biased towards head orientation, Cline, 1967; Otsuka et al., 2014; Otsuka et al., 2016). The repulsive effect occurs in experimental manipulations that reduce the amount of information available from the eye region when the head is rotated, because the eye region is partially occluded (as in Gibson & Pick, 1963). The attractive effect occurs when the amount of information available from the eye region is spared (i.e., by cropping identical eye regions onto rotated heads; Cline 1967; Otsuka et al., 2014; Otsuka et al., 2016). This isolates the effect of only incongruent information coming from the head without manipulating the amount of information available from the eyes. The effect of head direction on perceived gaze direction occurs along one of these two routes – either by changing the amount of information available from the eyes. The effect of head orientation (Otsuka et al., 2014).

The dual-route model of gaze perception alludes to the high degree of spatial integration used in eye gaze processing, which my first study will aim to measure in DP and control participants. This is perhaps most obvious when considering the effect of head orientation – local information about gaze conveyed by the eyes is integrated with global information conveyed by the head. A powerful task used to quantify this eye-head integration is the Wollaston task. The task is based on Wollaston's illusion – in which physically direct gaze presented in the context of an averted head appears averted (Todorovic, 2006; Wollaston, 1824). An example of Wollaston's original engravings demonstrating this effect is shown in Figure 4. Wollaston tasks generally aim to preserve the amount of information available from the eye region in order to isolate the true effect of head direction on perceived eye gaze, leading to the attractive effect. The Wollaston task was employed in this first study to measure the degree of integration between the eye region and the whole head in DP and control participants. **Figure 4.** 

Demonstration of the Wollaston Illusion.



*Note.* A sample of Wollaston's (1824) original illustrations. The two eye regions are completely identical, but changing the angle of the nose (one cue to head direction) greatly influences the perceived eye gaze.

Another form of spatial integration that may be taking place during gaze perception is integrating gaze information from the two eyes. Studies show that humans have a left visual field advantage for eye gaze – their judgements of another person's gaze are influenced more by the eye in their left visual field than the eye in their right visual field (Ricciardelli et al., 2002). For the most part, using only one eye to make judgements of gaze direction may not necessarily be problematic as the eyes tend to look in the same direction. But what happens when someone is looking at something right in front of them, causing their gaze to converge? Or if they have a medical condition such as strabismus, in which the eyes do not look in congruent directions? Detecting such instances requires a form of local spatial integration, in which information conveyed by one eye is integrated with information conveyed by the other. To measure this form of eye-eye integration, I used a task in which DP and control participants had to identify faces with strabismic gaze (each eye gazes in a different direction; Kanai et al., 2012). I also included trials in which the faces were inverted, a classic experimental manipulation used to disrupt spatial integration of faces as a whole (Yin, 1969). Inverted trials will assess whether this local spatial integration of eye gaze interacts with the spatial integration of face processing in general.

Study 1 administered these two tasks – the strabismus and Wollaston tasks – to measure the degree of spatial integration in the perception of eye gaze in DP and control participants. These tasks have the advantages of also measuring invariant and changeable information in eye gaze processing – strabismus is largely invariant information as it is tied to one's identity and does not change from moment-to-moment, while Wollaston's illusion accesses a changeable form of gaze perception as a person's head and eye gaze direction changes often. Normal performance by DP participants would support a dissociation between gaze and identity processing, whereas impaired performance by DP participants would be consistent with the notion that gaze and identity processing rely on common mechanisms.

### 2.2 Method

#### **2.2.1 Participants**

Participants were 101 adults with DP ( $M_{age} = 39.50$  years, SD = 8.96 years, 26 male, 68 female, 7 other) and 97 control participants ( $M_{age} = 39.10$ , SD = 8.18, 24 male, 73 female, 0 other). The control group was matched with the DP group on age and gender, such that there were no significant differences in gender ( $\chi^2(1) = 0.21$ , p = .647) or age (t(196) = 0.33, p = .742) between the groups.

DP participants were recruited via faceblind.org, an online prosopagnosia database. All participants met the typical diagnostic criteria for DP (Barton & Corrow, 2016; Bowles et al.,

2009) across a battery of tests: The Prosopagnosia Index 20-item scale (Shah et al., 2015), the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006), a recognition of famous faces test (FFT; Duchaine & Nakayama, 2005). Participants were excluded if they reported having previous brain injuries or a neurological disorder, or if their scores on the Leuven Perceptual Organisation Test (L-POST; Torfs et al., 2014) suggested broader deficits in low/mid-level visual processing. Participants outside of the ages 18 to 51 at the time of screening were excluded, as their poor face recognition abilities could reflect underdevelopment or cognitive decline of the face recognition system (Germine et al., 2011). DP participants were recruited from the United States, the United Kingdom, Australia, Canada Germany, France, and the Netherlands. They received a voucher for the equivalent of \$5 USD from their local Amazon.com store for their participation. Control participants were recruited through Testable Minds (minds.testable.org). Controls were screened for atypical face recognition abilities by completing the CFMT after the experimental tasks. CFMT scores for controls and DPs can be found in Appendix A.1. Controls received US\$4.50 for their participation. All participants provided informed consent.

All participants completed two tasks, the order of which was counterbalanced between participants. Tasks were completed online via Testable (<u>www.testable.org</u>; Rezlescu et al., 2020), an online platform for running sensitive cognitive and behavioural tasks, in the participant's own time and on their personal computer. Ethical approval for this study was granted by the School of Psychology Human Ethics Committee, on delegated authority by the Victoria University of Wellington Human Ethics Committee.

#### 2.2.2 Strabismus Task

### Stimuli

I used the stimuli developed by Kanai and colleagues (2012) for the strabismus task. These included 22 target images of faces with strabismus, which were created by manipulating images of people without strabismus. Each target identity was also presented as a distractor image without strabismus, so participants could not rely on the identity of the faces to decide which had strabismus (an example of this can be seen in Figure 5 below). Each target image was presented three times in each orientation (upright and inverted) – once on the left, once in the middle, and once on the right. The images measured 300 x 400 pixels each.

## Figure 5.

Example Stimuli from the Strabismus Task.



Note. One identity used in the strabismus task as a target (left) and a distractor (right).

## Procedure

Before beginning the task, participants were told what strabismus is and were shown examples of people presenting with strabismus. Each trial in the strabismus task showed three faces that could be looking in any direction. One face would be presenting with strabismus. Participants had to use the 1, 2, and 3 keys on the keyboard to report which face they believed had strabismus (left, right, or middle face, respectively). The faces were presented for two seconds, and participants had unlimited time to respond either during or after stimulus presentation. Participants completed 132 trials in four blocks of 33 trials and were given the opportunity to take a self-terminated break between blocks. In two blocks, the faces were presented upright. In the other two blocks, the faces were presented upside-down. The inverted trials were identical to the upright trials, except that all three images were orientation inverted. The order of the trials was completely randomised within the blocks and the order of blocks was counterbalanced. This task took participants around 10 minutes. An example of an upright trial is presented in Figure 6.

## Figure 6.

Strabismus Task Trial Diagram.



*Note*. Example of a single trial in the strabismus task.

## 2.2.3 Wollaston Task

## Stimuli

For the Wollaston task, six individual identities with forward-facing heads were created using FaceGen Modeller (Singular Inversions, 2019). Each identity had nine eye gaze deviations, ranging between  $-16^{\circ}$  (left) and  $+16^{\circ}$  (right) in 4° intervals. The eyes from these forward-facing heads were then cropped and merged onto faces with their heads averted 20° left or 20° right. Using identical eye regions with averted heads means that the total amount of information available from the eye region was not changed in the averted heads, which should lead to a direct effect of head direction on perceived eye gaze per the dual route model (Otsuka et al., 2014). This also means that the head-left and head-right conditions used identical eye regions, so the conditions differed only in the type of head direction information displayed (Palmer et al., 2018b). For each identity, there were 18 possible combinations of head direction and eye deviation (example for one identity shown in Figure 7). Each combination was presented twice, resulting in (18 combinations x 6 identities x 2 repeats) 216 trials in total. The face stimuli were presented at 945 x 845 pixels.

## Figure 7.



Example Stimuli from the Wollaston Task.

*Note.* All possible combinations of head and eye direction for one identity in the Wollaston task. Top row shows  $-20^{\circ}$  averted heads ('head left' condition). Bottom row shows  $+20^{\circ}$  averted heads ('head right' condition).

As the perception of eye gaze can be sensitive to the position of the viewer, the stimuli used in this task were created with such a vergence that the eyes of direct gazes should be looking directly at the viewer when the viewer is seated 80 cm away (Palmer et al., 2018b). As the participants completed the task privately in their own homes, viewing distance and position could not be controlled. However, participants were instructed before the task and in every break to view the monitor from an arm's length away, with their head looking straight ahead, and at such a height that their eyes were level with the centre of the screen.

#### Procedure

Each trial consisted of a face presented for 1500 ms, after which the participant was asked to categorise the eye gaze as left, direct, or right by pressing the left, down, or right arrow keys on their keyboard. There was no time limit in which to make a response. Trials were separated by a 500ms inter-trial interval. The order of the trials was randomised. Each participant received four opportunities to take a break, occurring at random times throughout the experiment. The Wollaston task took participants around 15 minutes. An example trial is shown in Figure 8.

#### Figure 8.

Example of a Single Trial from the Wollaston Task.



*Note*. Example of a single trial from the Wollaston task.

### 2.3 Results

Statistical analyses were conducted in Jamovi version 1.2 (Jamovi project, 2020) unless otherwise stated. Welch's *t*-tests were used instead of Student's *t*-tests where the assumption of equal variances was violated. Bonferroni-corrected *t*-tests were used to follow up all analyses of variance (ANOVAs). Modelling was done in MATLAB 2020a (MathWorks, 2020), and model fitting used the non-linear least squares method.

Bayes factors were used to quantify all statistical evidence beyond the acceptance or rejection of the null hypothesis. A non-significant *p*-value does not allow us to distinguish between absence of evidence or evidence of absence, but a Bayes factor can indicate whether there is more evidence for the null hypothesis, the alternative hypothesis, or neither (Keysers et al., 2020). Bayes factors were implemented in JASP (JASP Team, 2020) and interpreted according to conventions (e.g., Biel & Friedrich, 2018; Jeffreys, 1998; Keysers et al., 2020; Lee & Wagenmakers, 2014).

Descriptive statistics for DP participants' and controls' performance are reported in Appendix A.1. My analyses are focused on accuracy (for the strabismus task) or the size of the Wollaston effect, but RT analyses can be found in Appendix A.2 and distribution comparisons in Appendix A.3.

## 2.3.1 Strabismus Task

I compared accuracy in a 2 (group: DP, control) x 2 (condition: upright, inverted) mixed measures ANOVA. Data are shown in Figure 9. A main effect of orientation (F(1, 196) =344.48, p < .001,  $\eta^2_p = 0.64$ ) revealed higher accuracy in the upright condition (M = 76.62%, SD = 0.11%) than the inverted condition (M = 65.97%, SD = 0.12%), t(196) = 18.56, p < .001. The main effect of group was not significant (F(1, 196) = 2.47, p = .118,  $\eta^2_p = 0.01$ ), but the interaction of group and condition was significant (F(1, 196) = 5.01, p < .026,  $\eta^2_p = 0.03$ ). Follow-up t-tests showed that DP accuracy was slightly reduced compared to control accuracy in the upright condition (DP M = 74.87%, SD = 10.40%; Control M = 78.44%, SD = 10.41%), t(255.9) = 2.29, p < .001, but not the inverted condition (DP M = 65.48%, SD = 11.53%; Control M = 66.48% SD = 11.61%), t(255.9) = 0.64, p = 1.000. The group difference in the upright condition was small in terms of magnitude (4%) and effect size ( $\eta^2_p = 0.03$ ). Bayes factor indicated only anecdotal evidence for the interaction between group and condition (BF<sub>incl</sub> = 1.76; absence of evidence).

#### Figure 9.

DP and Control Accuracy in the Strabismus Task.



*Note.* Small dots represent individual data points and larger circles represent group means. Control data is shown in light grey and DP data in dark.

## 2.3.2 Wollaston Task

I analysed the Wollaston data using two approaches: psychophysical modelling and the centroid method. Both approaches allow me to quantify the effect of head direction on perceived eye gaze as captured by the Wollaston illusion. Palmer and colleagues (2018b) note that the psychophysical model can overestimate the effect of head direction on perceived eye gaze when participants are noisy in their responding, or only categorise extreme gazes as "direct" (i.e., show a large effect of the illusion). In contrast, the centroid method uses the midpoint of the data, so it is constrained by the range of eye gaze deviations tested in the task and is therefore more likely to underestimate the effect of head direction on perceived eye gaze estimate of the strength of the Wollaston illusion in the DP and control groups.

#### Psychophysical Modelling

For each participant's data, I modelled the proportion of "direct" responses to each eye gaze deviation in the head left and head right conditions separately using a Gaussian function:

$$p(Direct) = \int_{P_0 - (\frac{W}{2})}^{P_0 + (\frac{W}{2})} G(\theta_{stim}, \sigma_{rep}) d\theta$$

p(Direct) is the probability of a participant responding "direct" to the eye gaze deviation  $\Theta_{\text{stim}}$ . The Gaussian distribution (*G*) is centred over the eye gaze deviation and has a standard deviation of  $\sigma_{\text{resp}}$ , corresponding to variability in the participant's categorisation. The category boundaries are the midpoint of the category (*P*<sub>0</sub>) and the width of the category (*w*). An example of this model fit to an individual's data from each group is shown below in Figure 10 below.

## Figure 10.





*Note.* The cone model fit to the data of a single participant from the control (left) and DP (right) groups.

The point at which the function shows the highest proportion of "direct" responses was taken as the estimate of the participant's perceived direct gaze in each condition. To estimate the participant's overall perceived direct gaze, the estimates for the head left and head right conditions were averaged. This measure is referred to as the *cone model half-difference*, and it represents how much on average head direction influenced eye gaze perception. For example, a cone model half-difference of 5° means that head direction pulled perceived gaze direction by 5°. A smaller cone model half-difference indicates a smaller influence of head direction. This measure was calculated for each participant. Plots for each participant's data can be found in Appendix A.4.

The model fit the data equally well for both groups, with an average Adjusted R<sup>2</sup> value of .93 (SD = 0.07) for the control group and .94 (SD = 0.07) for the DP group, t(196) = 0.16, p = .871, d = 0.02. Plots of the model fit to each group's data are shown in Figure 11 below. The mean cone model half difference was similar for the control group ( $M = 8.74^\circ$ ,  $SD = 4.66^\circ$ ) and the DP group ( $M = 9.31^\circ$ ,  $SD = 3.68^\circ$ ), t(182.61) = 0.96, p = .339, d = 0.14. This result suggests that head direction pulled perceived gaze direction by around 9° in both groups. Bayes factors indicated moderate evidence for this lack of group difference, BF<sub>10</sub> = 0.16 (evidence of absence). The group comparison is shown in Figure 12.

