Audiovisual Integration after Late Monocular Enucleation

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Abstract

People who underwent monocular enucleation, the surgical removal of one eye, exhibit altered sensory processing compared to people with binocular vision. Most research has focused on early monocular enucleation, which occurs during critical periods in visual development and leads to more balanced processing of audiovisual stimuli. I investigated whether audiovisual integration is altered after late monocular enucleation, which occurs after completed visual development. Susceptibility to the sound-induced flash illusion and the McGurk effect was compared between people who underwent late monocular enucleation and binocular viewing control participants. People who underwent late monocular enucleation were less susceptible to the sound-induced flash illusion but were susceptible to the McGurk effect, whereas control participants were susceptible to both. These findings suggest altered audiovisual integration for low-level audiovisual stimuli but unaltered audiovisual integration for high-level audiovisual speech stimuli. This may reflect compensatory adaptations and underscores the importance of timing in monocular enucleation research.

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1. Introduction

The visual system is the most extensively studied sensory system (Hutmacher, 2019), with sight often described as the most important sense for daily life in humans (Enoch et al., 2019). Among many other functions, it provides an efficient and accurate spatial representation of one's surroundings (Shioiri et al., 2018). This facilitates interactions with the environment that enable abilities like traversal (Ekstrom, 2015), object identification (Bracci & De Beeck, 2023) and threat detection (Quinlan, 2013). Vision therefore has an important role in guiding daily actions and behaviours which facilitate an individual's lived experiences (reviewed in Land, 2009). Visual impairment results in a substantial reduction in quality of life (Enoch et al., 2019; Langelaan et al., 2007) and therefore warrants research that investigates different types of vision loss (Hutmacher, 2019).

1.1. Visual System Development

Neurodevelopment is a complex process that entails the concurrent development of multiple sensory systems. Neuroplasticity is the ability of the brain to grow or reorganize its structure and functional connectivity patterns that underlie neurodevelopmental processes including the maturation of the visual system (reviewed in Ismail et al., 2017). Vision comprises various abilities which inform a viewer of different properties of an object, like its colour and shape, that emerge and develop over the course of early childhood and early adulthood (reviewed in Daw, 2014). These developmental processes mirror those of other abilities that are similarly absent or immature at birth, like speech, the acquisition of which occurs through years of experience and learning (reviewed in Werker & Hensch, 2015). The gradual development of visual

abilities after birth occurs through neuroplasticity mechanisms that are driven by an interplay between biological factors and visual experiences from the environment (Ismail et al., 2017).

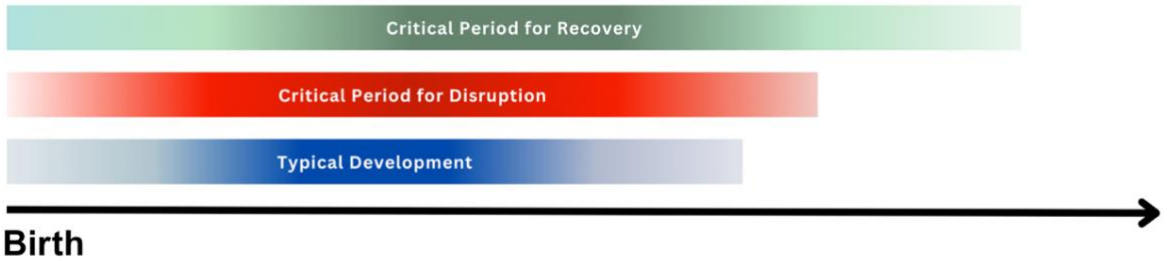
1.1.2. The Period of Typical Development and Critical Periods in Visual Development

Each visual ability has a period of typical development during which it matures to adult levels of function (Daw, 2014). There also exist critical periods for each visual ability during which neuroplasticity in response to visual experience is heightened (reviewed in Lewis & Maurer, 2005; Mitchell & Maurer, 2022). This increased neuroplasticity enables greater cortical reorganization, which are changes in cortical areas in response to experience, within the visual cortex (reviewed in Voss & Zatorre, 2012).

There are two types of critical periods, which often coincide with, yet are distinct from, its corresponding period of typical development (Mitchell & Maurer, 2022) as depicted in Figure 1.1. During critical periods for disruption, the absence or reduction of appropriate visual experiences results in atypical development, and thus atypical function, of the affected visual ability (Daw, 2014). During critical periods for recovery, exposure to typical visual experiences or some other therapeutic intervention can reverse the influence of previous atypical visual experiences, such that the affected visual ability subsequently develops typically (Mitchell & Maurer, 2022). After these critical periods for recovery, the altered development of a visual ability is generally considered permanent and irreversible. The development of visual abilities is therefore less sensitive to visual experiences outside of both types of critical periods. These periods do not necessarily coincide temporally (Lewis & Maurer, 2005); instead, critical periods may entirely occur during a period of typical development or extend beyond it.

Figure 1.1

Period of Typical Development and Critical Periods in Visual Development



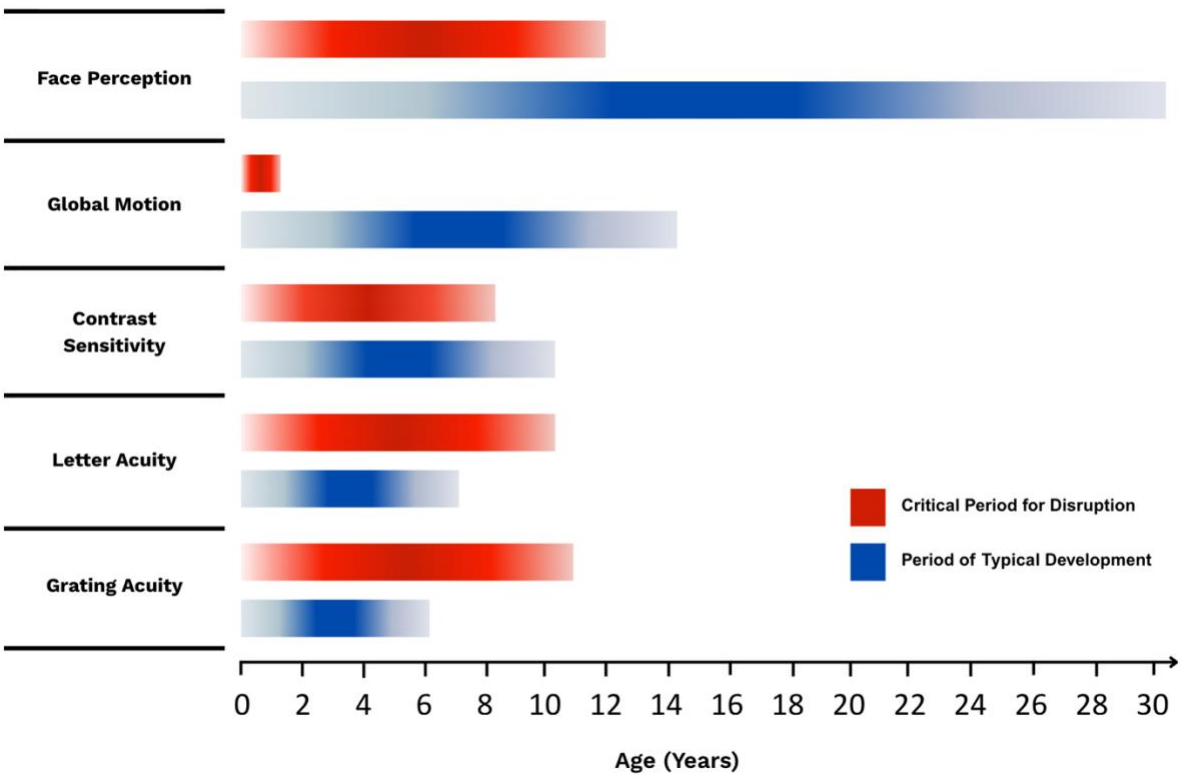
Note. A conceptual illustration of the period of typical development, critical period for disruption, and critical period for recovery, in the development of a visual ability after birth.

1.1.3 Development of Visual Abilities in Humans

The development of visual abilities and their respective critical periods comprise multiple concurrent timelines in humans (reviewed in Maurer & Lewis, 2013; Mitchell & Maurer, 2022). This can be demonstrated by a brief outline of some periods of typical development in which several visual abilities mature to adult levels of function and their corresponding critical periods for disruption that are illustrated in Figure 1.2. The critical periods for recovery are relatively less understood and are not included in this outline (Mitchell & Maurer, 2022).

Figure 1.2

Periods of Typical Development and Critical Periods for Disruption of Some Visual Abilities in Humans



Note. An illustration depicting the estimated periods of typical development (blue bars) and critical periods for disruption (red bars) of various visual abilities in human visual development. The depicted periods of typical development of face perception (Carnevali et al., 2022; Germine et al., 2011; McKone et al., 2012), global motion (Bogfjellmo et al., 2014; Hadad et al., 2011, 2012; Parrish et al., 2005), contrast sensitivity (Ellemberg et al., 1999; Silvestre et al., 2020), letter acuity (Maurer & Lewis, 2013; Simons, 1983), and grating acuity (Ellemberg et al., 1999) are based on evidence of when these abilities fully mature to adult levels. The depicted critical periods for disruption of face perception (McKone et al., 2019; Pascalis et al., 2020), global motion (Ellemberg et al., 2002), contrast sensitivity (Maurer et al., 2006; Mitchell & Maurer, 2022), letter

acuity (Maurer & Lewis, 2001b, 2001a), and grating acuity (Ellemberg et al., 2002) are based on evidence from visual deprivation studies.