#### Figure 11.

Super-Subject Plots Fit with the Cone Model.



Note. Super-subject plots showing the cone model fit to the data of the whole control (left) and

DP (right) groups. Error bars represent  $\pm 1$  SEM.

## Figure 12.

*Cone Model Half-Difference (CMHD) and Centroid Half-Difference Values in the DP and Control Groups.* 



*Note*. Cone model half-difference (left) and centroid half-difference (right) values in the control and DP groups. Small dots represent individual data points and the larger circles represent the group means.

#### **Centroid Method**

I calculated the centroid of each participant's data in each head direction condition using the sum of the proportion of direct responses at each eye gaze deviation multiplied by the corresponding eye gaze deviation, divided by the sum proportion of direct responses across all gaze deviations. The average of this measure in each head direction condition is the *centroid half-difference*, another estimate of the effect of head direction on perceived eye gaze. A smaller centroid half-difference value means a weaker integration of the head and eye region.

Data from the centroid method are shown in Figure 12. The mean centroid halfdifference was comparable for the DP group (M =  $7.98^\circ$ ,  $SD = 3.04^\circ$ ) and the control group (M =  $8.02^\circ$ ,  $SD = 3.51^\circ$ ), t(196) = 0.11, p = .916, d = 0.02. Bayes factors again indicated moderate support for the lack of group difference (BF<sub>10</sub> = 0.16).

#### 2.3.2 Follow-up Analyses of the Strabismus Task

The upright data in the strabismus task suggested some evidence of a small reduction in accuracy in the DP group. To follow-up this finding I examined two factors that could have contributed to this finding: prosopagnosia severity and autism traits. The reduced accuracy in the DP group may be linked to the severity of face recognition deficits in DP, so I investigated whether scores on the CFMT could predict strabismus accuracy. DP participants also frequently report a higher incidence of autism and/or trait autism than the general population, and deficits in eye gaze processing are common in autism (Senju & Johnson, 2009). During their screening for our database, all DP participants completed the Subthreshold Autism Traits Questionnaire (SAT-Q; Kanne et al., 2012). To see if strabismus performance was related to autism traits, I looked at whether SAT-Q scores could predict strabismus accuracy. To examine the contributions of both factors simultaneously, I ran a multiple regression using strabismus upright accuracy as the dependent variable and CFMT and SAT-Q scores as independent variables. The overall model was significant (F(2, 98) = 4.61, p = .012), but these factors explained only 7% of the variance in strabismus accuracy (Adj  $R^2 = .07$ ), indicating minor contributions. CFMT scores positively predicted strabismus performance ( $\beta = 0.20$ , SE= 0.002, p = .048) but SAT-Q scores did not ( $\beta = -0.19$ , SE > .001, p = .060). This finding suggests that the severity of face recognition deficits may be related to strabismus performance in the DP group, but the effect is small.

## **2.4 Discussion**

The main aim of Study 1 was to examine whether DP participants showed a similar degree of spatial integration in the perception of eye gaze as controls. I measured spatial integration with two tasks. The strabismus task measures integration between the two eyes. The Wollaston task measures integration between eye deviation and head direction. The strabismus task revealed a slightly weaker integration in DP that was potentially driven by a subset of the most severe DP cases. The Wollaston task revealed strong effects of the illusion in both groups, with an average effect of head direction on eye gaze of 8.38° in controls and 8.65° in DPs (averaged across both measures). There were no group differences. Overall, the results suggest that DP is not generally associated with impairments of spatial integration in eye gaze processing. This interim discussion will link these findings back to what is known about spatial integration in the perception of face identity and how this is used by people with DP, and therefore what these results suggest about functional specificity in eye gaze processing.

Effective face identity processing involves a high degree of spatial integration between different regions of the face, also known as holistic processing of the face. Evidence for this comes from three classic paradigms of holistic processing (shown in Figure 13). The first of these is the inversion effect, in which orientation inversion hinders recognition by disrupting the spatial relationships between facial features (Figure 13A; Yin, 1969). Second is the composite task: when presented with two perfectly aligned faces with the same top half but different bottom halves, the different bottom halves affect the perception of the identical top halves. In the same trial with the two face halves misaligned, this perceptual integration does not occur, and it is easier to identify that the two faces have the same top half (Figure 14B; Young et al., 1987). In the part-whole task (Figure 13C), participants must recognise a feature (e.g., Larry's nose) when presented alone (e.g., Larry's nose versus Bob's nose) or in the context of a face (Larry's face with Larry's nose versus Bob's nose). Participants are better at recognising features when presented in the context of a face rather than in isolation (Tanaka & Farah, 1993). These tasks demonstrate that when the whole face context is removed or changed, features alone are not sufficient for good face recognition.

## Figure 13.





*Note.* Examples of control and test conditions in the inversion task (A), the composite task (B) and the part-whole task (C). Sourced from DeGutis and colleagues (2013).

This holistic processing may specifically involve integrating the eyes with the rest of the face. Some evidence for this comes from EEG studies of the N170 component, implicated in the structural encoding of faces (Bentin et al., 1996). The N170 component to isolated eye regions is comparable or even larger than that to whole faces (Itier et al., 2007); N170 components are larger when participants fixate on the eye region (de Lissa et al., 2014); and selectively manipulating the contrast of or removing the eyes delays and reduces the N170 component (Eimer, 2000; Fisher et al., 2016). The degree of modulation of the N170 response to contrast-negated eyes can positively predict scores on a face perception task – participants more affected by the negation of the eye area have better face perception (Fisher et al., 2016).

People with DP have a particular deficit in holistic processing (Avidan et al., 2011; Barton, 2009; Lobmaier et al., 2010). Most people with DP show atypical effects of inversion, composite faces, and part-whole faces (Avidan et al., 2011; DeGutis et al., 2013; Palermo et al., 2011; Rezlescu et al., 2017; Ross et al., 2015; Tanaka & Farah, 1993; Yin, 1969; Young et al., 1987, but see Biotti et al., 2017; Susilo et al., 2010). The holistic deficit in DP is most pronounced when integrating eyes with the rest of the face (DeGutis et al., 2013). In the partwhole task, control participants experience a benefit of the whole-face context for all features tested (nose, eyes, and mouth), but people with DP only experience a slight benefit for nose and mouth – their accuracy at discriminating eyes is identical with or without the face context. This finding suggests that, when recognising face identity, people with DP process eyes separately from the rest of the face. Similarly, in EEG experiments of the N170 face component, DP participants are not affected by the contrast negation of the eyes as controls are. DP and control participants do not differ in their modulation of the N170 response when
selective changes to contrast negation occurred over other features of the face (Fisher et al., 2017).

Given this evidence that people with DP have an impairment in holistic processing, particularly of the eyes with the rest of the face, the results from this first study strongly suggest that the spatial integration used in eye gaze processing differs from that used in face identity processing. This conclusion is strengthened by data from a subset of my DP participants who completed the part-whole task as part of another study (Chapman et al., 2018). These DP participants showed a greatly reduced part-whole effect, in contrast to their normal performance on the Wollaston task (supplemental analysis in Appendix A.5). This finding may have implications for our understanding of holistic processing. Some authors (e.g., Maurer et al., 2002; Rezlescu et al., 2017) suggest that there are different types of holistic processing used in face recognition. An example of three such types may be a sensitivity to the first-order relations of a face (the arrangement of two eyes above a nose and mouth), integrating these features into a holistic percept via gestalt principles, and sensitivity to the second-order relations of a face (analysing the distances between features; Maurer et al., 2002). Evidence for different types of holistic processing comes from individual differences studies of the inversion, composite, and part-whole tasks - there are small to non-existent correlations between these tasks, and they do not equally predict face recognition abilities (Rezlescu et al., 2017). My study adds to this research by further fractionating holistic processing of the eyes depending on whether this is for gaze or identity processing.

A potential limitation to Study 1 is in assuming that the strabismus task measures one's ability to integrate gaze information contained within the eye region, and that this is an invariant element of gaze perception. That it involves gaze processing is a relatively safe assumption, as you must be able to tell that the two eyes are not looking in the same direction in order to detect strabismus. However, it may be more closely related to other invariant aspects of face

processing such as identity. Presumably, strabismus is a characteristic one is more likely to notice when making judgements about a person's identity than where they are looking. It is entirely possible that this task measured an aspect of identity recognition more than eye gaze processing. The relationship between strabismus task performance and CFMT scores suggests this may be the case.

Future studies should look into issues of spatial integration not studied here. One is crowd perception: how eye gaze is integrated *across* faces, rather than *within* faces. Evidence suggests that the visual system rapidly pools eye gaze information being conveyed by many different faces in a crowd into an efficient and accurate estimate of the crowd's average eye gaze direction – a process called ensemble coding (Sweeny & Whitney, 2014). Inversion reduces this crowd benefit, suggesting that high-level face processing mechanisms are involved. There is also evidence that DPs show weaker ensemble coding of face identity (Robson et al., 2018). There is no evidence to suggest that one's sensitivity to individual gaze predicts one's sensitivity to crowd gaze, or what the social or attentional consequences of this might be. The relationship between individual gaze coding, ensemble gaze coding, and holistic face processing could be explored in future research using participants with DP.

Another is the different types of cues, processed at different levels, that give rise to the Wollaston effect (Langton et al., 2004). The contour of the head is one cue to head direction that seems to be processed at a lower level (it is not affected by inversion), while the angle of the nose relative to the head is another potential cue that is processed at a higher level, where mechanisms become more selective to the upright orientation (it is affected by inversion). My study is not able to tease apart the influence of these two cues, so it is possible that DP participants could complete this task using only low-level cues, rather than the high-level cues that are similar to those used in face identity processing. Manipulating the images through inversion and/or filtering them to maintain only the contour of the head or nose (as in Langton

et al., 2004) could be an interesting follow-up to explore whether the DP and control participants used the same information to complete the task.

To conclude the first study, there was no convincing evidence for a difference in spatial integration of eye gaze processing between DP and control participants. This would suggest that the integration mechanisms at work in eye gaze processing are distinct from those used in face identity processing, as suggested by traditional face perception models (e.g., Bruce & Young, 1986; Haxby et al., 2000). This holds true even for aspects of eye gaze processing that may revolve around more invariant information, such as the perception of strabismus.

### Chapter 3: Study 2

#### **3.1 Temporal Integration**

Eye gaze and face identity processing both involve temporal integration. Here, this refers to how the perception of a stimulus is modulated by stimuli seen in the recent past. This chapter will focus on two types of temporal processes in eye gaze perception, namely adaptation and serial dependence.

Adaptation refers to a reduction in the responsiveness of neurons after prolonged exposure to the stimulus that those neurons are sensitive to, and how that influences the way one views subsequent stimuli. Adaptation is seen throughout different stages of visual processing, impacting the perception of a wide range of stimuli from low-level attributes like orientation and colour to complex objects like faces and eye gaze (Webster & MacLeod, 2011). For example, if one views a tilted line for several seconds, any vertical lines seen soon after will appear tilted in the opposite direction. This is a negative or repulsive aftereffect – the neutral test stimulus (the vertical line) is biased to look less like the adapted stimulus (the tilted line; Gibson & Radner, 1937). Adaptation also occurs for complex stimuli such as face identity (prolonged exposure to a face with a thin nose and high eyes would cause an average face to perceived as a person with a broad nose and low eyes; Leopold et al., 2001; Rhodes & Jeffery, 2006) and eye gaze (prolonged exposure to leftward-averted gaze would cause direct gaze to appear rightward-averted; Calder et al., 2008).

Adaptation studies can provide insight into the organisation of visual information in the brain. In the case of eye gaze, adaptation provides evidence for the existence of distinct channels of neurons responding preferentially to different eye gaze directions, in line with neural studies of the STS (Calder et al., 2007). When participants were adapted to leftward gaze (they looked at leftward gaze for a long time), the parts of the STS that responded preferentially to leftward gaze were less responsive compared to those that responded

preferentially to direct or rightward gaze. Behavioural responses in this study and others demonstrate the perceptual consequences of this adaptation: adapting to leftward gaze causes viewers to report that subsequent leftward gazes are looking directly at them, and direct gazes are looking to the right (Calder et al., 2008; Jenkins et al., 2006; Palmer et al., 2018a; Palmer et al., 2018). Adapting to direct gaze leads to a decrease in the responsiveness of the "direct" channel of neurons, causing the range of eye gaze deviations one would categorise as "direct" to narrow (Calder et al., 2008). These are negative aftereffects, as the perception of subsequent test stimuli is biased look less like the adaptor.

Adaptation studies suggest that eye gaze is associated with multichannel neural coding. This means gaze is coded by multiple pools of neurons, each with a bell-shaped tuning curve centred over a different value (i.e., the left, direct, and right tuning curves depicted in Figure 14; Calder et al., 2008). The perception of the eye gaze is determined as the normalised sum of responses across three channels responding preferentially to left, direct, and right gaze. Repeated exposure to one gaze causes the corresponding channel of neurons to become less responsive, changing the normalised sum of responses that occur to subsequent gaze stimuli (Palmer et al., 2018a; Palmer et al., 2018).

### Figure 14.



Schematic of Multichannel Processing of Eye Gaze.

*Note.* Schematic of hypothetical neural channels responding preferentially to leftward (red), direct (black), and rightward (blue) gaze. Direct responses predominate in the shaded grey region. The bars above each schematic represent the relative responsiveness of each channel at the five gaze directions used in the example (-10, -5, 0, +5, and +10 degrees). Sourced from Calder and colleagues (2008).

Another temporal process is serial dependence. Serial dependence describes the opposite effect to adaptation, whereby new stimuli appear *more* similar to just-seen stimuli than they really are (Fisher & Whitney, 2014). Like adaptation, serial dependence has been observed across different stages of the visual hierarchy. Different stimuli presented one after another within a temporally tuned spatial field (termed a "continuity field") can appear similar or even identical, for low-level features such as numerosity all the way to more complex features like face identity. When participants were asked to adjust a random "adjustment face" to match "target face", these adjustments were often skewed to look like the identity of faces shown on previous trials (Liberman et al., 2014). Unlike adaptation, serial dependence does not require a long period of exposure and can occur to stimuli shown over 6-15 seconds after the inducer stimulus (Liberman et al., 2018; Liberman et al., 2014).

Serial dependence has been demonstrated in eye gaze perception (Alais et al., 2018). Participants briefly saw a face, then adjusted a pointer on a sphere to correspond to where they thought the eyes of the face were looking. The difference between where the pointer was placed and where the eyes of the face objectively looked on each trial (error) was plotted against the difference between the eye gaze on the current trial and the previous trial. When the change in eye gaze between the previous and current trial was small, around 4°, the eye gaze on the current trial was skewed towards that on the previous trial. For example, if the eye gaze on the previous trial was around 4° more leftward than the current trial, then the eye gaze in the current trial then appeared more leftward than it was (Alais et al., 2018).

Why is eye gaze perception subject to both adaptation and serial dependence when they have opposing effects on perception? One possibility is that adaptation and serial dependence reflect different goals of the visual system. When looking at the same stimulus for a long time, the visual system adapts in order to maximise sensitivity to changes, as these changes are ordinarily meaningful (Fischer & Whitney, 2014; Fritsche et al., 2017). For example, if the person you are making eye contact with suddenly looks just over your shoulder, that is a meaningful difference that you need to be sensitive to. Likewise, if you look between two different faces, then the changes in facial features are meaningful and need to be noticed. On the other hand, small changes can occur in the stimuli we are looking at that are not meaningful, and our perception of these stimuli will be less noisy if these small changes are factored out (Alais et al., 2018; Fischer & Whitney, 2014; Fritsche et al., 2017). When making eye contact with someone, their eyes will constantly be making small saccades independent of gaze direction. If someone moves their head while talking to you and the new perspective dramatically changes the way they look, you wouldn't want to mistake that for a change in identity. In these ways, adaptation and serial dependence function together to maximise changes that are meaningful and minimise changes that are meaningless.

A handful of studies have looked at adaptation in DP. They generally found atypical adaptation to face identity (Palermo et al., 2011; Steeves et al., 2009, but see Nishimura et al., 2010; Susilo et al., 2010) but typical adaptation to gaze (Duchaine et al., 2009). This finding supports a dissociation between identity and gaze processing, but the small sample of the gaze study (N=7) prevents strong conclusions to be drawn. Serial dependence has not been studied in DP, but face recognition skills in the typical population are positively correlated with the strength and narrow tuning of serial dependence effects to face identity. That is, those with better face recognition abilities showed a larger effect of serial dependence on face identity, but only when the sequential faces were already highly similar (Turbett et al., 2019). This

finding suggests that serial dependence to face identity is related to face recognition abilities, so is likely to be reduced in DP.

Study 2 aimed to test the temporal integration of eye gaze in DP by looking at adaptation and serial dependence in eye gaze perception. A subset of the participants in Study 1 completed an adaptation task (Palmer et al., 2018a; Palmer et al., 2018) and a serial dependence task (modelled off Liberman et al., 2014). Normal performance by DP participants would support a dissociation between gaze and identity processing, whereas impaired performance by DP participants would be consistent with the notion that gaze and identity processing rely on common mechanisms.

#### 3.2 Method

### **3.2.1** Participants

All participants from Study 1 were invited back to complete the adaptation task from Study 2. Those who returned included 45 adults with developmental prosopagnosia ( $M_{age}$  = 41.56,  $SD_{age}$  = 8.74, 10 male, 34 female, 1 other) and 45 control participants ( $M_{age}$  = 39.76,  $SD_{age}$  = 7.70, 11 male, 34 female). There were no significant differences in sex ( $\chi^2(2) = 0.03$ , p = .849) or age (t(88) = 1.04, p = .303) between the groups. The DP and control participants were recruited as in Study 1 so met the same exclusion criteria; the CFMT screening scores for these new groups can be found in Appendix B.1. Participants with DP received a voucher worth US\$2.70 for their participation in the adaptation task. Control participants received US\$1.50.

All participants who completed the adaptation task were later invited to complete the serial dependence task. The participants did not complete both tasks in the same session due to the length of the serial dependence task and the potential for adaptation effects to carryover between tasks. Of the sample that completed the adaptation task, 19 participants with DP ( $M_{age}$  = 41.53,  $SD_{age}$  = 9.09, 4 male, 14 female, 1 other) and 22 control participants ( $M_{age}$  = 41.32,  $SD_{age}$  = 7.36, 3 male, 19 female) returned. They were again matched on age (t(39) = 0.08, p =

.936) and sex ( $\chi^2(2) = 1.69$ , p = .430). Before reaching this sample, two DP participants and one control were excluded for being statistical outliers (2 SDs above or below the group mean). This was important for this particular task as the much smaller sample size made it more susceptible to skewness from outliers. Participants with DP received a voucher worth US\$6.00 for their participation, while control participants received US\$4.50.

Participants completed the tasks online on Testable (<u>www.testable.org</u>), in their own time and on their own computer. Ethical approval for this study was granted by the School of Psychology Human Ethics Committee, on delegated authority by the Victoria University of Wellington Human Ethics Committee.

### **3.2.2 Adaptation Task**

## Stimuli

I used the same 6 face identities from the Wollaston task in Study 1. This time, all heads were forward-facing. The test faces had eye gazes averted between  $-16^{\circ}$  (left) and  $+16^{\circ}$  (right) in 4° intervals, whereas the adaptor faces had eye gazes averted to  $\pm 30^{\circ}$ . The faces were presented at the same size as in the Wollaston task other than the adaptor faces, which were 25% smaller. This was to reduce the effects of adaptation to lower-level retinotopic representations (Palmer & Clifford, 2017a, Jenkins et al., 2006; Webster & MacLeod, 2011). Additionally, the position of the test faces was randomly jittered by up to 50 pixels vertically and/or horizontally from the centre of the screen. The identities of adaptor and test faces also differed, further ensuring that adaptation was not also occurring to high-level representations of face identity.

### Procedure

The adaptation task followed a similar procedure to that of Palmer and colleagues (2018a; Palmer et al., 2018) and Palmer and Clifford (2017). This consisted of three phases: (1) a pre-adaptation test of perceived gaze direction, (2) an adaptation period in which

participants were adapted to left- or right-averted gaze, and (3) a post-adaptation test of aftereffects on perceived gaze direction. Figure 15 below demonstrates an example trial with all three phases.

# Figure 15.

Adaptation Task Trial Diagram.



*Note.* Example of a single trial from (A) the pre-adaptation phase, (B) the adaptation phase, and (C) the post-adaptation phase.

In the pre-adaptation phase, participants viewed a test face for 500 ms then were asked to report whether the face was looking left, direct, or right by pressing the left, down, and right arrow keys on their keyboard, respectively. Three face identities were used. Each identity could be looking in nine directions:  $16^{\circ}$ ,  $12^{\circ}$ ,  $8^{\circ}$ ,  $4^{\circ}$  left or right, or  $0^{\circ}$  (direct). Each direction was repeated 12 times, resulting in 108 trials (3 identities x 9 directions x 12 repeats). Trials were presented in a random order. Participants were given the opportunity to take a self-terminated break halfway through. This phase took participants around five minutes to complete. In the adaptation phase, participants saw an adaptor face for 4 seconds. On one-fifth of trials the eyes of the face would flash from dark brown to light brown for 200 ms. After every trial, participants were asked whether they had seen the eyes change colour during the trial, and replied by pressing 'Y' for "yes" and 'N' for "no". This task ensured that participants were attending to the eyes during adaptation, and served as an attention check. Three face identities, different to the identities used in the pre-adaptation phase, were used as adaptor faces. Each identity was presented five times, resulting in a total of 15 trials. Trials were presented at random. Half of the participants in each group adapted to faces looking 30° left (Adapt Left condition); the other half adapted to faces looking 30° right (Adapt Right condition). This phase took around a minute to complete.

The post-adaptation phase used the exact same 108 trials as the pre-adaptation phase, except for two differences designed to maintain the effects of adaptation. First, a "top-up" adaptor was shown for 4 seconds before each trial. Second, participants completed the entire adaptation phase again halfway through. The post-adaptation phase took around 10 minutes to complete. Overall, the adaptation task took around 20 minutes to complete.

### 3.2.3 Serial Dependence Task

### Stimuli

The same identities as in Study 1 and the adaptation task were used again. All faces were looking straight forward and had eye gazes averted between  $-20^{\circ}$  (left) and  $+20^{\circ}$  (right) in 5° intervals. The serial dependence task also used the scrambled face shown in Figure 16 as a mask. This stimulus was a single face identity with direct gaze, scrambled using the created using the "Scramble" function on webmorph.org.

### Figure 16.

Scrambled Face Stimulus Used as a Mask in the Serial Dependence Task.



*Note.* This scrambled face, made using the "scramble" function on WebMorph.org, was displayed after every face in the serial dependence task.

# Procedure

This task was modelled after Experiment 2 in Liberman and colleagues' (2014) study of serial dependence in face identity processing. I used this study as a model as it includes a categorical response method that lends itself more easily to online experiment platforms than the method of adjustment used in the previous study of serial dependence in eye gaze processing (Alais et al., 2018).

Each trial presented participants with a sequence of two faces with different eye gazes and identities. Face 1 was presented for 1 second, followed by a scrambled face mask (Figure 16) for 1 second. After a 250 ms ISI during which a fixation cross was presented, Face 2 was shown for 500 ms, followed by the same mask for 1 second. After this, half of the participants were asked which face looked *more* right (Right condition); the other half were asked which face looked *more* left (in the Left condition). They responded by pressing "1" for Face 1 or "2" for Face 2. This was followed by a 500 ms ITI. Example trial sequences are illustrated in Figure 17.

### Figure 17.

Trial Diagram for the Serial Dependence Task.



*Note*. Illustration of two possible trial sequences in the serial dependence task (Right condition).

The eye gaze of Face 1 in a trial could differ from the eye gaze of Face 2 in one of five ways. The eye gaze of Face 1 could be  $\pm 10^{\circ}$ ,  $\pm 5^{\circ}$ , or  $0^{\circ}$  more/less averted than the eye gaze of Face 2. A negative difference means that Face 1 looked more to the left than Face 2, and a positive difference means that Face 1 looked more to the right than Face 2. A difference of  $0^{\circ}$  means the first and second face had the same eye gaze. Trials could either be "Right-previous" or "Left-previous", depending on whether the eye gaze direction of Face 1 in the trial prior to the current trial (the 1-back trial) was looking *more* rightward or *more* leftward than the current trial's first face. We are interested in the effect that the eye gaze of Face 1 in the 1-back trial has on the perception of Face 1 in the current trial.

Again, the image presentation was manipulated in such a way as to minimise dependencies to low-level image attributes instead of to high-level eye gaze representations. The position of Face 2 in each trial varied randomly by up to 80 pixels in the horizontal and/or vertical planes. Participants completed 50 practice trials followed by 360 test trials. This task took participants around 45 minutes to complete.

#### **3.3 Results**

All analyses were conducted in Jamovi version 1.1.9 (Jamovi project, 2020) or JASP version 0.13.1 (for Bayesian analyses; JASP Team, 2020) unless otherwise stated. Modelling was conducted in MATLAB 2020a (MathWorks, 2020) and model fitting used the nonlinear least squares method. Welch's *t*-tests were used in place of Student's *t*-tests wherever the assumption of equal variances was violated. Bonferroni *t*-tests were used to follow up significant ANOVAs. Descriptive statistics for DP and control performance on all tasks are in Appendix B.1. The measures I focused on are accuracy/response-based, but RT analyses can be found in Appendix B.2.

### 3.3.1 Adaptation Task

## Data Checks

Before measuring adaptation effects, I checked whether the DP and control groups were similarly attentive during the adaptation phase. An independent samples *t*-test revealed that the DP (M = 0.93, SD = 0.08) and control (M = 0.95, SD = 0.06) groups showed similar accuracy for detecting eye colour change during adaptation (t(88) = 1.25, p = .213), indicating similar levels of engagement with the adaptor faces. I also checked whether there were differences between the left and right adaptation conditions. A 2 (condition: right, left) X 2 (group: DP, control) X 2 (phase: pre-adaptation, post-adaptation) X 9 (direction:  $-16^{\circ}$ ,  $-12^{\circ}$ ,  $-8^{\circ}$ ,  $-4^{\circ}$ ,  $0^{\circ}$ ,  $4^{\circ}$ ,  $8^{\circ}$ ,  $12^{\circ}$ ,  $16^{\circ}$ ) mixed-measures ANOVA revealed no main effect of condition (F(1, 86) = 0.04, p = .836,  $\eta^2_p < .001$ ) and no interaction of condition and group (F(1, 86) = 0.26, p = .614,  $\eta^2_p < .001$ ), indicating comparable performance across conditions, which did not differ between the groups. Thus, in subsequent analyses, I collapsed across the right and left adaptation condition (i.e., so that  $-16^{\circ}$  became  $16^{\circ}$ ,  $-12^{\circ}$  became  $12^{\circ}$ , and so on).

### **Centroid Method**

I first analysed the adaptation effects using the centroid of participants' pre- and postadaptation data. The centroid was the sum of the proportion of "direct" responses at each eye gaze deviation multiplied by that corresponding eye gaze deviation, divided by the sum proportion of direct responses across all gaze deviations. A shift in this value between the preadaptation phase and the post-adaptation phase implies that the perception of eye gaze was skewed by adaptation -i.e., a rightwards/positive shift in this value after adapting to rightwards gaze implies that direct gaze now appears to be slightly leftward averted. I submitted the centroid values to a 2 (phase: pre-adaptation, post-adaptation) X 2 (group: DP, control) mixedmeasures ANOVA. This data is shown in Figure 18. There was a main effect of phase (F(1,88) = 280.05, p < .001,  $\eta^2_p = .46$ ), such that centroid values were lower (i.e., more leftward) in the pre-adaptation phase (M =  $0.09^{\circ}$ , SD =  $1.07^{\circ}$ ) compared to the post-adaptation phase (M =  $2.43^{\circ}$ ,  $SD = 1.40^{\circ}$ ), t(88) = 16.74, p < .001. There was no main effect of group (F(1, 88) = 0.18, p = .671,  $\eta^2_p = .002$ ) and no interaction (F(1, 88) = 0.30, p = .588,  $\eta^2_p = .003$ ), indicating that the change in centroid from pre- to post-adaptation did not differ between the groups. After adapting to 30° rightward gaze, the perception of direct gaze shifted to 2.43° rightward on average across the groups (i.e., truly direct gaze appeared slightly more leftward, a negative aftereffect). Bayes factors indicated strong evidence for the main effect of phase ( $BF_{incl} =$ 1.133e+14), and moderate evidence for no main effect of group ( $BF_{incl} = 0.23$ ) and no interaction ( $BF_{incl} = 0.20$ ).

## Figure 18.

Centroid Differences Compared Across the DP and Control Groups.



*Note*. Small dots represent individual data points and larger circles represent the group means. Control data are represented in light grey and DP data in dark grey.

# Parametric Method

To enhance the robustness of the results, I also analysed the data using a parametric method, following other eye gaze adaptation studies (e.g., Duchaine et al., 2009). I tested for differences in adaptation effects between the groups with a 2 (group: DP, control) X 2 (phase: pre-adaptation, post-adaptation) X 9 (direction:  $-16^{\circ}$ ,  $-12^{\circ}$ ,  $-8^{\circ}$ ,  $-4^{\circ}$ ,  $0^{\circ}$ ,  $4^{\circ}$ ,  $8^{\circ}$ ,  $12^{\circ}$ ,  $16^{\circ}$ ) mixed-measures ANOVA. The dependent variable was the proportion of direct responses at each gaze direction. Adaptation effects are indexed by changes in proportion of direct responses after adaptation. For example, after adapting to a rightward gazing adaptor, rightward gaze would appear more direct/less right, which would increase the proportion of direct responses to rightward gaze probes.