Visual acuity is a measure of clarity that refers to the precision in resolving fine details of a visual stimulus that can be tested using different methods (reviewed in de Jong, 2024). Using a sine wave grating paradigm, which presents alternating patterns of black and white stimuli of varying distances from one another, visual acuity develops to adult levels by around six years of age (Ellemberg et al., 1999). Its critical period for disruption starts shortly after birth and ends somewhere between the first five and 11 years of development (Ellemberg et al., 2002). Visual acuity for alphabetical letter stimuli reaches adult levels of maturity at around seven years of age (Simons, 1983, as cited in Maurer & Lewis, 2013). Its critical period for disruption begins shortly after birth and extends to approximately nine to 10 years of age (Maurer & Lewis, 2001b, 2001a).

Contrast sensitivity is a measure of the ability to discern between differences in the brightness of objects relative to their environment (Aleci & Rosa, 2022) which matures to adult levels by the age of seven years (Ellemberg et al., 1999) or, according to more recent research, 10 years (Silvestre et al., 2020). The precise temporal boundaries that define its critical period for disruption are unclear (Mitchell & Maurer, 2022). However, based on evidence from monocular deprivation research, it has been estimated to include at least the first eight years of development (Maurer et al., 2006).

Global motion perception is the ability to perceive the overall movement of an aggregate of smaller, local, motion stimuli and is commonly used to gauge motion perception abilities (reviewed in Burr & Thompson, 2011). This can be investigated using motion coherence tasks, which test the ability to perceive the direction of moving dot stimuli that vary in their speed and

density compared to other dot stimuli moving in random directions (Britten et al., 1992). Global motion abilities have been found to mature to adult levels around seven (Parrish et al., 2005), 12 (Hadad et al., 2011, 2012) or 14 (Bogfjellmo et al., 2014) years of age. There is also evidence for its critical period for disruption being contained within its and not extend past its period of typical development, from shortly after birth until one year of age (Ellemberg et al., 2002). As such, typical visual experiences may not be necessary for the entire period of typical development and instead be limited to a critical period for disruption that ends before the affected ability has matured.

Face perception abilities develop through visual input and learning, with the ability to learn and recognize new faces continuing to improve until around 30 years of age (Germine et al., 2011). However, there is evidence of earlier maturation of face recognition abilities, with estimates of its period of typical development ranging between three to five years of age (McKone et al., 2012). Similarly, there is evidence of the basic configuration of facial features maturing by one year of age (Carnevali et al., 2022).

The existence of critical periods for disruption in the development of face perception is disputed (Pascalis et al., 2020). The other race effect, a phenomenon whereby the discernment of different faces is more accurate in people of the same race as the viewer (Malpass & Kravitz, 1969), has been used to test the development of face recognition. This effect is reduced by exposure to faces of people from other races in the first 12 years of development, but not after that, suggesting the end of a critical period for disruption in this aspect of face perception (McKone et al., 2019).

Notably, the period of development for a given visual ability does not necessarily temporally coincide with its corresponding critical periods. For instance, critical periods for disruption may include and extend past its corresponding developmental period, as with letter

acuity (Maurer & Lewis, 2001b, 2001a), or be entirely contained within it, as with global motion (Ellemberg et al., 2002). Nevertheless, the periods of typical development and critical periods for disruption for many of the reviewed visual abilities are completed by 11 or 12 years of age (see Figure 1.2). This underscores the importance of exposure to typical visual experiences early in life since atypical visual experiences during development could permanently alter a wide range of visual abilities.

The periods of typical development in which visual abilities fully mature, and their corresponding critical periods for disruption, are not all precisely known (Mitchell & Maurer, 2022; Nelson & Gabard-Durnam, 2020). Much of the ambiguity in determining when critical periods occur is due to challenges in their experimental determination (Nelson & Gabard-Durnam, 2020). These periods are determined using evidence from visual deprivation that was experienced by children at different times (Daw, 2014; Mitchell & Maurer, 2022). It follows that ethical constraints limit investigators from incurring visual deprivation at different times in human development to determine precise temporal boundaries of critical periods (Nelson & Gabard-Durnam, 2020).

1.2 Atypical Visual Experiences and Atypical Visual System Development: Amblyopia

A range of pathologies can cause atypical visual experiences, like monocular deprivation, during human development. These include unilateral cataract, which manifests as clouding in the lens of one eye (reviewed in Liu et al., 2017; Mansouri et al., 2013), and strabismus, where both eyes do not point in the same direction (reviewed in Ticho, 2003). Atypical visual experiences during critical periods for disruption may lead to amblyopia, a developmental condition characterized by permanent impairments in visual abilities (reviewed in Levi, 2021). Also known

as ‘lazy eye’, amblyopia usually affects one eye and is a commonly used model for monocular deprivation.

Many of the previously described critical periods are based on research that investigated the timing and nature of atypical visual experiences that resulted in amblyopia (as reviewed in Mitchell & Maurer, 2022). For example, the critical period for disruption of letter acuity is based on the timing of visual deprivation caused by unilateral in children which led to the development of amblyopia (Maurer & Lewis, 2001b, 2001a). Amblyopic deficits are neurological in nature since they are the result of altered visual development in the brain and not due to defects in one or both eyes (Levi, 2021). Visual deficits like the loss of visual acuity in people with amblyopia therefore cannot be corrected by eyeglasses. Instead, therapeutic strategies for amblyopia aim to reverse the altered visual development in the brain during critical periods for recovery (reviewed in Papageorgiou et al., 2019).

Not all forms of monocular deprivation are equal; rather, the atypical visual experiences caused by different pathologies may differ in their timing, duration and degree of deprivation which influence the severity of amblyopic deficits (Levi, 2021). Consider the monocular deprivation caused by unilateral cataracts (reviewed in Liu et al., 2017; Mansouri et al., 2013). The timing of both the onset and surgical removal of a unilateral cataract is important for its effects on visual development (Mitchell & Maurer, 2022). A unilateral cataract in a child is likely to disrupt the development, and thus function, of a visual ability if it coincides with its corresponding critical period for disruption (Mansouri et al., 2013). However, a unilateral cataract is less likely to disrupt the development and function of a visual ability if it occurs in an older child or adult, for whom the relevant critical period for disruption has already passed.

If a unilateral cataract does coincide with the development of a visual ability, the earlier removal of the cataract would minimize its impaired function (Ruth & Lambert, 2006). Unilateral cataracts also differ in the degree of monocular deprivation they cause, due to differences in factors like its size, position and opacity (Liu et al., 2017). Larger and more centrally located unilateral cataracts are more likely to lead to greater amblyopic deficits (Dixit et al., 2017). More opaque unilateral cataracts cause a greater degree of visual obstruction that result in greater visual amblyopic deficits (Smith et al., 2000) that persist into adulthood (Daw, 2014; Hensch & Quinlan, 2018).

1.3. Atypical Visual Experience: Monocular Enucleation

Monocular enucleation is the complete surgical removal of one eye which may be conducted as a last resort treatment for a variety of reasons (reviewed in Moshfeghi et al., 2000). Two of the most common reasons are ocular malignancies, like retinoblastoma present in young children (reviewed in Warda et al., 2022), and traumatic injuries that may occur at any age (Gauthier et al., 2020). The resulting loss of one half of visual input to the brain is unlike the previously described forms of visual deprivation which result in amblyopia (Levi, 2021). People who underwent monocular enucleation provide researchers with a uniquely complete and irreversible model for monocular deprivation (reviewed in Steeves et al., 2008). The consequences of monocular enucleation are notably distinct from amblyopia (Steeves et al., 2008) and have extensively been studied in non-human mammals (reviewed in Nys et al., 2015) and humans (reviewed in Kelly et al., 2013; Nys et al., 2015; Steeves et al., 2008)

1.3.1. Early and Late Monocular Enucleation

The timing of eye removal in reference to visual development can be used to categorize two types of monocular enucleation. Early monocular enucleation is the removal of one eye prior

to the completion of visual development during early childhood and coincides with the critical periods for disruption of most visual abilities (Kelly, Moro, et al., 2013; Steeves et al., 2008). Late monocular enucleation could be defined as the removal of one eye after visual development is relatively completed, during adolescence or adulthood, when the critical periods for disruption of most visual abilities have passed. Importantly, these types of monocular enucleation lack a single codified definition. The age at enucleation that delineates early from late monocular enucleation varies across studies.

Most monocular enucleation research has focused on people who underwent early monocular enucleation and its developmental consequences (reviewed in Kelly, Moro, et al., 2013; Steeves et al., 2008). These studies have primarily tested participants who had one eye removed by five or six years of age (González et al., 2002, 2014; Hoover et al., 2012; Kelly et al., 2012, 2014, 2015; Kelly, Zohar, et al., 2013; Moro et al., 2014, 2015, 2019; Moro & Steeves, 2012, 2013, 2018b, 2018c, 2018a; Steeves et al., 2002). However, this tendency may be explained by the fact that many of these participants had one eye removed to treat retinoblastoma. This rare cancer usually develops in young children (reviewed in Warda et al., 2022) by four (Walker et al., 2025) or five (Broaddus et al., 2009) years of age. Clinical guidelines recommend its screening in genetically predisposed children for up to seven years of age since its onset does not usually extend past this age (Skalet et al., 2018).