The parametric analysis is shown in Figure 19. There was a main effect of block (*F*(1, 88) = 58.06, p < .001,  $\eta^2_p = .40$ ), such that the proportion of direct responses was higher after adaptation (*M* = 0.47, *SD* = 0.08) than before adaptation (*M* = 0.39, *SD* = 0.06) (*t*(88) = 7.62, p < .001). There was no interaction of block and group (*F*(1, 88) = 0.56, p = .458,  $\eta^2_p = .01$ ),

indicating this did not differ between DP and control participants. There was a significant main effect of direction (F(8, 704) = 1003.77, p < .001,  $\eta^2_p = .92$ ), indicating that the proportion of direct responses differed across the range of eye gaze directions, which again did not differ between the groups (no interaction of gaze and group, F(8, 704) = 1.18, p = .311,  $\eta^2_p = .01$ ). There was a main effect of group (F(1, 88) = 4.31, p = .041,  $\eta^2_p = .05$ ), such that DP participants (M = 0.45, SD = 0.10) made a slightly higher proportion of direct responses overall than controls (M = 0.41, SD = 0.08), t(88) = 2.08, p = .041. Critically, there was an interaction between phase and direction (F(8, 704) = 75.87, p < .001,  $\eta^2_p = .46$ ), indicating that the proportion of direct responses at different directions changed differently after adaptation, reflecting adaptation effects. As expected for rightward gazing adaptor, the proportion of direct responses decreased at  $-8^{\circ}$  and  $-4^{\circ}$  (*p*-values < .001) and increased at  $4^{\circ}$ ,  $8^{\circ}$ ,  $12^{\circ}$ , and  $16^{\circ}$ degrees (p-values < .05). There was no three-way interaction of phase, direction, and group, indicating that the adaptation effects were similar for the DP and controls groups. Bayes factors suggested moderate evidence for no interaction of block and group ( $BF_{incl} = 0.12$ ), strong evidence for no interaction of gaze and group ( $BF_{incl} = 0.01$ ), strong evidence for an interaction of block and gaze ( $BF_{incl} = 2.232E+85$ ), and strong evidence for no three-way interaction of block, gaze, and group ( $BF_{incl} = 0.01$ ).

#### Figure 19.

Comparison of Direct Responses Across the Pre- and Post-adaptation Blocks.



*Note.* DP data is represented in red and control data in blue. Pre-adaptation data is indicated by dashed line and post-adaptation data by solid lines. Locations of significant differences are indicated by the asterisks – these signal the significant differences in direct responses between the pre- and post-adaptation blocks, and do not differ between the groups.

# **3.3.2 Serial Dependence Task**

# **Estimating Serial Dependence**

To measure serial dependence in eye gaze processing, I used the same method used by Liberman and colleagues (2014) to measure serial dependence in face identity processing. I sorted trials into Right-previous and Left-previous trials based on whether the 1-back first face looked relatively more right or more left than the current trial's first face. For each participant, I fit separate psychometric functions to the proportion of "1" responses on Right-previous and Left-previous trials using the equation:

$$P(respond \ 1 \ on \ trial \ n) = \frac{1}{1 + e^{-a(x_n - b)}}$$

Where  $x_n$  is the difference in eye gaze between Face 1 and Face 2 on trial n (-10°, -5°, 0°, 5°, or 10°), parameter a scales with the slope, and b is the point of subjective equality (PSE; Liberman et al., 2014). An example of these curves can be seen in Figure 20 below.

# Figure 20.

Examples of Logistic Functions Fit to a Single Participant's Serial Dependence Data.



*Note.* Examples of the function fit to an individual's data in the "Left" condition (left) and the "Right" condition (right). Blue points and lines represent data from Left-previous trials, red points and lines represent data from Right-previous trials, and yellow points and lines represent a function fit to all "1" responses, blind to the previous trial. The PSE values come from the point on the x-axis corresponding to 0.5 on the y-axis. A positive PSE difference (Left-previous minus Right-previous) represents positive serial dependence, as shown in both graphs above.

I tested the significance of the difference between Right- and Left-previous PSEs for each individual participant by calculating a bootstrapped distribution of PSE values from their data. Within each trial type (Right-previous and Left-previous) and gaze difference ( $-10^{\circ}$ ,  $-5^{\circ}$ ,  $0^{\circ}$ ,  $5^{\circ}$ , and  $10^{\circ}$ ), I resampled the data with replacement for 10,000 iterations using the *bootstrp* function in MATLAB 2020a. I then fit a psychometric function to each new combination of proportions to come up with 10,000 new Right-previous PSE values and 10,000 new Leftprevious PSE values. To test that the difference in PSE values between the Right- and Leftprevious functions was significant, I ran a premutation analysis using *permutationTest* in MATLAB 2020a, shuffling the "Right-previous" and "Left-previous" labels. This resulted in a null distribution of 10,000 permutated PSE difference values for each subject to compare to their observed PSE difference.

## Data Checks

I performed several checks to ensure that the serial dependence data are appropriate for comparing effects across groups. First, I checked whether the condition the participants were assigned to affected task performance. I submitted the PSE difference values to a 2 (group: DP, controls) X 2 (condition: "Right", "Left") ANOVA. There was no main effect of condition  $(F(1, 37) = 0.59, p = .447, \eta^2_p = .02, BF_{incl} = 0.32)$  and no interaction of condition and group  $(F(1, 37) = 1.32, p = .259, \eta^2_p = .03, BF_{incl} = 0.26)$ , indicating that the condition a participant was in did not influence their performance, and this did not differ between the DP and control groups.

I also checked that the average first face gaze direction did not differ between Rightprevious and Left-previous trials in either group with a 2 (group: DP, controls) X 2 (trial type: Right-previous, Left-previous) mixed measures ANOVA. There was no main effect of group  $(F(1, 39) = 0.01, p = .942, \eta^2_p < .001, BF_{incl} = 0.20)$  or trial type  $(F(1, 39) = 0.64, p = .429, \eta^2_p = .02, BF_{incl} = 0.24)$ , and no interaction  $(F(1, 39) = 0.59, p = .449, \eta^2_p = .02, BF_{incl} = 0.09)$ , indicating that the stimuli in each trial type and each group was balanced.

I then checked that model fits were adequate overall. As there is no consensus on the best measure of a logistic model's predictive power or goodness-of-fit, a conservative approach is to ensure a model passes multiple tests. In Table 3 below I report some common statistics for goodness-of-fit (Pearson's  $\chi^2$  and its corresponding *p*-value; average deviance at the solution vector), predictive ability (pseudo- $R^2$ ), and the quality of the model for the supplied

data (Akaike Information Criterion, corrected for small samples [AICc]). All values indicate that the logistic functions fit the data well and the values did not differ significantly between the groups.

## Table 1.

Average Goodness-of-Fit and/or Predictive Power Statistics for Logistic Models.

		V	alue	Group difference	
Measure	Direction of Measure	DP	Control	( <i>p</i> -value)	
Pearson's $\chi^2$	$\uparrow = worse$	0.08	0.11	.095	
Pearson's $\chi^2 p$ -value	$\uparrow$ /non-sig = better	0.885	0.844	.615	
Deviance	$\uparrow = $ worse	1.74	1.57	.287	
Pseudo- $R^2$	↑ = better	0.97	0.95	.089	
AICc	$\uparrow = $ worse	13.00	13.03	.839	

## Serial Dependence Effects

Serial dependence occurs when there is a positive change in the PSE between the Rightprevious and Left-previous functions (see Figure 20). The Left-previous PSE should be *larger* than the Right-previous PSE, creating a positive PSE difference score when the Right-previous PSE is subtracted from the Left-previous PSE. On Right-previous trials, serial dependence would make the participant less able to discriminate the two faces when Face 1 was objectively looking slightly more *leftwards* than Face 2, because the rightward looking Face 1 in the 1back trial caused Face 1 in the current trial to appear more right than it actually was.

I tested whether these PSE difference values were equal across the groups with an independent samples *t*-test (Figure 21 below, plots for each individual are in Appendix B.3, Figures B2 and B4). There were no differences between the groups (t(36.38) = 1.33, p = .193, d = .40), indicating that PSE differences did not differ between DP participants (M = 3.12, SD = 2.18) and controls (M = 4.28, SD = 3.36). Bayes factors indicated anecdotal evidence for the null hypothesis (BF<sub>10</sub> = 0.59).

### Figure 21.





Note. Small dots represent individual data points and larger circles represent the group means.

I computed the effect size of the serial dependence effect by bootstrapping the observed Right- and Left-previous PSE values yielded by each participant within each group 10,000 times, then permutating the condition labels 10,000 times to create a null distribution of PSE differences. The serial dependence effect size was 8.23 in the DP group and 4.19 in the control group. This is shown in Figure 22 below. That the effect size was larger for DP participants compared to controls despite no group differences could be due to the much larger standard deviation in the control group, as visible in Figure 21 above.

# Figure 22.

Comparison of Group PSE Differences to Bootstrapped and Permutated Null Distributions.



*Note.* The result of bootstrapping and permutating the difference score of the Right-previous PSE subtracted from the Left-previous PSE, in control (left) and DP (right) participants. The blue bars represent the null distribution, and the red dot represents the average difference score. The effect size refers to Cohen's *d*: the observed difference between the two measures divided by the pooled standard deviation.

To examine the results further, I analysed the data at the single subject level. I used the bootstrapping and permutation methods described above to see whether each *individual's* PSE difference was significantly greater than 0. I was interested in whether the number of participants demonstrating a significant, positive PSE difference was equal between the groups. A Chi-square test revealed that the DP and control groups had a similar proportion of participants showing serial dependence (19/19 DP participants and 20/22 controls;  $\chi^2(1) = 0.03$ , p = .873). Plots of the outcome of the bootstrapping and permutation can be found in Appendix B.3, Figures B3 and B5.

#### **3.3.3** Alternative Explanations for the Serial Dependence Effect

The above analyses indicate no difference between the groups in the magnitude of serial dependence for eye gaze. However, this conclusion assumes that the effect was driven by serial dependence rather than alternative processes that might produce similar-looking effects, particularly priming and response hysteresis. I examined these alternative explanations below.

# Priming

A key issue in serial dependence research is whether the effect can be explained by priming (Fisher & Whitney, 2014; Liberman et al., 2014; Liberman et al., 2018). Priming occurs when the repeated presentation of a stimulus makes it easier to detect or recognise (Henson, 2003; Schacter & Buckner, 1998; Tulving & Schacter, 1990). In my study, priming would make participants more likely to identify the first face as looking more rightward when the 1-back first face was looking right because they are *primed* to detect and respond to rightward gaze, which occurs at the level of response generation, rather than because their perception had been skewed by the previously seen rightward gaze. This would result in a similar effect as is predicted for serial dependence. However, priming and serial dependence can be dissociated by looking at response time and stimulus discriminability.

**Response Time.** Priming improves the response time to primed stimuli (Fischer & Whitney, 2014) as the motor response can be prepared ahead of time. This predicts that in the "Right" condition, "1" responses should be made faster when the 1-back first face was looking rightwards (primed trials) as opposed to leftwards (unprimed trials), and vice versa in the "Left" condition. Serial dependence, on the other hand, makes no predictions about response times. A 2 (group: DP, control) X 2 (response: primed, unprimed) mixed measures ANOVA revealed no main effect of response (F(1, 39) = 1.24, p = .271,  $\eta^2_p = .03$ , BF<sub>incl</sub> = 0.29) or group (F(1, 39) = 0.41, p = .525,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.41 [absence of evidence]), and no interaction (F(1, 39) = 0.41, p = .525,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.41 [absence of evidence]), and no interaction (F(1, 39) = 0.41, p = .525,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.41 [absence of evidence]), and no interaction (F(1, 39) = 0.41, p = .525,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.41 [absence of evidence]), and no interaction (F(1, 39) = 0.41, p = .525,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.41 [absence of evidence]), and no interaction (F(1, 39) = 0.41, p = .525,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.41 [absence of evidence]), and no interaction (F(1, 39) = 0.41, p = .525,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.41 [absence of evidence]), and no interaction (F(1, 39) = 0.41, p = .525,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.41 [absence of evidence]), and no interaction (F(1, 39) = 0.41, p = .525,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.41 [absence of evidence]), and no interaction (F(1, 39) = 0.41]

39) = 0.46, p = .501,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.15). This suggests comparable response times for primed and unprimed trials in both groups (Figure 23).

### Figure 23.

DP and Control Response Times (Primed and Unprimed)



Note. Small dots represent individual data points and larger circles represent the group means.

**Stimulus Discriminability.** Priming and serial dependence also differ in terms of their effects on stimulus discriminability. Priming *improves* the discriminability of repeated stimuli, while serial dependence *reduces* the discriminability of repeated stimuli by altering their appearance (Fischer & Whitney, 2014). Stimulus discriminability can be measured through the slope of the psychometric function, where a steeper slope represents better discrimination. Since priming improves discriminability, the slopes of the Right- and Left-previous functions should be steeper than the slope of a function fit to the entire dataset regardless of the previous trial (Fischer & Whitney, 2014). In contrast, serial dependence predicts that the slope of the Right- and Left-previous functions should be shallower than that of the function fit to the entire dataset.

I averaged the slopes of the functions fit to the Right- and Left-previous trials for each participant to create an overall "split" slope value, and fit a function to all of the participant's trials (i.e., collapsed across Right- and Left-previous trials) to get a "combined" slope value. If the split slope is larger (steeper) than the combined slope, this suggests better discrimination when the data is split by the previous trial (i.e., there is priming). To test for differences between the groups, I implemented a 2 (group: DP, control) X 2 (function: split, combined) mixed measures ANOVA on the slope values. This is shown in Figure 24. There was a main effect of function (F(1, 39) = 52.65, p < .001,  $\eta^2_p = .58$ , BF<sub>incl</sub> = 974848.04), such that split slopes (M = 0.28, SD = 0.08) were slightly but significantly steeper than combined slopes (M = 0.25, SD = 0.08), t(39) = 7.26, p < .001. I found no main effect of group (F(1, 39) = 0.29, p = .591,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.66) or function X group interaction (F(1, 39) = 0.60, p = .442,  $\eta^2_p = .02$ , BF<sub>incl</sub> = 0.65). This suggests that discrimination was higher when the data is split by the effect of the previous trial, as predicted by priming, and that this did not differ between the groups.

### Figure 24.





*Note*. Small dots represent individual data points and larger circles represent the group means.

Following previous literature (Fischer & Whitney, 2014), I used a second method to determine whether the difference between the slopes of the split and combined function was different in the two groups. I compared the observed difference between the functions (combined slope minus split slope) to a null distribution of difference scores, created by bootstrapping the data 10,000 times then permutating the slope labels on each iteration using *bootstrp* and *permutationTest* functions in MATLAB 2020a. The results showed that the average difference score was significantly different from zero for DP and control participants, indicating priming effects in both groups. The results of the permutation tests are shown in Figure 25.

### Figure 25.





*Note.* The result of bootstrapping and permutating the slope difference score (combined slope minus the Right- and Left-previous average slope) in control (left) and DP (right) participants.

The blue bars represent the null distribution, and the red dot represents the average difference score. The effect size refers to Cohen's *d*.

The effect size of priming for DP participants (d = 1.85) was slightly larger than that for controls (d = 1.58). However, these effect sizes were much smaller than the effect sizes for serial dependence, which were d = 8.23 for DP participants and d = 4.19 for controls (section 3.3.2). Since Cohen's d values can be readily compared to one another, the effect size for priming is clearly much smaller than the effect size for serial dependence. This suggests that priming cannot account for the entirety of the serial dependence effects in either group.

**Summary**. While RT analyses suggested that priming did not occur, slope analyses suggested that DP and control participants showed some effects of priming. However, effect size comparisons indicated that the effect of priming was much smaller than the effect of serial dependence in both groups, suggesting that priming cannot entirely explain the results.

## **Response Hysteresis**

Another mechanism frequently discussed in serial dependence experiments is response hysteresis (Fischer & Whitney, 2014; Liberman et al., 2014). Response hysteresis is the tendency for previous responses to influence the current response, which could produce results similar to those generated by serial dependence. To disentangle response hysteresis and serial dependence, I simulated data for each participant that included varying degrees of response hysteresis, and then compared the simulated results with actual results (as in Liberman et al., 2014). To simulate data with x% of response hysteresis, I replaced x% of the actual responses with repeats of the response made on the previous trial. For example, to simulate a dataset with 10% response hysteresis, 90% of trials had the correct response (i.e., responding "1" in the "Right" condition when the first face was indeed looking more right) and the other 10% of trials simply repeated the response made on the previous trial. I then coded and analysed this data for each level of hysteresis as in the previous analyses to determine the magnitude of the serial dependence effect for each participant, including the bootstrapping and permutation to determine the effect size and significance of the PSE differences.

Following Liberman and colleagues (2014), I initially simulated this data with 7 levels of response hysteresis (10% - 70%). I used the same goodness-of fit tests as in section 3.3.2 to assess these new datasets and compare them to the same measures applied to the real data using 2 (group: DP, control) X 8 (dataset: actual, 10%, 20%, 30%, 40%, 50%, 60%, 70% hysteresis) mixed-measures ANOVAs. All ANOVAs returned a main effect of dataset only (ps < .001), with *post hoc* tests revealing that the simulated data displayed worse fits on almost all measures for all simulated datasets. This is shown in Table 2 below.

### Table 2.

Model Fit Measures at Each Level of Simulated Hysteresis (%).

Measure	Pearson's $\chi^2$		<i>p</i> -value		Deviance		Pseudo- <i>R</i> <sup>2</sup>		AICc	
Dataset	DP	Control	DP	Control	DP	Control	DP	Control	DP	Control
Actual	0.14	0.20	.340	.386	0.08	0.11	0.97	0.94	13.00	13.01
10%	3.74*	3.77*	.054*	.054*	0.25*	0.29*	0.97	0.97	17.41*	17.40*
20%	2.69*	2.71*	.104*	.102*	0.27*	0.33*	0.93	0.92	18.13*	18.13*
30%	1.96*	2.01*	.165*	.160*	0.23*	0.27*	0.90*	0.89*	18.57*	18.56*
40%	1.37*	1.38*	.248*	.245*	0.18*	0.23*	0.86*	0.84*	18.91*	18.92*
50%	0.92*	0.94*	.344*	.341*	0.14*	0.19*	0.84*	0.79*	19.15*	19.16*
60%	0.59*	0.61*	.454*	.445*	0.10*	0.14*	0.80*	0.75*	19.32*	19.32*
70%	0.34*	0.35*	.576*	.568*	0.07*	0.11*	0.73*	0.66*	19.44*	19.45*

\* significantly different from the actual dataset at p < .001.

**Summary.** The logistic model of serial dependence effects did not fit the simulated data as well as the actual data, meaning that comparing the PSE values between the actual data and the simulated data might not be a legitimate comparison. In itself, this suggests that response hysteresis could not have explained the observed results.

### 3.3.4 Follow-up Analyses of the Serial Dependence Effect

So far, I have established that DP and control participants showed a similar amount of serial dependence for eye gaze, and that this effect could not be accounted for entirely by

priming or response hysteresis. However, the effects in the two groups could have arisen through different mechanisms or occurred over different timescales. These possibilities were examined in further follow-up analyses.

### Dependence on Face 1 versus Face 2

The structure of the serial dependence task is such that dependence should be more likely to occur to the 1-back first face instead of the 1-back second face. This is because the first face is presented for longer than the second face, and it is seen around 6 seconds before the current-trial's first face. The 1-back second face is seen around 4.75 seconds before the current-trial's first face, which has been considered too short a timeframe for dependence to occur within (Liberman et al., 2018; Xia et al., 2016). This is the reason why all the analyses so far have assumed serial dependence due to the 1-back first face. However, if the nature of the dependence shown by DP and control participants differed – for example, if their continuity field was maximally tuned to a different temporal timeframe – dependence effects could be stronger to the 1-back second face. In this analysis I examined whether the DP and control groups differed on this issue.

To determine whether serial dependence occurred to the 1-back second face, the same procedure used for analysing Right- and Left-previous PSE values based on the gaze direction of the 1-back first face was applied to the data based on the gaze direction of the 1-back second face. Plots of each individual's 1-back second face data can be found in Appendix B.3, Figures B6 and B8.

To see if PSE differences were similar when looking at the gaze direction of the 1-back first face, I used a 2 (group: DP, control) X 2 (face: 1-back first, 1-back second) mixed measures ANOVA. This is shown in Figure 26. There was no main effect of group (F(1, 39) = 2.96, p = .093,  $\eta^2_p = .07$ , BF<sub>incl</sub> = 0.84), no main effect of face (F(1, 39) = 0.36, p = .552,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.23) and no interaction of group and face (F(1, 39) = 2.60, p = .115,  $\eta^2_p = .06$ , BF<sub>incl</sub> = 0.31),

demonstrating that neither group showed a smaller or larger PSE difference when the data was split by the gaze direction of the 1-back second face.

### Figure 26.

PSE Differences Based on the Direction of Gaze of the 1-back First or Second Face.





I used the same methods to see for how many participants the change in PSE based on the gaze of 1-back second face was significant and positive (Appendix B.3, Figures B7 and B9). A Chi-square test suggested the proportion of participants with a significant positive PSE shift did not differ between the DP and control groups, ( $\chi^2(1) = 0.03$ , p = .869), indicating that the proportion of participants with significant dependence to the 1-back second face was similar between the groups (18/19 DP and 19/22 control participants).

**Summary.** DP and control participants did not differ in the degree to which their perception was pulled by the first and second face of the previous trial, which could suggest no difference in the temporal tuning of the continuity field. Interestingly, for both groups, there

was strong evidence to suggest that perception was not being pulled *more* by the 1-back first face than the 1-back second face. Overall, there is little to suggest that the 1-back second face could not have an *equally* large effect on the perception of eye gaze.

## Modulation by Face Identity

In typical participants, serial dependence for facial expression can be enhanced when the identities of the faces are more similar; for example, when they are the same gender (Liberman et al., 2018). Motivated by this finding, I examined whether serial dependence for eye gaze was also modulated by identity similarities in either group.<sup>1</sup> To do this, I split the trials by whether the identity of the 1-back first face matched or mismatched the current first face. I then fitted Right- and Left-previous functions for each kind of trial as described previously (individual plots can be found in Appendix B.3, Figures B10-B17).

These data are likely to be noisier than data from all trials as the pool of responses which can be included is reduced, and unevenly so, when splitting them into match and mismatch trials. Identity matches were relatively rare, occurring on 59.57/360 trials on average (around 17%). For this reason, I made sure to compare the same model fit values between the match and mismatch trials to ensure that these two conditions were equally suited to the analysis, as well as comparing the fits of both of these conditions to the fit of the functions fit to the entire data. I used a series of 2 (group: DP, control) X 3 (dataset: all, identity match, identity mismatch) mixed measures ANOVAs to do this. There were main effects of dataset in all analyses except when using the Pearson  $\chi^2 p$ -value. There were no main effects of group and no interactions. The results are summarised in Table 3 below.

#### Table 3.

<sup>&</sup>lt;sup>1</sup> I completed the same analyses splitting the data by whether the gender of the two first faces was matched or mismatched. This meant the trial numbers were more balanced between conditions: gender matches occurred on 191.13/360 trials on average (53%), whereas identity matches occurred on 59.57/360 trials on average (17%). The main findings did not differ, so in the interests of brevity I report only the identity analyses here, as these are more relevant to a study with DP participants.

Measure	Pearson's $\chi^2$		<i>p</i> -value		Deviance		Pseudo- <i>R</i> <sup>2</sup>		AICc	
Dataset	DP	Control	DP	Control	DP	Control	DP	Control	DP	Control
Actual	0.14	0.2	.340	.386	0.08	0.11	0.97	0.94	13	13.01
ID match	0.55**	0.54**	.989	.887	1.98*	1.71*	0.83**	0.75**	12.82*	12.86*
ID mismatch	0.11	0.15	.885	.864	1.74	1.58	0.96	0.93	13.00	13.03

Model Fit Measures for Identity Match and Mismatch Datasets.

\*\* significantly different from the actual dataset at p < .001.

\* significantly different from the actual dataset at p < .050.

The identity match data displayed significantly worse goodness-of-fit values (Pearson's  $\chi^2$  and deviance) and predictive abilities (Pseudo- $R^2$ ) than the actual dataset. This result was expected given the relatively few trials used in the identity match condition. Interestingly, the AICc values – indicating the relative quality of the data for the model – were significantly better (lower) for identity match data compared to the actual dataset. However, as this difference in AIC values is < 2, it is considered negligible (Duong, 1984). I then used the PSE values in a 2 (group: DP, control) X 2 (identity: match, mismatch) mixed measures ANOVA. There was no main effect of group (F(1, 39) = 0.44, p = .510,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.24) or of identity (F(1, 39) = 0.26, p = .616,  $\eta^2_p = .01$ , BF<sub>incl</sub> = 0.20), and no interaction (F(1, 39) = 0.84, p = .365,  $\eta^2_p = .02$ , BF<sub>incl</sub> = 0.10), suggesting that identity did not modulate serial dependence in either group. This is shown in Figure 27 below.

# Figure 27.

PSE Differences on Identity Match and Mismatch Trials.



Note. Small dots represent individual data points and larger circles represent the group means.

I also used the bootstrapping and permutation methods described previously to measure for how many individual participants in each group the PSE differences were significant and positive when the face identities were matched and mismatched (Appendix B.3, Figures B10 to B17). If serial dependence is modulated by identity, the proportion of participants showing a positive PSE difference should be greater for match compared to mismatch trials. If serial dependence is not modulated by identity, then the proportion of participants with a positive PSE difference should be similar for both types of trials.

For controls, the proportion of individuals showing positive PSE differences was similar for identity match (17 significant, 5 non-significant;  $\chi^2(1) = 6.55$ , p = .011) and identity mismatch (19 significant, 3 non-significant;  $\chi^2(1) = 11.64$ , p < .001) trials,  $\chi^2(1) = 0.11$ , p = .739. Similarly, for DP participants, the proportion of individuals with positive PSE differences was comparable for both identity match (15 significant, 4 non-significant;  $\chi^2(1) = 6.37$ , p = .012) and identity mismatch (17 significant, 2 non-significant;  $\chi^2(1) = 11.84$ , p < .001) trials,  $\chi^2(1) = 0.13$ , p = .724.

**Summary**. Identity did not have an effect on the magnitude of the serial dependence effect in either group. This could suggest that serial dependence in the perception of eye gaze does not interact with the processing of face identity. Alternatively, that this analysis was *post hoc* rather than being planned from the outset meant that the pool of identity match trials was severely limited, potentially limiting the legitimacy of these analyses. This is reaffirmed by the poor goodness-of-fit measures which suggested the identity match data was too noisy, yet the AICc values indicated that following up this analysis could be interesting.

### **3.4 Discussion**

The aim of Study 2 was to determine if DP participants showed normal adaptation and serial dependence in eye gaze perception. The adaptation task shows that DP participants have an intact ability to adapt to eye gaze information. Similarly, DP participants showed intact serial dependence, which could not be explained by priming or response hysteresis. This interim discussion will link these findings back to how temporal integration is used in the perception of face identity and what this means for functional specificity in eye gaze processing.

The data from the adaptation task show that DP participants have intact adaptative coding of eye gaze direction. This extends the finding of Duchaine and colleagues (2009) who found typical eye gaze adaptation in a sample of seven DP participants. Together, these results show that gaze adaptation is not impaired in DP. This finding dissociates from studies of adaptation to face identity in DP, which have reported mixed results. Some people with DP showed impaired face identity adaptation (Palermo et al., 2011; Steeves et al., 2009), while others showed normal adaptation (Nishimura et al., 2010; Susilo et al., 2010). That this study found intact adaptation to eye gaze direction in DP provides evidence for functional specificity in eye gaze processing – adaptive processes used for eye gaze perception differ from those used in face identity perception.

The adaptation task also allowed me to measure of the cone of direct gaze (Appendix B.4). This refers to the range of physically averted eye gaze deviations that a person will report as looking directly at them (Gamer & Hecht, 2007). The cone of gaze typically ranges from around -10° to +10° (Balsdon & Clifford, 2018). The cone of direct gaze is often taken as a general measure of typical eye gaze categorisation ability, and it can be atypical in populations with deficits in processing the eye region (such as people with autism and schizophrenia; Hooker & Park, 2005; Senju et al., 2005; Tso et al., 2012; Vida et al., 2013). I measured the average cone of direct gaze and found comparable results across DP and control groups (Appendix B.4). This analysis further suggests that eye gaze processing is typical in DP. That the DP group made slightly but significantly more "direct" responses overall than the control group may be because they may be less confident in their responses on face tasks (e.g., Stumps et al., 2020) and direct responses tend to increase with uncertainty (Mareschal et al., 2013a).