Late monocular enucleation has been less extensively researched than its early counterpart and its consequences are therefore less understood. Some studies have included participants in this group who had one eye removed at 45 (Steeves et al., 2002) and 50 (Kelly et al., 2015) years of age. These ages at enucleation are well into adulthood and ostensibly many years after visual development is completed. The youngest age at enucleation that has been included in a late

monocular enucleation group is 11 years of age (Nicholas et al., 1996). This is consistent with evidence of the completion of visual development corresponding with 11 years of age (Garey & de Courten, 1983, as cited by Kelly et al., 2015). This age approximately coincides with the end of the period of typical development and critical periods for disruption of several previously reviewed visual abilities, like contrast sensitivity (Maurer et al., 2006) and grating acuity (Ellemberg et al., 2002), by around 11 or 12 years of age (see Figure 1.2). My research is consistent with previous studies (Day, 1995; Kelly et al., 2015; Nicholas et al., 1996) and defines late monocular enucleation as the removal of one eye including and after 11 years of age. Early monocular enucleation consequently refers to the removal of one eye preceding this range, namely before 11 years of age.

1.3.2. Terminology in Monocular Enucleation Research

Monocular enucleation research generally includes control participants with binocularly intact vision who underwent typical visual development. These participants are tested with their appropriate optical corrections like eyeglasses, if needed, and are often split into two groups. Binocular viewing control participants complete the given task with both eyes open and unobstructed. Monocular viewing control participants have one eye physically obstructed using an eye patch for the duration of the experiment. This provides investigators the opportunity to compare the results of participants with one eye to those with two intact eyes but are experiencing monocular vision, albeit transiently and with a less complete degree of monocular deprivation (Steeves et al., 2004).

1.4. Visual Processing after Monocular Enucleation

A review of existing literature on visual abilities in the years following monocular enucleation provides insights into its long-term implications beyond the reduction of visual input

following the removal of one eye. This research has primarily tested adults who underwent early monocular enucleation using behavioural, structural, and functional measures (reviewed in Kelly, Moro, et al., 2013; Steeves et al., 2008). Differences observed in these measures, compared to binocularly intact control participants, are indicative of altered visual development and highlight the crucial role of intact binocularity for typical visual development. Visual research involving people who underwent monocular enucleation has led to novel findings in spatial vision (Kelly et al., 2012; Kelly, Zohar, et al., 2013; Nicholas et al., 1996), motion processing (González et al., 2002, 2014; Steeves et al., 2002), and the morphology of the visual system (Beatty et al., 1982; Goldby, 1957; Horton, 1997; Kelly et al., 2014, 2015).

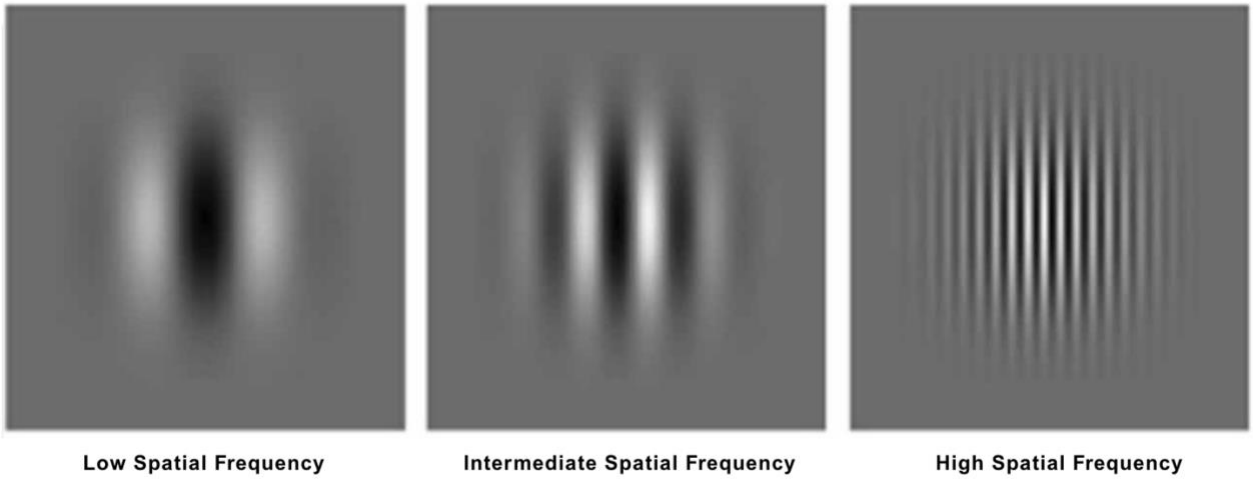
1.4.1 Spatial Vision Abilities

Spatial vision refers to a broad category of visual abilities which entail the processing of the spatial distribution of light stimuli that is captured by the retina and the location of the stimuli in a three-dimensional environment (De Valois & De Valois, 1980; Ferwerda, 1998). Also known as pattern vision, the scope of its definition is usually limited to the perception of non-moving stimuli (Varadharajan, 2012). Low-level spatial vision refers to the fundamental aspects of vision that involves the detection and recognition of basic visual elements like luminance and colour (Groen et al., 2017). Low-level spatial abilities entail early processing in the visual cortex and serve as scaffolding for further visual processing in higher areas of the visual cortex (Yamins & DiCarlo, 2016). High-level spatial vision involves more semantic and cognitive information and includes processes such as the identification of objects like letters and faces (Peirce, 2015). The abilities included in this general hierarchy work together to enable the perception of different objects and scenes in an environment (Groen et al., 2017).

1.4.1.1. Contrast Sensitivity. Contrast sensitivity is the ability to discern differences in brightness and is an important low-level spatial vision feature (Varadharajan, 2012). This is because the visual perception of objects relies upon their illumination, which is usually not uniform in different environments. Contrast sensitivity can be tested using sine wave gratings that vary in contrast (reviewed in Pelli & Bex, 2013; Robson, 1993). In one method, participants are presented with a pair of sine wave gratings that differ in contrast (Robson, 1993). They are then tasked with identifying in which of the presented pair of visual stimuli a sine wave grating was perceived. Contrast sensitivity can be tested at varying spatial frequencies, which refers to the distance between the alternating black and white stripes of a presented sine wave grating (Pelli & Bex, 2013; Robson, 1993). A sine wave grating with a low spatial frequency has wide stripes, which are spread out, whereas a high spatial frequency has thin stripes which are closely spaced as depicted in Figure 1.3.

Figure 1.3

Sine Wave Gratings at Different Spatial Frequencies for Testing Contrast Sensitivity



Note. Illustrated examples of sine wave grating stimuli that can be used to test contrast sensitivity at varying spatial frequencies. The depicted stimuli demonstrate the differences between low, intermediate, and high spatial frequencies. Adapted from "Beauty and the beholder: the role of visual sensitivity in visual preference" by B. Spehar, S. Wong, S. van de Klundert, J. Lui, C. W. G. Clifford and R. P. Taylor, (Spehar et al., 2015), Frontiers in Human Neuroscience, 9:514, p. 8 (https://doi.org/10.3389/fnhum.2015.00514). CC BY 4.0.

People who underwent early monocular enucleation have exhibited comparable contrast sensitivity to monocular viewing control participants at low (Kelly, Zohar, et al., 2013; Nicholas et al., 1996) and high (Nicholas et al., 1996) spatial frequencies (see Figure 1.3). At intermediate spatial frequencies, however, this group has demonstrated improvements in contrast sensitivity compared to both binocular and monocular viewing control participants (Nicholas et al., 1996).

People who underwent late monocular enucleation did not exhibit the same improvements in contrast sensitivity as people who underwent early monocular enucleation (Nicholas et al., 1996). Contrast sensitivity in people who underwent early monocular enucleation was superior to monocular viewing control participants at all the tested intermediate spatial frequencies. Contrast sensitivity in people who underwent late monocular enucleation was instead superior to monocular viewing control participants at one, but not all, tested intermediate spatial frequencies. Similarly, people who underwent early, but not late, monocular enucleation exhibited superior contrast sensitivity compared to binocular viewing control participants at one of the tested intermediate spatial frequencies. These findings collectively indicate that earlier monocular enucleation results in greater improvements in contrast sensitivity. Early monocular enucleation therefore results in unique developmental consequences (Kelly, Zohar, et al., 2013; Nicholas et al., 1996) which do not occur after late monocular enucleation (Nicholas et al., 1996).

1.4.1.2. Visual Acuity. Visual acuity is the precision with which spatial stimuli are resolved and is highest at the centre of the visual field as opposed to its periphery (Barbot et al., 2021). Foveal acuity refers to the centre of the visual field (reviewed in Stewart et al., 2020) whereas eccentric acuity refers to its periphery (reviewed in Rosenholtz, 2016). Letter acuity is a measure of visual acuity that is considered a high-level spatial vision ability since it involves the recognition of shapes and letters (Aleci & Rosa, 2022). This can be tested with the presentation of the tumbling E optotype chart, which comprises rows of the capital letter ‘E’ arranged at different orientations and sizes (reviewed in Aleci & Rosa, 2022; de Jong, 2024). Participants are then instructed to report the direction of the three perpendicular line segments, or ‘legs’, of the letter ‘E’ in its appropriate orientation at a given letter size as illustrated in Figure 1.4. This is also known as an illiterate E optotype chart since it does not require the identification of specific letters (Aleci &

Rosa, 2022; de Jong, 2024). Snellen optotype charts can also be used but require literacy since they present a range of alphabetical letters.