One interesting result from the adaptation task is the pattern of responses after adaptation. Not only did the proportion of direct responses to rightward-looking gaze probes increase after adaptation, but this proportion also *decreased* to leftward-looking gaze probes. A multichannel model with three distinct channels encoding left, right, or direct gaze would predict no effect to leftward-looking stimuli if they are far enough away from the rightward adaptor, because the leftward-tuned gaze channel should not be adapted. However, this assumes that the gaze probes that I used, ranging from  $-16^{\circ}$  to  $+16^{\circ}$ , capture a large amount of averted eye gaze deviations. But this may not be the case. People are willing to accept eye gaze deviations of up to  $10^{\circ}$  as looking directly at them (Balsdon & Clifford, 2018), so  $16^{\circ}$  may not be averted enough. Given a narrow range of test stimuli and three broadly tuned neuron channels, the leftward gaze channel could easily have become slightly adapted, leading to the observed aftereffects at  $-4^{\circ}$  and  $-8^{\circ}$ .
Previous studies show that adaptation to face expression can be selective to the identity of the face (Campbell & Burke, 2009; Ellamil et al., 2008; Fox & Barton, 2007; Fox et al., 2008; Schweinberger et al., 1999; Schweinberger & Soukup, 1998; Wild-Wall et al., 2008). In my study I changed the face identities between the adaptation and test stimuli to isolate an effect of eye gaze adaptation that was not confounded by adaptation to face identity. Now, with the knowledge that eye gaze adaptation is typical in DP, follow-up studies can investigate whether these adaptation effects are similarly tuned to face identity in DP and control participants.

The data from the serial dependence task show that DP participants also show typical effects of serial dependence to eye gaze direction. It is more difficult to say whether this result dissociates from serial dependence in face identity perception, as this has not yet been studied in DP. However, face recognition skills in the typical population are positively correlated with serial dependence for face identity; people with better face recognition abilities show a larger effect of serial dependence on face identity (Turbett et al., 2019). This finding raises the possibility that serial dependence for identity would be abnormal in DP. If so, then my finding of intact serial dependence for gaze perception in DP would provide further evidence for functional specificity in eye gaze processing.

The potential interaction between face identity and eye gaze in serial dependence is a question worth pursuing. Since eye gaze direction *within* an individual should be more autocorrelated than eye gaze direction *across* individuals, serial dependence for eye gaze *should* be stronger for same identity faces. This selectivity for same identity faces would better facilitate social functioning. My analysis of this was limited as it was *post hoc* and reduced in power by the relative rarity of identity match trials. Future studies with equal numbers of match and mismatch trials, along with a larger sample, will be needed to address this issue thoroughly.

Future studies should also examine the effects of serial dependence and adaptation within the same task, as demonstrated by Taubert and colleagues (2016). The authors asked participants to make judgements about both the gender *and* the expression of each face presented and examined the effect of the gender/expression of previously presented faces on these responses. They predicted that the visual system should consolidate information for invariant attributes like gender (show positive serial dependency) while contrasting information for changeable attributes like expression (show negative adaptation). It would be interesting to look for both effects within the same task in DP. In fact, adaptation likely was occurring to a small degree and at different time courses throughout the serial dependence task (as in orientation studies; Alais et al., 2017, Fischer & Whitney, 2014; Fritsche et al., 2017) but the task design and behavioural responses did not allow me to pick up on this (Liberman et al., 2018). *Ex ante* manipulation of face identity matches, as well as collecting behavioural responses to eye gaze *and* identity, might yield insight into the distinction between invariant and changeable information within the visual system, and whether this distinction is spared in DP.

There are some limitations to Study 2. One is the lack of a continuous response measure in either task (as in Alais et al., 2018; Palmer et al., 2018a; Palmer et al., 2018). In the studies by Palmer and colleagues (2018a; Palmer et al., 2018), the authors were able to model the pattern of adaptation and compare this to a simulated model of how a subject with reduced divisive normalisation would respond, building a convincing argument for intact divisive normalisation in autism and schizophrenia. Another limitation is that while I could rule out priming and hysteresis as accounting for the entirety of the serial dependence effect, I cannot rule out potential response or memory biases. My study did not include blank trials that would have allowed me to rule out response biases, or memory trials to exclude effects of memory confusion (for example, where a participant might recall a gaze from the 1-back trial in place of the current trial's first face gaze). Finally, the serial dependence task collected data from only 18 DP participants and 22 controls<sup>2</sup>. Small samples can be limited in their ability to detect differences between control and DP participants and may be insensitive to potential heterogeneity within DP (Barton et al., 2019; Behrmann & Geskin, 2018; Towler & Tree, 2017). This concern is mitigated by the relatively large number of trials (360), the bootstrapping of the data, and the individual-level analysis, but a larger sample will be needed to draw a firmer conclusion about DP as a whole.

To conclude the second study, there was no convincing evidence for a difference in adaptation or serial dependence effects to eye gaze direction between DP participants and controls. This would suggest that the mechanisms used for temporal sensitivity and stability in eye gaze processing are independent from those used for face identity processing.

<sup>&</sup>lt;sup>2</sup> More DP data are currently being collected for the serial dependence task.

### **Chapter 4: General Discussion**

In this thesis, I examined the degree of functional specificity in eye gaze processing by asking whether gaze processing could be intact while a related function, face identity processing, is impaired. In Study 1, participants with DP and control participants completed two tasks assessing the use of spatial integration in eye gaze processing. There were no differences between the groups in their ability to integrate information being conveyed independently by each eye of the face, and to integrate eye region information with head direction information. In Study 2, DP and control participants completed two tasks assessing the use of temporal integration in eye gaze processing. Again, DP and control participants did not differ in their use of adaptation or serial dependence in eye gaze processing. Overall, my thesis demonstrates spatial and temporal integration in eye gaze processing can be intact where they are impaired for face identity processing, indicating a high degree of functional specificity in the processing of the eyes.

In this general discussion, I will relate my findings to three central areas of application. First, I will consider how these results address the overarching question of whether the mechanisms used in eye gaze processing are functionally specific from those used in face identity processing. Next, I will consider how my results inform the literature on eye gaze processing more generally. Finally, I will consider how my results advance knowledge on the nature and selectivity of face processing deficits in DP.

### 4.1 Functional Specificity in Eye Gaze Processing

The overarching aim of this thesis was to examine functional specificity in eye gaze processing – whether processing of eye region for gaze information can be intact when this is impaired for face identity processing. Overall, my results suggest a high degree of functional specificity in eye gaze processing. This finding has implications for prominent models of face and eye gaze processing, raises questions about how the use of the eyes for other purposes might dissociate from face identity processing, and suggests how this specificity might arise during development. These implications are discussed in the following sections.

# Models of Face Processing

The finding that DP participants had intact eye gaze processing despite impaired face identity processing accords with prominent models of face processing explained in the introduction – Bruce and Young's (1986) cognitive model and Haxby and colleagues' (2000) neural model (Figure 28). Both models posit that changeable aspects of the face such as eye gaze are processed separately from invariant aspects such as identity. This is also consistent with EEG studies showing that substantially earlier ERP components are influenced by face identity adaptation (150-200 ms) versus gaze adaptation (250-350 ms) (Nummenmaa & Calder, 2008; Schweinberger et al., 2007), and that eye gaze and identity are coded in fundamentally different ways – i.e., by multichannel versus opponent coding (Calder et al., 2008; Rhodes & Jeffery, 2006), and with an emphasis on horizontal versus vertical information (Goffaux, 2019). **Figure 28.** 

## Haxby and Colleagues' (2000) Distributed Human Neural System for Face Perception.



*Note.* Sourced from Haxby and colleagues (2000). The point of interaction between the changeable and invariant aspect streams has been circled in red.

Previous studies have indicated that the changeable and invariant information streams can interact. Adaptation to emotional expression can be selective to the identity of the face (Campbell & Burke, 2009; Ellamil et al., 2008; Fox & Barton, 2007; Fox et al., 2008; Schweinberger et al., 1999; Schweinberger & Soukup, 1998; Wild-Wall et al., 2008), and serial dependence effects to emotional expressions can rely on the invariant aspect of gender (Liberman et al., 2018). Gaze direction has also been shown to influence the magnitude of face identity aftereffects (Kloth et al., 2015). Moreover, evidence suggests that the visual system could aim to minimise its sensitivity to changes in invariant information such as gender and identity (show positive serial dependency), while maximising its sensitivity to changes in changeable attributes such as expression (show negative adaptation; Taubert et al., 2016). Having established that DP participants show typical patterns of eye gaze adaptation independently of face identity, and that they show typical patterns of serial dependence independently of adaptation, future studies should combine identity, eye gaze, and varying time delays to ask whether the communication between the changeable and invariant processing streams is preserved in DP.

The results of such a study would add greatly to models of face processing. While Bruce and Young's (1986) cognitive model does not explicitly consider the interaction between processing streams, Haxby and colleagues' (2000) neural model does (indicated by the red circle in Figure 28). For example, the fusiform face area (which is mainly involved in processing face identity) may play a supportive role in facial expression processing, as different individuals may have characteristic expressions (Haxby et al., 2000). Face processing regions may also support eye gaze perception, as various changes in gaze direction may be more or less meaningful *within* identities, as opposed to *across* identities. While I cannot conclude that serial dependence in the perception of eye gaze relies on face identity, there is evidence that this is true for the perception of facial expression (Liberman et al., 2018); in this case the continuity field of serial dependence could act to maintain the stability of changeable features in addition to identity. In other words, the continuity field may be a mechanism by which the two core systems for changeable and invariant aspects interact. A future experiment with DP participants that manipulates information from both processing streams could indicate just how closely these two streams interact – i.e., whether both the changeable system *and* the interaction between the systems may be preserved in DP, meaning deficits can be highly selective to the invariant stream only.

Itier and Batty (2009) note that a high degree of functional specificity in eye gaze processing may make models such as Bruce and Young's (1986) and Haxby and colleagues' (2000) dated. Assuming the human brain has a specialised system for detecting and processing eyes (e.g., the eye direction detector [Baron-Cohen, 1994] discussed in section 4.2) and that this is different from the face processing system (as my data suggests), these models may need to be revised. Face processing may not be the result of integrating equally important features, but may instead result from a system dedicated to eye processing working together with a system dedicated to processing the rest of the face (Itier & Batty, 2009).

Figure 29 is an example of how such a revised model might look. Rather than beginning with the early perception of all face features, as Haxby and colleagues' model does, this model begins with the early detection and encoding of only the eyes. The inferior occipital gyrus (IOG) and posterior STS may be involved at this early stage. The IOG is implicated in the early structural encoding of faces (Haxby et al., 2000; Hoffman & Haxby, 2000), which research suggests may in fact be an early eye-specificity (Itier et al., 2007; Itier et al., 2006; Itier et al., 2011), and the posterior STS both categorises gaze as averted or direct (Nummenmaa & Calder, 2008; Pelphrey et al., 2004; Pfeiffer et al., 2013) and contains a face selective region (Fox et

al., 2009; Pinsk et al., 2009; Pitcher et al., 2011). These two processes are known to interact, as direct-gaze faces are better encoded and recognised than averted-gaze faces (Itier & Batty, 2009; Mason et al., 2004; Vuilleumier et al., 2005). Changeable aspects of eye region processing, such as using the eyes for gaze processing, would go on to occur in the anterior STS (Calder et al., 2008; Calder et al., 2007; Carlin & Calder, 2013; Carlin et al., 2012; Perrett et al., 1985; Perrett et al., 1992) then higher cognitive areas in the extended system (Haxby et al., 2000). Integrating the eye region with the rest of the face, such as in the processing of face identity, may make use of the fusiform and occipital face areas.

### Figure 29.

Proposed Neural Model Beginning with Eye Region Processing.



*Note.* The cortical areas implicated at each stage are speculative. The extended system remains the same as in Haxby and colleagues' (2000) model but has been condensed for clarity.

My data demonstrates that the processing of eyes for gaze is functionally specific from face identity processing, which Itier and Batty (2009) suggest is evidence for a system dedicated to eye processing before face processing. In the case of DP, where there is intact eye gaze processing and impaired face identity processing, this would suggest that the initial eye detection stage is intact. However, future studies involving neuroimaging and network analyses would be needed to test this model and validate this theory. This model also relates well to the argument that face recognition involves different types of holistic processing at several levels (Maurer et al., 2002; Rezlescu et al., 2017). DP participants were able to use spatial integration of the eye region in the Wollaston task, but they are frequently unable to do this in the part-whole task (DeGutis et al., 2013). Any holistic processing involved in the eye detection system (such as an initial sensitivity to first-order relations; Maurer et al., 2002) may be intact while any holistic processing occurring later in the invariant stream (e.g., integrating facial features; Maurer et al., 2002) may be impaired.

It is worth noting that Duchaine and Yovel (2015) have proposed an updated version of the Haxby model, in which the key distinction is between *dynamic* and *static* information, rather than changeable and invariant information (Figure 30). In the Haxby model, the fusiform face area is involved solely in identity processing, yet we know that it responds to the isolated eye region (Baron-Cohen et al., 2001; Tong et al., 2000) and also to facial expressions (Ganel et al., 2005), so long as the stimuli are static images. The model also views the STS as an area for processing solely changeable face aspects, but there is evidence for an identity selective region in the STS (Fox et al., 2009; Pinsk et al., 2009; Pitcher et al., 2011). Moreover, the STS responds strongly to dynamic face stimuli and less to static face stimuli, while the fusiform face area responds strongly to static face stimuli and less to dynamic (Fox et al., 2009). As I used only static stimuli, my study is not able to compare these two models and see which distinction – static versus dynamic, or changeable versus invariant – best describes the functional specificity in eye gaze processing or the nature of the impairment in DP.

### Figure 30.

Duchaine and Yovel's (2015) Revised Framework of Face-Selective Areas.



*Note.* This model proposes a ventral pathway (occipital face area, FFA, anterior temporal lobe face area) for the processing of static face information, and a dorsal pathway (posterior STS face area, anterior STS face area, and inferior frontal gyrus face area) for the processing of dynamic face information. Figure sourced from Duchaine and Yovel (2015).

The use of only static stimuli is a key limitation of this study, and much of eye gaze processing literature in general, as it strips away the real-world dynamics of eye gaze movements. Related to this is the use of an "isolation paradigm", again both in these studies and the literature at large, in which participants view detached and inert stimuli (Becchio et al., 2010). These limitations mean that social cognition is studied without social interaction – gaze processing in real life always involves at least two individuals who are engaged with each other and move and change in real time, reciprocating the gaze cues conveyed by one another (Becchio et al., 2010; Pfeiffer et al., 2013). Future experiments with interactive gaze paradigms – with another person or a gaze-contingent avatar – would be valuable. For example, gaze processing areas in the brain such as prefrontal cortex and ventral striatum respond differentially when one is engaging with another's gaze (joint attention) versus their own gaze (non-joint attention; Schilbach et al., 2010), and when they are the initiator versus the receiver of joint attention (Schilbach, 2015). Interactive gaze paradigms may be more important when

studying complex gaze functions like mindreading over more basic functions like judging gaze direction (Schilbach et al., 2013), but the differences between the tasks I asked my participants to complete and the way that gaze interactions work in real life should be acknowledged.

### The Processing of Eyes for Different Functions

The eyes are a critical feature in face identity processing (Abudarham et al., 2019; Abudarham & Yovel, 2016; Chelnokova & Laeng, 2011; Fisher et al., 2016; Itier et al., 2007; Lewis & Edmonds, 2003; McKelvie, 1976; Royer et al., 2018; Vinette et al., 2004; Wu et al., 2011). Beyond simply being present, the eyes must be integrated with the rest of the face in order to facilitate recognition (DeGutis et al., 2013; Ross et al., 2015; Rezlescu et al., 2017; Tanaka & Farah, 1993; Young et al., 1987).

People with DP have a particular deficit with the use of eye region for identity recognition. They do not integrate the eyes with the rest of the face in part-whole tasks, despite being able to do so for the mouth (DeGutis et al., 2013). DP participants are also less sensitive to contrast information in the eye region in studies of the N170 component looking at face identity matching (Fisher et al., 2016). Those with DP who are *more* sensitive to this information have better face perception abilities, suggesting that the way the eye region is processed in DP can predict face recognition skills (Fisher et al., 2016). Yet despite these deficits, DP participants showed normal processing of eyes for gaze perception. The Wollaston results are especially interesting given how DP participants perform in the part-whole task (DeGutis et al., 2013, and Appendix A.5) – while they are unable to integrate the eye region with the whole face for identity recognition, they are seemingly able to integrate the eye region with the head for gaze perception. The dissociation between part-whole and Wollaston results speak to the high degree of functional specificity in eye gaze processing, as two almost identical processes can be differentially impaired when used for different functions.

Another domain where the uses of eye region can dissociate is in ASD (Nation & Penny, 2008), where processing of eyes for gaze is typical, but processing of eyes for "mindreading" is not. People with ASD can show a typical ability to categorise gaze (Leekam et al., 1997), can display typical and reflexive effects of eye gaze cueing (Charwarska et al., 2003; Driver et al., 1999; Johnson et al., 2005; Senju et al., 2004), and can show normal adaptation to eye gaze (Palmer et al., 2018; but see Pellicano et al., 2013). Young children with ASD even show the same ERPs as typically developing children when looking at direct versus averted gaze (Grice et al., 2005). This last finding changes as children grow older, and a possible explanation for this is that young children have not yet learned to associate gaze with social intentions or "mindreading", so could be using non-gaze specific or non-social mechanisms at first (Nummenmaa & Calder, 2008). Evidence from macaques and chimpanzees show that apparently "social" gaze behaviour (such as following another individual's gaze) can arise without a representation of the other's mental state (Ferrari et al., 2000; Povinelli & Eddy, 1996; Povinelli & Eddy, 1997). Children with ASD are much worse at more obviously "social" aspects of gaze behaviour – they engage in less mutual gaze (Sigman et al., 1986; Volkmar & Mayes, 1990) and gaze-following behaviour (Leekam et al., 1997; Leekam et al., 1998; Leekam et al., 2000); they are less able to detect mutual gaze (Senju et al., 2003) and responses to mutual gaze are not lateralised to the right hemisphere as they are in typically developing children (Senju et al., 2005); and they don't engage in spontaneous shifts of attention to the target of others' attention (Leekam et al., 1997). This suggests that gaze perception can be normal without being social. As I did not include social gaze tasks or measures of the perception of mental states from gaze, I cannot speak to whether social gaze processing is normal in DP, though this dissociation would be an interesting idea for future research.

#### Development of Eye Gaze Processing

This thesis is focussed on people with *developmental* prosopagnosia – those who have never developed the ability to recognise faces. The developmental nature of the deficits in DP allows me to draw some inferences about the typical development of eye gaze processing<sup>3</sup>. The dissociation between eye gaze and identity processing in adults with DP suggests not only that the two functions rely on separate mechanisms, but that they also develop independently from one another.

Infant studies suggest that gaze and identity processing are associated in early life. Infants perceive illusory shifts of gaze in the Wollaston illusions only in the context of upright faces as 8 months, but not at 6 or 7 months. This suggests that the development of eye gaze processing coincides with the development of holistic face processing that is characteristic of identity recognition (Nakato et al., 2009). The N170 response to faces is enhanced by direct gaze at only 4 months, providing further evidence that gaze processing overlaps with face identity processing early in life (Farroni et al., 2004).

Taken together, the infant studies and my data raise the hypothesis that eye gaze and face identity processing branch off into separate developmental pathways early in life. Alternatively, eye gaze and face identity processing may continue to share a developmental trajectory, but eye gaze processing could be compensated for more easily or achieved through different mechanisms later in life. Support for this second hypothesis could come from testing eye gaze processing in children with DP. If both eye gaze and identity processing were impaired in children with DP, but only identity processing in adults with DP, this would suggest eye gaze processing can be compensated for later in life (as may be the case with face perception in DP; Dalrymple et al., 2014).

<sup>&</sup>lt;sup>3</sup> Thomas and Karmiloff-Smith (2002) caution against using developmental disorders to make inferences about the typical brain. Doing so assumes "Residual Normality" – that developmental disorders produce selective deficits while the rest of the system develops normally. However, Ramus (2002) demonstrates that a highly selective deficit can be at the core of some developmental disorders, such as dyslexia.

### 4.2 Models of Eye Gaze Processing

A second set of implications of my results is how they reaffirm and add to general theories about eye gaze processing. The eye direction detector theory (Baron-Cohen, 1994; Baron-Cohen & Ring, 1994) posits that humans have a system dedicated to identifying if we are the object of another's attention. This makes us extremely sensitive to whether someone is looking at us. From an evolutionary point of view, this sensitivity helps us to detect when we are in danger or are otherwise about to be engaged with by a conspecific. My results are consistent with this theory. First, the presence of a cone of gaze tuned to ensure that direct gaze is rarely missed was demonstrated in the Wollaston and adaptation tasks. Second, the presence of cells in the STS tuned to respond differentially to left, right, or direct gaze is commonly taken as evidence that there is a part of the brain with the primary function of detecting where another individual is looking (i.e., this is the EDD; Baron-Cohen & Ring, 1994; Perrett et al., 1992). The pattern of adaptation aftereffects in both groups is further evidence for such organisation in the brain as it corresponds to multichannel coding.

Another theory of gaze processing is the cooperative eye hypothesis (Tomasello et al., 2007). This theory relates the unique morphology of the human eye to the extent of reliance on eye gaze cues in humans, as well as the greater social complexity and cooperation seen in humans compared to non-human primates. Eye contact also increases co-operative and altruistic behaviour in humans but not non-human primates (Bateson et al., 2006; Ernest-Jones et al., 2011; Haley & Fessler, 2005; Nettle et al., 2013). Indeed, people with DP show milder or no social cognitive impairments compared to people with autism (Duchaine et al., 2009; Kracke, 1994). Both conditions present with atypical face identity processing, but only people with DP seemingly possess typical eye gaze processing abilities (Joseph et al., 2008; Leekam et al., 1997; Leekam et al., 1998; Leekam et al., 2000; Senju & Johnson, 2009; Senju et al., 2003; 2005; Sigman et al., 1986; Volkmar & Mayes, 1990; Weigelt et al., 2012). This could

suggest that intact eye gaze processing in DP contributes to preserved social functioning despite deficits in face recognition.

One interesting new direction in social cognition is cue integration, a Bayesian framework that seeks to explain the processing of complex social information (Zaki, 2013). In this framework, contexts and stimuli produce perceptual cues with conditional probabilities – for example, the probability of someone looking directly at you, P(direct gaze) – which are combined with the perceiver's prior knowledge – if it is more likely for the person approaching you to be looking directly at you, P(direct gaze | approaching). My serial dependence results fit this framework. The quality of the data for the logistic functions (AICc) was slightly better on identity match trials than on identity mismatch trials, which could suggest some interaction with identity. For example, insignificant changes in eye gaze such as the microsaccades that occur within an individual may be factored out of perception. In this case, the high probability of P(insignificant change | same identity) would overwhelm the low probability of P(insignificant change | different identity). Other studies of serial dependence and adaptation in the processing of changeable and invariant face features can also be explained in such terms: P(insignificant expression change | same identity) would be much higher than P(insignificant expression change | different identity) (Liberman et al., 2018; Taubert et al., 2016).

While the role of Bayesian inference and cue integration has been considered in social processes such as mentalising (Zaki, 2013) and in social impairments such as social anxiety (Foa et al., 1996), neither eye gaze processing nor prosopagnosia has been considered within this framework before. The results from the serial dependence task suggest that it could help us to understand the processes underlying serial dependence in the typical perception of eye gaze, but further study should investigate this area more.

### 4.3 Implications for Developmental Prosopagnosia

A final set of implications of this thesis are related to the nature of deficits in DP. This thesis used DP as a means for characterising the relationship between eye gaze and face identity processing, but the results also yield several insights into DP itself.

A central question in DP research is the extent to which the impairment is specific to faces. Some DP studies have reported broader deficits beyond recognising face identity, including perceiving emotional expressions (Biotti & Cook, 2016), gender (Marsh et al., 2019), attractiveness (LeGrand et al., 2006), and trustworthiness (Todorov & Duchaine, 2008) in faces; recognising bodies (Biotti et al., 2017); or recognising everyday objects in general (Barton et al., 2019; Duchaine & Nakayama, 2006). Other studies argue that the deficits in DP are highly specific and are mostly restricted to face identity (Barton et al., 2019; Bell & Suilo, 2018; Carbon et al., 2010; Chatterjee & Nakayama, 2012; DeGutis et al., 2012; Duchaine & Nakayama, 2006; Duchaine et al., 2003; LeGrand et al., 2006; Rezlescu et al., 2013; Todorov & Duchaine, 2008).

My findings of normal gaze processing in DP align more with highly specific view. Compared to other facial aspects that have previously been studied (such as gender and attractiveness), eye gaze processing could be considered more closely related to face identity processing because of the common reliance on the eye region. As such, the dissociation between gaze and identity processing in DP attests to the high degree of functional specificity in eye gaze processing. If the serial dependence effect is revealed to be selective to same identity faces in future studies, this would argue even more strongly for a highly specific deficit. If serial dependence functions as an integration mechanism between the identity and eye gaze processing streams (as theorised in section 4.1), this would suggest that the DP impairment is specific to just the invariant stream, sparing areas where this stream interacts with other streams (such as that for eye gaze processing).

Why might my studies have yielded a face-specific effect while others have not? One possibility is that there could simply be less overlap between face identity and eye gaze processing than there is between, for example, face identity and object processing, or face identity and expression processing. However, there are some other key differences between my study and previous studies that could account for this. Some of these are related to common issues in DP research that I have combatted from the outset of this thesis. I used a much larger sample size than is common, allowing for increased statistical power, as well as considering the role of subthreshold autism traits, which could have explained any differences in eye gaze processing (as they could any deficits in emotion, body, or personality processing). This thesis is also made more statistically robust by the use of multiple measures to test each hypothesis: null-hypothesis tests and Bayesian tests; parametric and nonparametric measures of the Wollaston and adaptation effects; and group-level and individual-level analyses. Another limitation in DP research that I have addressed is the issue of stimulus similarity. Prior studies might have found face-specific deficits in DP because they did not equate stimulus variation faces are all very similar to one another, while a category such as objects tends to have greater stimulus variation (Campbell & Tanaka, 2018). This is not the case in my study, since the eye gaze stimuli often differed by only 5°, a very small variation compared to the typical stimulus variation for identity.

Another central idea in face recognition is that face processing relies on holistic mechanisms much more so than non-face object processing (Avidan et al., 2011; Towler et al., 2018; Tanaka & Sengco, 1997). There is evidence that eye gaze processing also requires some holistic processing (Jenkins & Langton, 2003; Langton et al., 2004). The strabismus and Wollaston tasks were those most likely to require holistic processing in these studies. Both involve spatial integration of different parts of the head or face with one another; they would not have been able to be completed by processing one eye independently from the other, or the

eye region independently from the rest of the head. If we assume that these tasks did indeed require holistic processing of the eye region, then this seems to be intact in DP. This is further evidence for the argument that DP is face-specific, as it would exclude the possibility that people with DP have a general deficit in holistic processing that is simply most apparent for faces. This conclusion is supported by research showing that holistic processing of a related feature, gender, is intact in DP (Chatterjee et al., 2011), and may provide support for the view that holistic processing is several independent mechanisms rather than a single process (Maurer et al., 2002; Rezlescu et al., 2017).

In saying this, the involvement of holistic processing in these tasks remains an assumption. The inclusion of inverted trials in the strabismus task yielded an inversion effect, a hallmark of holistic processing. However, without similar trials in the Wollaston task, we are unable to say whether holistic processing was being used. Similar studies that have included inverted trials report that some upright-specific processing is used in the Wollaston effect in some cases, but not always. Langton and colleagues (2004) used inverted stimuli to gauge the degree of upright-specific processing used in the task – the more performance is affected by inversion, the more upright-specific processing is involved. They manipulated the images with a high-pass filter to preserve only the eyes and the shape of the head and found that the integration of the eyes and head was not upright-specific because it was not affected by inversion. Manipulating the angle of the nose suggested that integrating nose and eye information was upright-specific because it was affected by inversion. This upright specificity is not necessarily holistic, but including inverted trials and employing similar image manipulations in future iterations of the Wollaston task would allow me to further examine upright-specific, and potentially holistic, processing for eye gaze in DP.

My results also have implications for theories about the causes of DP, such as the neural migration theory (Ramus, 2004; Susilo & Duchaine, 2013). When the brain develops, neurons

migrate from where they are generated to where they need to be to complete neural circuits and facilitate cognition. Neural migration disorders arise when this migration occurs abnormally. Evidence from dyslexia shows that different symptoms in dyslexia (such as phonological deficits) result from neural migration errors, and the genes implicated in dyslexia are most often responsible for neural migration (Galaburda et al., 2006; Galaburda et al., 1985; Humphreys et al., 1990; Ramus, 2004). Applied to neurodevelopmental disorders more generally, neural migration errors in focal cortical regions would disrupt cognitive abilities with a high degree of specificity, such as in face recognition. Errors in the face processing stream or the fusiform gyrus would lead to selective deficits with face identity, whereas more widespread errors would result in broader deficits with emotional expression, gender, body, or object recognition (Barton et al., 2019; Biotti & Cook, 2016; Biotti et al., 2017; Duchaine & Nakayama, 2006; Marsh et al., 2019). This theory could account for the findings that face-specific deficits are present in some but not all DP participants. In this case, individuals are not inheriting DP itself, but rather a susceptibility to neural migration errors, which may be a common risk factor for DP as well as developmental body or object agnosia (Germine et al., 2011; Gray & Cook, 2018).

Applied to my data, the neural migration errors likely occur after the early processing of facial features in the inferior occipital gyrus, which the Haxby model considers as the initial stage of both eye gaze and face identity processing (Figure 27). This would leave the eye gaze processing stream intact while the face processing stream is impaired.