Figure 1.4

Tumbling E Optotypes

Note. An illustration of a Tumbling E optotype in four orientations that can be used to test visual acuity using optotype charts.

Letter acuity has been tested in people who underwent early monocular enucleation and people with strabismus compared to binocular and monocular viewing control participants (González et al., 2002; Reed et al., 1996, 1997). Foveal acuity in people who underwent early monocular enucleation is comparable to that of people with strabismus and monocular viewing control participants (González et al., 2002). Foveal acuity in people who underwent early monocular enucleation in low and high contrast conditions is comparable to binocular viewing control participants (González et al., 2002; Reed et al., 1997), but superior to monocular viewing control participants (González et al., 2002; Reed et al., 1996) and people with strabismus (Reed et al., 1996). Eccentric acuity in people who underwent early monocular enucleation is superior to people with strabismus and comparable to monocular viewing control participants (González et

al., 2002). However, eccentric acuity in people who underwent early monocular enucleation is superior to monocular viewing control participants at lower contrasts.

The findings of these studies suggest that early monocular enucleation and strabismus result in unique developmental consequences. Early monocular enucleation, unlike strabismus (Reed et al., 1996), does not disrupt letter acuity and instead enhances letter acuity at certain contrasts (González et al., 2002; Reed et al., 1996, 1997). This is noteworthy considering that strabismus may result in the development of amblyopia (Levi, 2021). The reviewed evidence therefore indicates that early monocular enucleation is unique from forms of visual deprivation which may result in amblyopia (González et al., 2002; Reed et al., 1996, 1997).

1.4.1.3. Face Perception. Face perception is a high-level spatial vision ability that involves all levels of visual processing to varying degrees (Cox, 2014). Faces comprise an amalgamation of features that are processed by higher cortical regions to form a unified and semantically meaningful percept (reviewed in Tsao & Livingstone, 2008). Face perception has been investigated in people who underwent early monocular enucleation using three measures of facial processing: feature, feature-spacing, and holistic face processing (Kelly et al., 2012).

Participants were presented with faces that differed by the mouth and eyes, and the spaces between the eyes, for feature and feature-spacing perception, respectively (Kelly et al., 2012). To gauge holistic face processing, the composite face effect was tested (Kelly et al., 2012; Young et al., 1987). In this phenomenon, replacing the bottom half of a face with another face creates the illusion of a distinct face, where it becomes difficult to identify the top half as being identical to that of the unaltered face (Young et al., 1987). When the different halves of the faces are spatially offset, it becomes easier to perceive the top halves as being identical or distinct from one another. This effect is exhibited in people with typically developed visual systems and implies that

individual facial features are perceived collectively, rather than independently, to form a holistic facial percept (reviewed in Rossion, 2013).

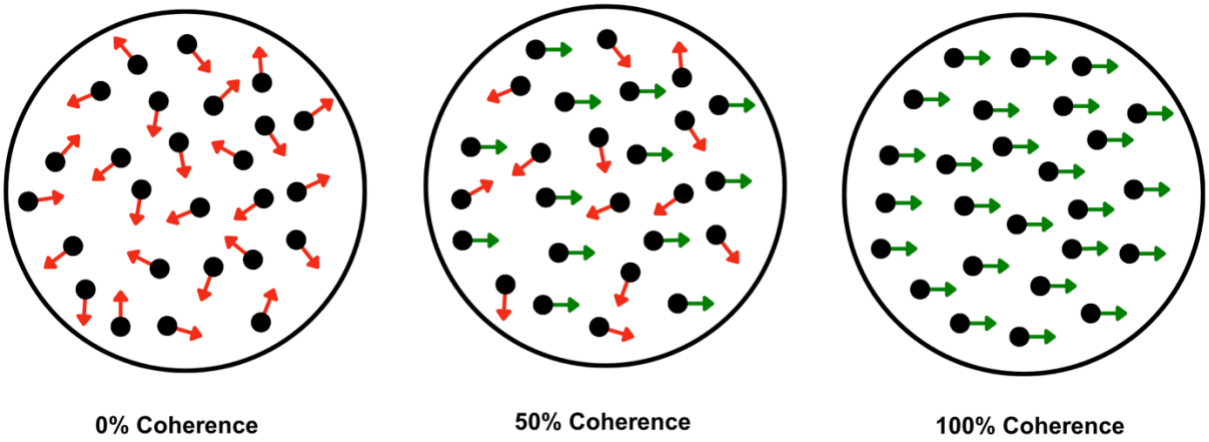
People who underwent early monocular enucleation exhibited impaired performance across the three tested measures of facial processing compared to binocular viewing control participants (Kelly et al., 2012). People who underwent early monocular enucleation exhibited significantly longer response times than binocular viewing control participants in the feature task and the feature-spacing task. People who underwent early monocular enucleation did not exhibit a composite face effect, unlike binocular viewing control participants, which suggests impaired holistic face processing. The investigators also employed control tasks using non-facial stimuli which confirmed that the impairments in facial processing were specific to facial stimuli and not due to general impairments in spatial vision.

1.4.2. Motion Perception

The detection and processing of moving visual stimuli is an integral function of vision which facilitates a variety of abilities including threat evasion and traversal (reviewed in Burr & Thompson, 2011; Sekuler et al., 2002). Global motion has been investigated with a motion coherence task (Britten et al., 1992) in people who underwent early monocular enucleation compared to binocular and monocular viewing control participants (González et al., 2014; Steeves et al., 2002). In this experiment, a group of scattered black dots moved in a unified direction amid other dots which moved in random directions (González et al., 2014; Steeves et al., 2002). The proportion of dots moving in a unified direction relative to the dots moving in random directions was varied across trials to create different levels of motion coherence (see Figure 1.5).

Figure 1.5

Coherent Motion Task Stimuli



Note. A visual schematic of stimuli in a motion coherence task to test global motion coherent motion. The dots are depicted as black circles with different coloured arrows which indicate the direction of their movement. Red arrows are for dots that move in random, uncoordinated directions. Green arrows are for dots that move in a unified, coordinated, direction. The percent of coherence refers to the proportion of dots with green arrows that move in a unified direction. Adapted from "The analysis of visual motion: a comparison of neuronal and psychophysical performance" by K. H. Britten, H. Shadlen, M. N. Newsome, 1992, *Journal of Neuroscience, 12*(12), p. 4746 (https://doi.org/10.1523/JNEUROSCI.12-12-04745.1992). CC BY-NC-SA 4.0.

The thresholds for the detection of coherent motion were subsequently determined in the participants whereby a lower threshold indicated higher sensitivity to coherent motion (González et al., 2014; Steeves et al., 2002). In one study, people who underwent early monocular enucleation exhibited impaired sensitivity in the detection of coherent movement in the temporalward, but not nasalward, direction compared to binocular and monocular viewing control participants (Steeves

et al., 2002). This asymmetric impairment was, however, absent in a subsequent study which used similar methods (González et al., 2014).

The researchers posited that this conflicting finding could be attributed to differences in ages at eye enucleation between the groups across the two studies (González et al., 2014). The study which demonstrated impaired motion coherence detection (Steeves et al., 2002) tested a participant group that underwent early monocular enucleation at younger ages relative to the subsequent study which found no such impairment (González et al., 2014). The earlier ages at enucleation (Steeves et al., 2002) may have coincided with the critical periods for disruption which required intact binocularity for the typical development of coherent motion perception (González et al., 2014). The participant group that did not exhibit an impairment may have underwent early monocular enucleation after the completion of this critical period for disruption (González et al., 2014).