### **4.4 Conclusions**

The aim of this thesis was to study functional specificity in eye gaze processing by considering whether it can be intact while a separate but highly related process, face identity processing, is impaired. In Study 1, DP and control participants showed a similar degree of spatial integration in the perception of eye gaze. In Study 2, DP and control participants showed

adaptation and serial dependence of a similar strength and direction. This provides robust evidence that eye gaze processing can be intact where face identity processing is impaired, suggesting a high degree of functional specificity in eye gaze processing. These results support common models of face processing that suggest eye gaze and identity processing dissociate early, and add to them by suggesting that eye detection may be the first step in both of these processes. My results also add to theories that aim to define the purposes of eye gaze processing and provide insight into the nature of impairment in DP. Having established that eye gaze processing is typical in DP, this thesis provides a clear direction for future research that will improve popular models of face processing by establishing whether the eye region is first processed independently of other face features, and testing whether deficits in eye gaze and face identity processing are confined to their respective mechanisms or are likely to affect the connections between them.

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### **Appendix A: Study 1 Supplementary Analyses and Figures**

#### **A.1 Descriptive Statistics**

### Table A 1.

Descriptive Statistics of Group Performance on Screening Measures (CFMT)

	DP	Control	
	Mean (SD)	Mean (SD)	
CFMT # correct	35.23 (5.05)	54.05 (8.60)	

### Table A 2.

Descriptive Statistics of Group Performance in the Strabismus and Wollaston Tasks.

Variable	DP		Control	
	М	SD	M	SD
Strahismus upright accuracy	74 87	0.1	78 44	0.1
	65.40	0.12	70.11	0.12
Strabismus inverted accuracy	65.48	0.12	66.48	0.12
Wollaston CMHD	9.41	3.38	9.33	3.85
Wollaston centroid half-difference	7.98	3.04	8.03	3.51
Wollaston AdjR <sup>2</sup>	0.94	0.07	0.93	0.07

### **A.2 Reaction Time Analyses**

I used accuracy or the size of the Wollaston effect as the dependent measures for my main analyses. As my tasks were not speeded, they are limited in what can be concluded from the reaction times (RTs). However, RTs can also demonstrate the presence of an impairment – perhaps the DP participants can perform just as well as the controls, but they take twice the amount of time to reach that level of performance. For this reason, I repeated the main analyses from Study 1 using median RT as the dependent measure.

I first compared median RT for upright and inverted faces in the strabismus task using a 2 (group: DP, control) x 2 (condition: upright, inverted) mixed measures analysis of variance (ANOVA). There was no main effect of orientation (F(1, 195) = 1.21, p = .272,  $\eta^2_p = 0.01$ ) and no significant interaction (F(1, 195) = 0.96, p = .328,  $\eta_p^2 = 0.01$ ) The main effect of group was significant (F(1, 195) = 39.04, p < .001,  $\eta_p^2 = 0.17$ ). A follow-up Bonferroni-corrected *t*-test revealed that DP RTs (M = 2.49 s, SD = 0.34s) were longer overall than control RTs (M = 2.13s, SD = 0.45s), t(195) = 6.25, p < .001). The groups also differed significantly in RTs on the Wollaston task, as DP participants (M = 1.64 s, SD = 0.66s) were again significantly slower than controls (M = 1.43s, SD = 0.76s), t(190.3) = 3976, p = .022). These analyses are shown in Figure A1.

### Figure A1.

Median Response Times (RTs) in the Strabismus and Wollaston Tasks.



*Note.* Median RTs for the control and DP groups in strabismus (left; upright trials only) and Wollaston (right) tasks. Small dots represent individual data points and the larger circles represent the group means.

Overall, DP participants were significantly slower than controls across both tasks. This result is however difficult to interpret as our participants with DP are simply likely to take longer because they are more invested in the outcome of the task.

### A.3 Distribution Comparisons

Beyond just analysing mean group differences, I also checked to see if there were difference between the groups anywhere in their distribution of responses on various measures of performance on the strabismus and Wollaston tasks. I used Kolmogorov-Smirnov tests implemented with ks.test in R. The groups did not differ at all in their distributions of responses (all *p*-values > .05).

## A.4 Cone Model Fit to Each Individual's Data

### Figure A2.



Cone Model Fit to Each Individual DP's Data from the Wollaston Task.











*Note*. Each individual DP's data fit to the cone model. The proportion of direct responses are shown on the y-axis, and each level of eye gaze deviation is on the x-axis. Responses from the

Head Right condition are shown in red and responses from the Head Left condition are shown in blue.

# Figure A3.

Cone Model Fit to Each Individual Control's Data from the Wollaston Task.













*Note.* Each individual Control's data fit to the cone model. The proportion of direct responses are shown on the y-axis, and each level of eye gaze deviation is on the x-axis. Responses from the Head Right condition are shown in red and responses from the Head Left condition are shown in blue.

### A.5 Part-Whole Task

Twenty-five DP participants in this sample had previously completed the part-whole task (Tanaka & Farah, 1993) in a previous experiment. The part-whole task involves recognising face features when presented alone, or in the context of a whole face. Control participants typically experience a benefit from the whole-face context and find it difficult to recognise features presented in isolation. The measure taken from this take is the part-whole effect, which is theoretically assumed to index holistic processing (DeGutis et al., 2013; Tanaka & Farah, 1993). This effect is calculated by subtracting the accuracy for individual features from the accuracy for whole faces.

As another commonly used assessment of holistic face processing, a relationship between part-whole effect size and strabismus accuracy might also suggest whether the severity of the holistic deficits in DP can explain variation in strabismus performance. Additionally, a relationship between part-whole effect size and Wollaston effect size could suggest whether the Wollaston task makes use of holistic face processing mechanisms. I looked at both the overall part-whole effect size, and the effect for just the eyes of the faces. The results of these correlations are shown below.

### Figure A4.

Relationship Between Part-Whole Effect Size and Strabismus/Wollaston Performance.



*Note.* Correlation between strabismus upright accuracy (left) or Wollaston CMHD (right) and part-whole effect size (top = total, bottom = eye trials only). The shaded areas depict the 95% confidence interval (CI). The red text reports the correlation coefficients and CIs.

Neither strabismus nor Wollaston task performance predicted part-whole effect size, which could suggest that the spatial integration employed in each task was not the same holistic processing used in face recognition and captured by the part-whole task. However, evidence suggests that this sample size is too small to yield a reliable estimate of the relationship between the measures (Schönbrodt & Perugini, 2013).

# **Appendix B: Study 2 Supplementary Analyses and Figures**

### **B.1 Descriptive Statistics**

### Table B 1.

Descriptive Statistics of Group Performance on Screening Measures (CFMT)

	DP	Control
CFMT # correct	Mean (SD)	Mean (SD)
Adaptation sample	34.91 (4.70)	53.18 (8.01)
Serial dependence sample	35.74 (5.98)	52.23 (9.38)

### Table B 2.

Descriptive Statistics of Group Performance in Study 1 Tasks.

Variable	DP		Control	
	М	SD	М	SD
Adaptation centroid difference	2.42	1.47	2.26	1.17
Adaptation RT (ms)	480.03	165.42	445.26	124.69
PSE shift 1-back first face	3.12	2.18	4.28	3.36
PSE shift 1-back second face	2.50	1.63	4.55	4.03
Serial Dependence RT (ms)	511.79	198.82	497.81	235.70

### **B.2 Reaction time analyses**

I used the responses made – the proportion of direct responses in the adaptation task, and the proportion of "1" responses in the serial dependence task – as the dependent measure for my main analyses. Again, as my tasks were not speeded, caution needed to be exercised when looking at reaction times (RTs). However, RTs can also demonstrate the presence of an impairment where groups perform at a similar level of accuracy but take longer to do so. For this reason, I repeated the basic analyses from Study 2 using median RT as the dependent measure.

In the adaptation task, there was no difference between DP (M = 480.03 ms, SD = 165.42 ms) and control (M = 445.26 ms, SD = 124.69 ms) median RTs across all pre- and postadaptation trials, t(88) = 1.13, p = .263, BF<sub>10</sub> = 0.39 (anecdotal). In the serial dependence task, there was no difference between DP (M = 511.79 ms, SD = 198.82 ms) and control (M = 496.77ms, SD = 230.07 ms) median RTs across all trials, t(39) = 0.22, p = .826, d = 0.07, BF<sub>10</sub> = 0.31. These analyses are represented in Figure B1 below.

### Figure B1.

Median Reaction Times (RTs) in the Adaptation and Serial Dependence Tasks.



*Note.* Median RT for DP and control participants in the adaptation (left) and serial dependence (right) tasks. Small dots represent individual data points and the larger circles represent the group means.

## **B.3 Serial Dependence Figures**

### Figure B2.

Model Fit to Each DP's 1-back First Face Data.





*Note*. Each graph displays a single participant's Right-previous (blue), Left-previous (red), and combined (yellow) functions. Functions that begin and descend from the upper left corner indicate that the participant was in the "Left" condition.

# Figure B3.







*Note.* Each graph represents a single participant's observed PSE difference (red dot) compared to their bootstrapped and permutated null distribution (blue graphs). A positive observed difference and negative (left-aligned) null distribution indicates a significant positive PSE shift.

## Figure B4.

Model Fit to Each Control's 1-back First Face Data.





*Note*. Each graph displays a single participant's Right-previous (blue), Left-previous (red), and combined (yellow) functions. Functions that begin and descend from the upper left corner indicate that the participant was in the "Left" condition.

# Figure B5.

*Observed PSE Difference Compared to Permutated Null Distribution for each Control (First Face Data).* 




*Note.* Each graph represents a single participant's observed PSE difference (red dot) compared to their bootstrapped and permutated null distribution (blue graphs). A positive observed difference and negative (left-aligned) null distribution indicates a significant positive PSE shift. **Figure B6.** 

Model Fit to Each DP's 1-back Second Face Data.





*Note*. Each graph displays a single participant's Right-previous (blue), Left-previous (red), and combined (yellow) functions. Functions that begin and descend from the upper left corner indicate that the participant was in the "Left" condition.

## Figure B7.

Observed PSE Difference Compared to Permutated Null Distribution for each DP (Second

Face Data).





*Note.* Each graph represents a single participant's observed PSE difference (red dot) compared to their bootstrapped and permutated null distribution (blue graphs). A positive observed difference and negative (left-aligned) null distribution indicates a significant positive PSE shift.

## Figure B8.

Model Fit to Each Control's 1-back Second Face Data.





*Note*. Each graph displays a single participant's Right-previous (blue), Left-previous (red), and combined (yellow) functions. Functions that begin and descend from the upper left corner indicate that the participant was in the "Left" condition.

## Figure B9.

Observed PSE Difference Compared to Permutated Null Distribution for each Control

(Second Face Data).





*Note.* Each graph represents a single participant's observed PSE difference (red dot) compared to their bootstrapped and permutated null distribution (blue graphs). A positive observed difference and negative (left-aligned) null distribution indicates a significant positive PSE shift.

## Figure B10.

Model Fit to Each DP's Data on Identity Match Trials.





*Note*. Each graph displays a single participant's Right-previous (blue), Left-previous (red), and combined (yellow) functions for identity match trials only. Functions that begin and descend from the upper left corner indicate that the participant was in the "Left" condition.

# Figure B11.

*Observed PSE Difference Compared to Permutated Null Distribution for each DP (Identity Match Data).* 





*Note.* Each graph represents a single participant's observed PSE difference (red dot) compared to their bootstrapped and permutated null distribution (blue graphs). A positive observed difference and negative (left-aligned) null distribution indicates a significant positive PSE shift.

## Figure B12.

Model Fit to Each Control's Data on Identity Match Trials.





*Note*. Each graph displays a single participant's Right-previous (blue), Left-previous (red), and combined (yellow) functions for identity match trials only. Functions that begin and descend from the upper left corner indicate that the participant was in the "Left" condition.

# Figure B13.

Observed PSE Difference Compared to Permutated Null Distribution for each Control

(Identity Match Data).





*Note.* Each graph represents a single participant's observed PSE difference (red dot) compared to their bootstrapped and permutated null distribution (blue graphs). A positive observed difference and negative (left-aligned) null distribution indicates a significant positive PSE shift.

## Figure B14.

Model Fit to Each DP's Data on Identity Mismatch Trials.





*Note*. Each graph displays a single participant's Right-previous (blue), Left-previous (red), and combined (yellow) functions for identity match trials only. Functions that begin and descend from the upper left corner indicate that the participant was in the "Left" condition.

# Figure B15.

*Observed PSE Difference Compared to Permutated Null Distribution for each DP (Identity Mismatch Data).* 





*Note.* Each graph represents a single participant's observed PSE difference (red dot) compared to their bootstrapped and permutated null distribution (blue graphs). A positive observed difference and negative (left-aligned) null distribution indicates a significant positive PSE shift.

## Figure B16.

Model Fit to Each Control's Data on Identity Mismatch Trials.





*Note*. Each graph displays a single participant's Right-previous (blue), Left-previous (red), and combined (yellow) functions for identity match trials only. Functions that begin and descend from the upper left corner indicate that the participant was in the "Left" condition.

# Figure B17.

Observed PSE Difference Compared to Permutated Null Distribution for each Control (Identity Mismatch Data).





*Note.* Each graph represents a single participant's observed PSE difference (red dot) compared to their bootstrapped and permutated null distribution (blue graphs). A positive observed difference and negative (left-aligned) null distribution indicates a significant positive PSE shift.

## **B.4** Cone of Direct Gaze

While not relevant to the main question this study asks, the adaptation task also allowed me to examine the average cone of direct gaze of the two groups. This cone of gaze refers to the range of physically averted eye gaze deviations that a person will report as looking directly at them (Gamer & Hecht, 2007). This measure increases with uncertainty, becoming larger when noise is added to eye images (Mareschal et al., 2013a; 2013b), and is sometimes atypical in populations with marked deficits in processing the eye region (such as people with autism and schizophrenia; Hooker & Park, 2005; Senju et al., 2005; Tso et al., 2012; Vida et al., 2013). It is often taken as a general measure of typical eye gaze categorisation ability.

This measure can be accessed by looking at the proportion of left, right, and direct responses to all eye gaze deviations presented in the pre-adaptation block. Logistic functions are fitted to each response across deviations for each participant (as shown in Figure B18). The distance between the intersection of the left and direct functions and the right and direct functions is taken as the width of the cone of gaze.

#### Figure B18.

Demonstration of the Cone of Direct Gaze.



*Note.* Three logistic functions fit to the pre-adaptation data of a single DP participant. The cone of gaze is the area in which the proportion of direct responses is larger than the proportion of left or right responses – corresponding to the range of gaze deviations of participant categorises as "direct".

There was no difference between DP ( $M = 14.65^\circ$ ,  $SD = 3.47^\circ$ ) and control ( $M = 13.44^\circ$ ,  $SD = 3.02^\circ$ ) participants in the average width of the cone of gaze, t(88) = 1.76, p = .081 (BF<sub>10</sub> = 0.86). I found no evidence that DP participants showed atypical eye gaze processing in comparison to the control group (Figure B19).

#### Figure B19.

Cone of Gaze Values Compared Across the DP and Control Groups.



Note. Small dots represent individual data points and larger circles represent the group means.