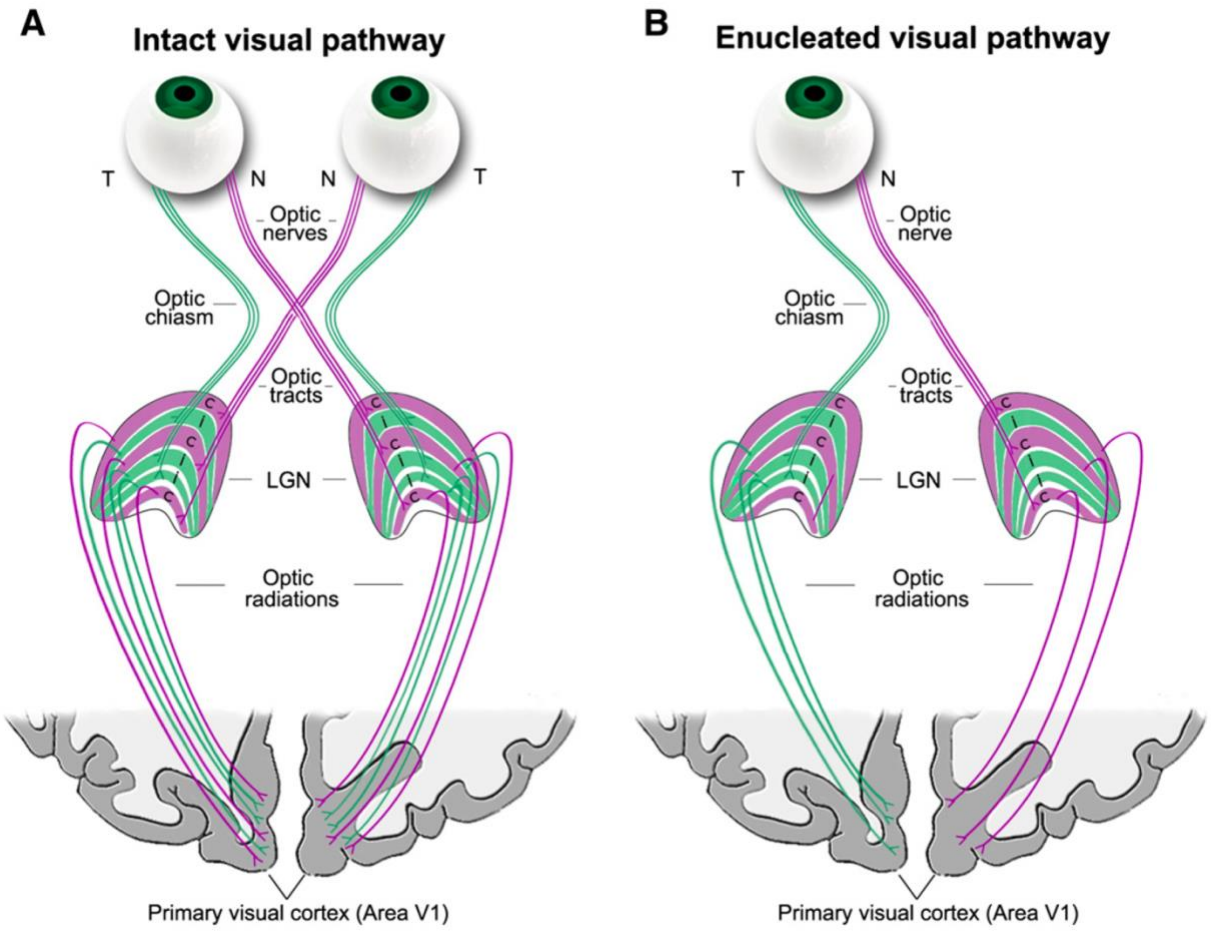
1.4.3. Visual System Morphology

The structural properties and organization of the brain in people who underwent monocular enucleation provides insights into the long-term effects of their monocular deprivation. Studies that used post-mortem dissection and subsequent staining of the brains of people who underwent late monocular enucleation have revealed structural aberrations in the visual pathways of the brain (see Figure 1.6). These include the bilateral atrophy of the optic chiasm (Horton, 1997), optic tracts (Beatty et al., 1982), and lateral geniculate nucleus (LGN) of the thalamus (Beatty et al., 1982; Goldby, 1957). The examined brain specimens in these studies belonged to people who had an eye removed due to trauma sustained across a range of ages, from 15-19 years of age (Goldby, 1957) up until 88 years of age (Horton, 1997). The observed degeneration of visual pathways affects both

hemispheres of the brain for people who underwent late monocular enucleation (Beatty et al., 1982; Goldby, 1957; Horton, 1997).

Figure 1.6

Visual Pathways before and after Early Monocular Enucleation



Note. Illustrations of the visual pathways of the brain in (A) people with binocularly intact vision and (B) people who underwent early monocular enucleation. Visual information from each eye is transmitted through the optic nerve in temporal (green) and nasal (purple) fibres for further processing in other structures of the visual pathway. (T = temporal retinal fibres; N = nasal retinal

fibres; LGN = lateral geniculate nucleus). From "Altered anterior visual system development following early monocular enucleation" by K. R. Kelly, L. McKetton, K. A. Schneider, B. L. Gallie and J. K. E. Steeves, 2014, *NeuroImage: Clinical, 4,* p. 73 (https://doi.org/10.1016/j.nicl.2013.10.014). CC BY 4.0.

Magnetic resonance imaging has also been used to examine the effects of monocular enucleation on the development of visual structures in the brain as illustrated in Figure 1.6 (Kelly et al., 2014, 2015). Evidence of neurodegeneration has been observed in both people who underwent late and early monocular enucleation in the anterior visual system, which includes the optic nerves, optic chiasm, optic tracts, and LGN (Kelly et al., 2014). Symmetric bilateral degeneration of the LGN has been exhibited after late monocular enucleation (Kelly et al., 2014), consistent with previous post-mortem studies (Beatty et al., 1982; Goldby, 1957; Horton, 1997). An overall degeneration of the anterior visual pathways has also been exhibited after early monocular enucleation (Kelly et al., 2014, 2015).

Structural asymmetries have been observed which are unique to early, and not late, monocular enucleation. The optic tract and LGN of people who underwent early monocular enucleation were significantly more reduced contralateral to the enucleated eye (Kelly et al., 2014). This means that the pathway contralateral to the remaining eye, which transmits signals for the remaining eye, is relatively spared. Significantly larger cortical surface area and gyrification have also been observed in visually relevant areas of the cerebral cortex of the brain contralateral to the remaining eye (Kelly et al., 2015). These findings are consistent with other asymmetries observed in this group such as a nasalward preference for coherent motion (Kelly et al., 2014; Steeves et al., 2002) and asymmetric facial processing deficits (Kelly et al., 2012, 2015).

The observed relative sparing of pathways contralateral to the remaining eye (Kelly et al., 2014) and increase in cortical surface area and gyrification contralateral to the remaining eye (Kelly et al., 2015) are possibly due to heightened neuroplasticity during development. This neuroplasticity may have enabled reorganization in which regions of the brain previously associated with the removed eye were recruited to support processing of vision from the remaining eye (Kelly et al., 2014, 2015). The lack of similar evidence of reorganization in the brain of people who underwent late monocular enucleation suggests that late monocular enucleation does not result in the same structural changes as early monocular enucleation.

1.5. Auditory Processing after Monocular Enucleation

Audition is a fundamental sense, like vision, that facilitates abilities like verbal communication through vocal speech stimuli (reviewed in Lotto & Holt, 2016). Sensory systems are often studied independently of one another, which has provided meaningful insights into the basic processing of unisensory stimuli (Purves et al., 2018). However, this approach may neglect the relationships between sensory systems and the multisensory connectivity that exists therein that enables the coordinated perception of different stimuli in an environment (Alais et al., 2010). The visual and auditory systems are interlinked and feature some commonalities despite processing distinct types of stimuli (Rauschecker, 2015). For instance, both systems involve the thalamus, a part of the brainstem that acts as an early relay processing centre after which signals are transmitted to their respective cortices for further processing (reviewed in Bartlett, 2013; Usrey & Alitto, 2015).

The deprivation of visual input may result in neuroplasticity in other sensory systems which may serve as an adaptation for the experienced loss of vision (reviewed in Bavelier & Neville, 2002; Lee & Whitt, 2015). As such, people who are blind in both eyes are commonly considered

to have enhanced audition, compared to people with intact binocular vision, that partially compensates for their visual impairment (reviewed in Sabourin et al., 2022). Evidence for enhanced auditory abilities in people with early blindness include improvements in spatially locating sound (Battal et al., 2020; Lessard et al., 1998; Röder et al., 1999; Voss et al., 2004) and recognizing different voices (Föcker et al., 2012; Pang et al., 2020). Similar results have been observed in people with late blindness for both sound localization (Abel et al., 2002; Voss et al., 2004) and voice recognition (Pang et al., 2020). Monocular enucleation results in the loss of visual input from one eye, which resembles the little to no visual input received by people who are blind in both eyes. Evidence of altered auditory systems in people who are blind in both eyes sets a precedent for the possibility of altered auditory systems in people with one eye and warrants investigation (Hoover et al., 2012).

1.5.1. Sound Localization

Sound localization is the ability to spatially locate the source of an auditory stimulus (reviewed in Middlebrooks, 2015). This ability has been investigated in people who underwent early monocular enucleation compared to binocular and monocular viewing control participants (Hoover et al., 2012). Participants were tasked with localizing auditory stimuli through an array of hidden speakers arranged in front of them along a horizontal plane. Binaural and monaural conditions were tested, wherein the latter entailed the occlusion of one ear with headphones and an earplug. In both binaural and monaural hearing conditions, people who underwent early monocular enucleation exhibited improved sound localization relative to binocularly intact control participants in most speaker locations that are central relative to the participant. However, people who underwent early monocular enucleation exhibited reduced accuracy for localizing auditory stimuli in the extreme periphery.

Monocular viewing control participants exhibited asymmetric performance in the binaural condition whereby accuracy was improved on the side of the viewing eye and reduced on the side of the patched eye (Hoover et al., 2012). This asymmetry is ostensibly the result of the transient monocular vision loss emulated by monocular patching. Investigators concluded that the absence of this asymmetry in people who underwent early monocular enucleation could be evidence of a multisensory adaptation for the loss of one eye during visual development in this group.

1.5.1. Auditory System Morphology

Structural differences have been observed in the auditory systems of people who underwent early monocular enucleation compared to binocularly intact control participants. Increased surface area has been observed in the supramarginal gyrus (Kelly et al., 2015). This is a cortical region that has been implicated with the processing of auditory stimuli including language (Paulesu et al., 1993, as cited in Kelly et al., 2015). A unique asymmetry in the volume of the medial geniculate body (MGB), an area of the thalamus involved in auditory processing (reviewed in Bartlett, 2013), has also been observed in this group (Moro et al., 2015).

Some of the observed structural differences in the auditory systems (Kelly et al., 2015; Moro et al., 2015) of people who underwent early monocular enucleation are analogous to those observed in their visual systems (Kelly et al., 2014, 2015). Increases in the surface area and gyrification of the supramarginal gyrus are akin to those observed in the visual cortex (Kelly et al., 2015). Asymmetric volumes have also been observed in the auditory area of the thalamus, the MGB, (Moro et al., 2015) and visual area of the thalamus, the LGN (Kelly et al., 2014).

The asymmetries however differ in that increases in LGN volume are ipsilateral to the removed eye (Kelly et al., 2014), whereas the left MGB is significantly larger than its right hemispheric counterpart, regardless of which eye was removed (Moro et al., 2015). This eye

agnostic asymmetry is interesting given that the left hemisphere of the brain plays a role in processing language (Knecht et al., 2000) (reviewed in Riès et al., 2016). The observed asymmetry has been suggested to serve as a compensatory adaptation (Moro et al., 2015) for deficits in facial recognition in this group (Kelly et al., 2012). People who underwent early monocular enucleation may better recognize other people using auditory speech stimuli instead of visual face stimuli (Moro et al., 2015).

A positive correlation in the volumes of the MGB and LGN was also observed in this group (Moro et al., 2015). The concurrent increase in the volumes of thalamic regions was interpreted as evidence for increased neuroplasticity in both auditory and visual systems of the brain after early monocular enucleation. The observed differences in certain auditory (Kelly et al., 2015; Moro et al., 2015) and visual (Kelly et al., 2014, 2015) areas of the brain therefore suggest the altered development of both senses in people who underwent early monocular enucleation.

1.6. Audiovisual Integration

Environments are replete with multiple concurrently presented stimuli from different senses that are processed by their appropriate sensory systems. Multisensory processing in the brain enables the coordinated processing of stimuli to form a holistic and accurate representation of a given environment and the objects within it (reviewed in Alais et al., 2010). One important function of multisensory processing is the perceptual integration of stimuli from different senses if they are considered to originate from the same source (reviewed in De Gelder & Bertelson, 2003; Vroomen & Keetels, 2010). The integration of complementary sensory stimuli reveals different properties of what is being perceived and redundancies that confer a greater degree of reliability in the formed percepts. It follows that multisensory integration is foundational to many learned

and innate abilities like traversal (reviewed in Berthoz & Viaud-Delmon, 1999) and communication (Holler & Levinson, 2019; reviewed in Rosenblum, 2008).

Audiovisual integration is a subset of multisensory integration that is important for abilities which extract auditory and visual information from the environment (reviewed in Spence, 2007). Consider the perception of auditory speech, as vocal stimuli, and visual speech, as facial stimuli. The integration of these stimuli enhances speech comprehension especially when a vocal stimulus is unclear (Ross et al., 2007). The presentation of facial stimuli provides further phonetic information from the visual perception of articulatory mouth movements made during speech production (Rosenblum, 2008).

Difficulty in understanding the speech of someone wearing a face mask is one example that illustrates the importance of audiovisual integration. The use of a face mask reduces the quality of vocal stimuli being heard (Sönnichsen et al., 2022) and prevents facial stimuli from being seen entirely (Giovanelli et al., 2021; Sönnichsen et al., 2022). Both factors contribute to impairments in speech comprehension (Sönnichsen et al., 2022). However, the inability to integrate facial and vocal stimuli through lip reading has been shown to have a greater influence on the impairment of speech comprehension (Giovanelli et al., 2021). This example illustrates the importance of integrating auditory and visual stimuli for forming meaningful multisensory percepts. Audiovisual integration in people who underwent monocular enucleation warrants investigation given previously reviewed differences in unisensory, visual (see 1.4) and auditory (see 1.5), processing.

1.6.1. Audiovisual System Morphology after Early Monocular Enucleation

The structural architecture that underlies audiovisual integration is less defined than it is for unisensory processing and is more diffusely spread across the brain (Gao et al., 2023). Audiovisual neural pathways lack a single unified underlying construct and instead comprise a

mosaic of unisensory and multisensory areas of the brain that work together (reviewed in Schroeder & Foxe, 2005). These include subcortical areas like the thalamus, and cortical regions like primary sensory cortices and higher-level association areas (Gao et al., 2023). Activity in these areas is flexible and dependent on contextual factors such as stimulus complexity (reviewed in Van Atteveldt et al., 2014).

The processing of multisensory stimuli involves low-level, early cortical, unisensory areas which can feed into higher-level cortical areas of the brain for more complex processing (Gao et al., 2023; Schroeder & Foxe, 2005). Consequently, the reviewed changes after early monocular enucleation in thalamic (Kelly et al., 2014; Moro et al., 2015) and cortical (Kelly et al., 2015) structures involved in unisensory processing also constitute altered structure of audiovisual neural pathways (Gao et al., 2023). These findings are further supported by evidence of increased cortical surface area in the superior temporal sulcus, a high-level association region involved in audiovisual integration (Kelly et al., 2015).

1.6.2. Temporal and Spatial Principles of Audiovisual Integration

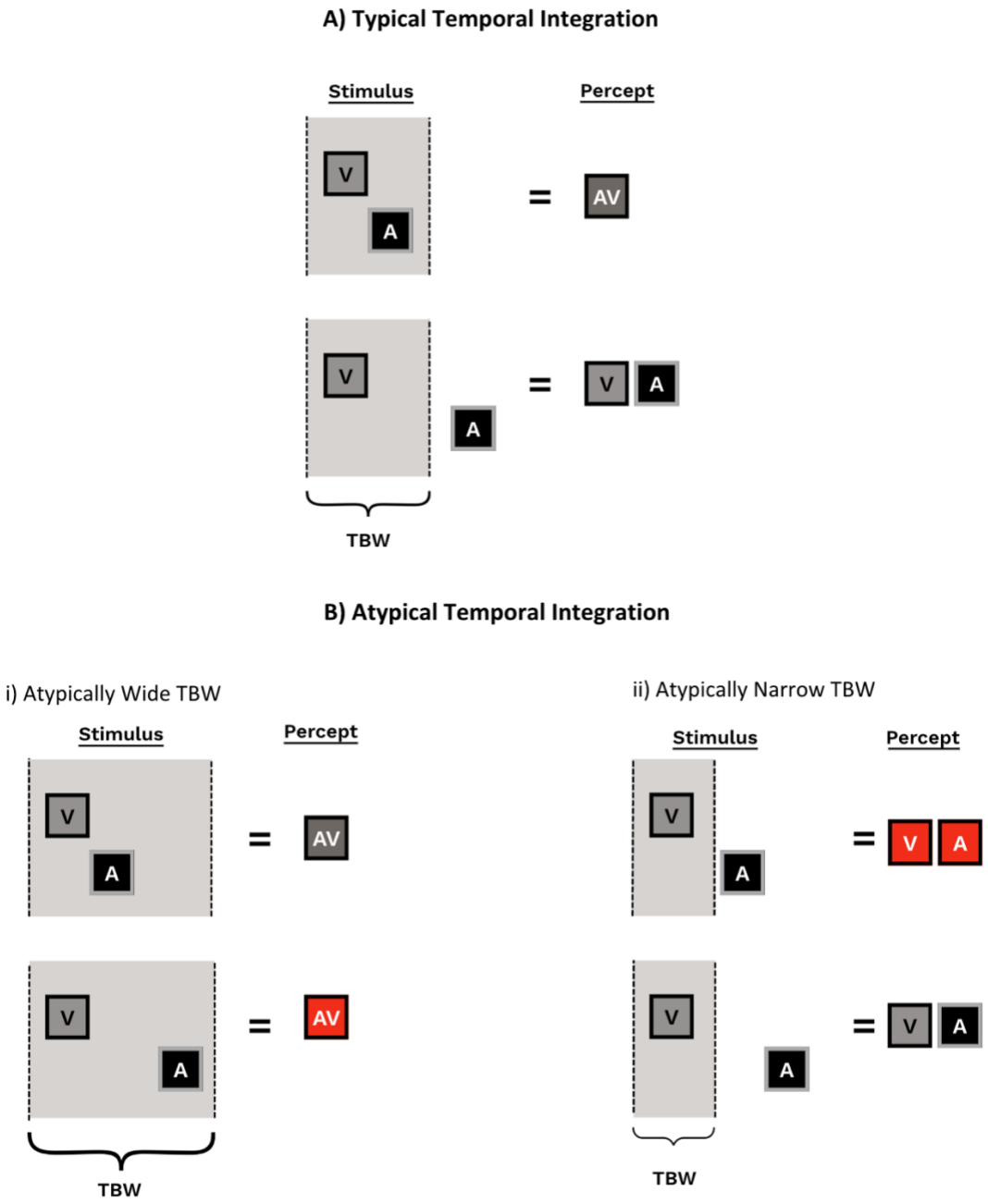
Auditory and visual stimuli are more likely to be integrated as a unified audiovisual percept when they are presented close to one another in time and space (Alais et al., 2010). This is in accordance with the temporal and spatial principles of audiovisual integration, respectively (reviewed in Holmes & Spence, 2005; Spence, 2007). These principles are foundational for determining whether different types of presented sensory stimuli are common or distinct in their origin. The integration of audiovisual stimuli in the temporal domain depends on temporal binding windows: the time during which auditory and visual stimuli are presented and tend to be perceived as a unified event (Jagini, 2021; reviewed in Wallace & Stevenson, 2014). Presentation of auditory and visual stimuli outside of the temporal binding window will be considered as separate events.

This is necessary to accommodate for any differences in the speeds of transmission of auditory and visual stimuli (King, 2005). For instance, the speed of light is faster than the speed of sound, which means that the visual and auditory components of an audiovisual stimulus may not be presented to an individual at the same time. This asynchrony is accounted for by the temporal binding window, which ensures that the stimuli are perceptually bound, or integrated, and perceived as a unified audiovisual event (Wallace & Stevenson, 2014).

1.6.2.1. Temporal Integration. Multiple temporal binding windows exist for the integration of auditory and visual stimuli that differ in their width according to factors like stimulus complexity (Stevenson & Wallace, 2013). The width of a temporal binding window refers to the range of stimulus onset asynchronies, the time between the presentation of stimuli, in which stimuli from different senses are perceived as simultaneously presented, as illustrated in Figure 1.7 (Wallace & Stevenson, 2014). Wider temporal binding window widths lead to the perceived simultaneity of sensory stimuli presented at larger stimulus onset asynchronies. More complex stimuli tend to have wider temporal binding windows for their integration (Stevenson & Wallace, 2013). Narrower temporal binding window widths facilitate the improved discernment of asynchrony between sensory stimuli. Less complex stimuli tend to have narrower temporal binding windows for their integration.

Figure 1.7

Typical and Atypical Temporal Integration of Audiovisual Stimuli



Note. The integration of audiovisual stimuli in the temporal domain is influenced by temporal binding windows of appropriate widths that ensure the veridical integration or segregation of

auditory and visual stimuli. (A) Illustration of temporal binding window width of appropriate resolution that veridically integrates and segregates stimuli.(B) Illustration of temporal binding window widths of atypical resolutions that tend to (i) erroneously integrate disparate stimuli and (ii) erroneously segregate stimuli from a common source (V = visual; A = auditory; AV = audiovisual; TBW = temporal binding window; red boxes = erroneous perception). Adapted from "Keeping time in the brain: Autism spectrum disorder and audiovisual temporal processing," by R. A. Stevenson, M. Segers, S. Ferber, M. D. Barense, S. Camarata and M. T. Wallace, 2016, *Autism Research, 9*(7), p. 721 (https://doi.org/10.1002/aur.1566). Copyright 2015 by John Wiley and Sons. Adapted with permission.

Temporal binding windows must be of an appropriate resolution to ensure the veridical perception of auditory and visual stimuli as disparate events or a unified audiovisual stimulus (see Figure 1.7) (Wallace & Stevenson, 2014). Atypically wide temporal binding window widths may result in the erroneous perceptual integration of disparate stimuli. Atypically narrow temporal binding window widths may conversely result in the erroneous perceptual segregation of a unified audiovisual stimulus.

The temporal integration of audiovisual stimuli in people who underwent early monocular enucleation has been studied with a task that briefly presented simple visual ring and auditory tone stimuli at a range of stimulus onset asynchronies (Moro & Steeves, 2018c). Participants were instructed to report when they perceived these low-level stimuli as simultaneously presented. The resulting data of perceived simultaneity at different stimulus onset asynchronies was used to determine the temporal binding window widths of participants. People who underwent early monocular enucleation had slower response times compared to binocular viewing control

participants. However, the temporal binding window widths in this group were comparable to binocular and monocular viewing control participants. This suggests that early monocular enucleation does not affect the temporal integration of low-level audiovisual stimuli.

1.6.2.2. Spatial Integration. The integration of audiovisual stimuli in the spatial domain can be studied using localization tasks which involve the integration of auditory and visual stimuli (Spence, 2007). Spatial localization experiments can exploit the ventriloquism effect (Howard & Templeton, 1966). This effect (reviewed in Kayser et al., 2019) refers to a phenomenon where the presentation of spatially displaced auditory and visual stimuli results in a single fused audiovisual percept, the location of which is ascribed to the visual component (Jack & Thurlow, 1973; Slutsky & Recanzone, 2001; Thurlow & Jack, 1973). This visual bias can be nullified by reducing the reliability of the visual stimulus by blurring it to a degree where localization is not biased towards a particular sense (Alais & Burr, 2004). This balanced sensory weighting of auditory and visual stimuli enables investigators to test the localization abilities of participants when integrating spatial stimuli from both senses.

The described paradigm has been used to study spatial integration of audiovisual stimuli in people who underwent early monocular enucleation compared to binocular and monocular viewing control participants (Moro et al., 2014). The experiment comprised unisensory, auditory and visual, and audiovisual trial conditions. The presented stimuli were a white visual blob and an auditory click. Participants were presented with stimuli in two intervals for the trials separated by an interstimulus interval of silence and a blank screen. In the unisensory trials, the first interval presented a centrally located stimulus, and the second interval presented a stimulus that was horizontally offset from the centre. In the audiovisual trials, one of the intervals presented spatially aligned auditory and visual stimuli, while the other interval presented auditory and visual stimuli

that were horizontally offset to varying degrees. Participants were instructed to report which of the presented stimulus intervals was located more leftward relative to the centre.

People who underwent early monocular enucleation spatially localized stimuli with comparable accuracy to binocularly intact control participants in both unisensory and audiovisual trial conditions (Moro et al., 2014). This suggests that audiovisual spatial integration abilities are intact after early monocular enucleation and information from both senses is weighted equally. It has been posited that the previously reviewed unisensory enhancement with sound localization (Hoover et al., 2012) could contribute to the preservation of audiovisual spatial integration in this group (Moro et al., 2014).

Faster response times for audiovisual trials compared to unisensory trials were observed in people who underwent early monocular enucleation and in the binocularly intact control participants (Moro et al., 2014). Spatial localization is thereby facilitated by the integration of auditory and visual stimuli in both groups. This is a phenomenon that is observed in people with typically developed visual systems (Nidiffer et al., 2016). The findings of the monocular enucleation study suggest that this audiovisual facilitation effect is intact after early monocular enucleation (Moro et al., 2014). The comparable accuracy and intact audiovisual facilitation collectively indicate that monocular enucleation does not impair the spatial integration of audiovisual stimuli.

1.6.3. Sensory Dominance

One sense may have a predominant influence over the other in the integration of multisensory stimuli, known as sensory dominance, in certain contexts (Hecht & Reiner, 2009). Consider the visual dominance exhibited in the ventriloquism effect, where the location of a formed audiovisual percept is attributed to the visual component of an audiovisual stimulus

(Howard & Templeton, 1966). Another example is the Colavita visual dominance effect (Colavita, 1974), which describes the tendency to exclusively perceive a visual stimulus despite the simultaneous presentation of an auditory stimulus (reviewed in Spence et al., 2012). This effect is notably absent in early childhood but develops over time and is commonly exhibited in adulthood (Hirst, Cragg, et al., 2018). It is therefore possible that its occurrence is altered in people who underwent atypical development of their sensory systems.

1.6.3.1. Colavita Visual Dominance Effect after Early Monocular Enucleation. The Colavita visual dominance effect has been investigated in people who underwent early monocular enucleation and compared to binocular and monocular viewing control participants (Moro & Steeves, 2012). Participants were presented with a series of auditory stimuli comprising commonly identifiable sounds. At the same time, participants were presented with a series of visual stimuli comprising commonly identifiable objects depicted as line drawings. Participants were assigned unisensory, auditory or visual, targets which were embedded within the series of stimuli. Audiovisual target stimuli were also assigned, which were a combination of an auditory and visual target stimulus. Participants were then instructed to report when the assigned unisensory target stimulus, or audiovisual target stimulus pairing, was perceived. The unisensory and audiovisual target stimuli were perceived comparably by the three participant groups in terms of accuracy and response time. The perception of audiovisual target stimuli was less accurate than unisensory target stimuli in all three participant groups.

The analysis of the errors in identifying the audiovisual target stimuli revealed that the binocular and monocular viewing control participants perceived the visual component of the paired audiovisual target stimuli more than the auditory component (Moro & Steeves, 2012). This is indicative of the Colavita visual dominance effect in the control participants. People who

underwent early monocular enucleation, however, did not exhibit a perceptual preference for one sense over the other when identifying an audiovisual target. This group therefore did not exhibit the Colavita visual dominance effect. Instead, their performance suggests a lack of sensory dominance where there is equal processing of the auditory and visual components of an audiovisual stimulus.

A follow-up study modified the Colavita experiment to increase the reliability of the auditory stimuli relative to the visual stimuli (Moro & Steeves, 2013). It was predicted that this modification could result in a reversed effect where there is auditory, instead of visual, dominance. Here, the Colavita visual dominance effect was reduced, although not reversed, in monocular and binocular viewing control participants. This suggests that the modified experiment was perceived with less visual dominance, and relatively more auditory dominance, in these binocularly intact control participants.

People who underwent early monocular enucleation did not exhibit the Colavita visual dominance effect or its reversal in this modified experiment (Moro & Steeves, 2013). The processing of auditory and visual stimuli was equal in this group despite a modification that induced less visual dominance and more auditory dominance in binocularly intact control participants. These findings collectively suggest that people who underwent early monocular enucleation possess balanced, unbiased, processing of visual and auditory stimuli in the Colavita experiment regardless of whether the experiments were designed to elicit visual (Moro & Steeves, 2012) or auditory dominance (Moro & Steeves, 2013).

1.6.3.2. Dynamic Visual Capture after Early Monocular Enucleation. Visual capture is a form of visual dominance in an integrated percept whereby the movement of a visual stimulus influences the perceived motion of a concurrently presented auditory stimulus (Mateeff et al.,

1985). This phenomenon has been studied in an experiment measuring looming or receding audiovisual stimuli in people who underwent early monocular enucleation compared to binocular and monocular viewing control (Moro & Steeves, 2018b). Participants were instructed to report the direction of the auditory stimulus' movement. The early monocular enucleation patient group, like both binocularly intact control groups, exhibited dynamic visual capture where the perceived auditory direction was dictated by the movement of the concurrently presented visual stimulus. This result was unexpected since it seemingly contradicts the previously noted equivalent processing of auditory and visual stimuli (Moro & Steeves, 2012, 2013) and instead shows dominance of visual over auditory stimuli (Moro & Steeves, 2018b). The intact dynamic visual capture could be an adaptation where attention is directed towards visual stimuli that are looming or receding, which are ecologically relevant since incoming objects could inflict harm (Moro & Steeves, 2018b).

1.6.3.3. Face and Voice Recognition after Early Monocular Enucleation. Person identification is a crucial function for fostering social relationships that is often facilitated through the recognition of visual facial stimuli and auditory vocal stimuli (Gokcekus et al., 2021). People who underwent early monocular enucleation have exhibited deficits in the processing of facial stimuli (Kelly et al., 2012, 2019) and altered processing of auditory stimuli (Hoover et al., 2012) despite evidence of intact audiovisual integration (Moro et al., 2014). In this context, the recognition of individuals using faces and voices has been investigated in people who underwent early monocular enucleation compared to binocular and monocular viewing control participants (Moro et al., 2019). Participants were presented with pairs of facial and vocal stimuli that they were instructed to learn as the identities of individuals. They were then tasked with identifying the

learned individuals interspersed within a series of other facial and vocal stimuli that were presented in unisensory and audiovisual stimulus conditions.

People who underwent early monocular enucleation and monocular viewing control participants were more sensitive to person identification in the unisensory vocal stimulus condition compared to binocular viewing control participants (Moro et al., 2019). This suggests an improved ability to identify individuals through auditory vocal stimuli alone. Binocular viewing control participants exhibited a visual dominance effect in the audiovisual stimulus condition. Specifically, person identification was improved in this group when facial stimuli were presented alongside vocal stimuli. People who underwent early monocular enucleation and monocular viewing control participants did not exhibit this visual dominance effect. Instead, these groups used both facial and vocal stimuli more equally than binocular viewing control participants in person identification. These findings collectively suggest the adapted use of auditory vocal stimuli and more balanced processing of visual and auditory stimuli in people who underwent early monocular enucleation and monocular viewing control participants.

1.7. Investigating Audiovisual Integration Using Audiovisual Illusions

An illusion is defined as a percept that objectively differs from a presented stimulus and thereby constitutes an inaccurate representation of reality (Gregory, 1968). Audiovisual illusions, which involve the presentation of audiovisual stimuli, have extensively been used to investigate audiovisual processing and integration (reviewed in Boyce et al., 2020). This is because the perception of an audiovisual illusion necessitates the processing and subsequent integration of auditory and visual stimuli. This integration is the result of multisensory processing mechanisms in the brain which attempt to reconcile simultaneously presented auditory and visual stimuli that are incongruent, mechanistically implausible, or otherwise atypical (Nour & Nour, 2015).

Susceptibility to an audiovisual illusion, which refers to the tendency to perceive it, is therefore commonly used as a measure of audiovisual integration.

1.7.1. Bayesian Causal Inference Explanation of Audiovisual Integration

The theory of Bayesian causal inference (Körding et al., 2007) has been used to explain various processes in the brain (reviewed in Shams & Beierholm, 2022) including audiovisual integration (Körding et al., 2007; Rohe & Noppeney, 2015) and by extension, the perception of audiovisual illusions, or the lack thereof (reviewed in Nour & Nour, 2015). Importantly, this theory also provides an explanation for how sensory dominance can occur based on the relative weighting of stimuli. The Bayesian causal inference model of audiovisual integration (Körding et al., 2007) has been described as a process with two stages: binding and fusion (Lindborg & Andersen, 2021).

The binding stage (Lindborg & Andersen, 2021) is where the brain determines the causal structure of the presented auditory and visual stimuli (Körding et al., 2007). This refers to whether the stimuli originate from common or independent sources (Körding et al., 2007).

Accordingly, the stimuli are perceptually integrated if common causal structure is inferred, otherwise they are perceptually segregated. The inference of causal structure is determined by prior expectations of whether the presented stimuli originate from a common or independent source. This prior expectation of causal structure, also known as binding tendency (reviewed in Quintero et al., 2022), is formed based on previous experiences of similar auditory and visual stimuli originating from common or independent sources (Körding et al., 2007).

The fusion stage (Lindborg & Andersen, 2021) is where auditory and visual stimuli are weighted based on their perceived relative reliability to form the resultant percept (Körding et al., 2007). The sense that provides more reliable information is assigned greater weight than the less reliable sense (Körding et al., 2007). This is referred to as relative reliability weighting (Rohe &

Noppeney, 2015), since the reliability of each sense is evaluated in relation to the other and the more reliable sense contributes more strongly to the resultant percept (Körding et al., 2007). According to this model, sensory dominance can be explained by the greater relative reliability weighting of the dominant sense (Körding et al., 2007).

Consider the perception of the ventriloquism effect (Howard & Templeton, 1966) as a demonstrative example of a Bayesian causal inference model for audiovisual integration (Körding et al., 2007). In this audiovisual illusion, spatially disparate auditory and visual stimuli are integrated as a unified percept in the binding stage (Lindborg & Andersen, 2021) partly because they are presented concurrently in terms of time (Körding et al., 2007). The perceived simultaneity confers high binding tendency for the two stimuli, so it is inferred that they originate from a common source. The visual stimulus is weighted more in terms of location (Körding et al., 2007) in the fusion stage (Lindborg & Andersen, 2021) because vision confers greater reliability in spatial information compared to audition (Alais & Burr, 2004; Metcalfe et al., 1981). The location of the resulting integrated audiovisual percept is therefore attributed to the presented visual stimulus (Körding et al., 2007) and the ventriloquism effect is described as a form of visual dominance (Howard & Templeton, 1966).

The ventriloquism effect would not be perceived if the inference for common causal inference is not made in the binding stage, or if the relative reliability of visual stimuli is not greater than auditory stimuli in the fusion stage (Körding et al., 2007). It follows that the reduced susceptibility to this illusion in an individual or group can reflect altered audiovisual integration. This could be the result of altered processing in inferring causal structure or in the relative reliability weighting of sensory stimuli compared to those who are susceptible to the illusion.

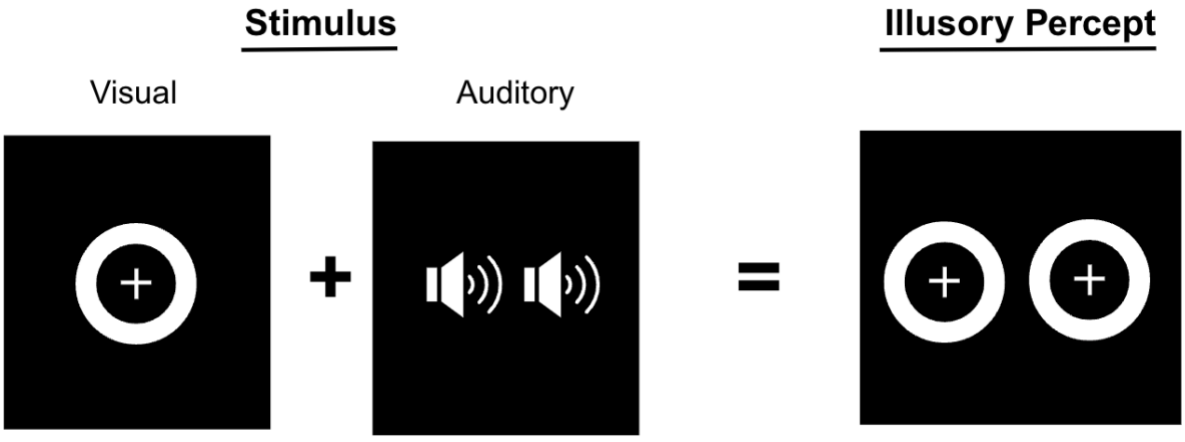
Susceptibility to other audiovisual illusions can be used in this way to compare audiovisual integration and sensory dominance across different groups in other contexts and types of stimuli.

1.7.2. The Sound-Induced Flash Illusion

The sound-induced flash experiment (Shams et al., 2000, 2002) is commonly used to study the integration of low-level auditory and visual stimuli (reviewed in Hirst et al., 2020; Keil, 2020). Participants of this experiment are presented with a single visual flash stimulus paired with multiple auditory beep stimuli and instructed to report the number of visual flashes that they see (Shams et al., 2000, 2002). Participants may perceive multiple illusory visual flashes, instead of one visual flash, which denotes the perception of the sound-induced flash illusion (see Figure 1.8).

Figure 1.8

Sound-Induced Flash Experiment Stimulus and Illusory Percept



Note. A schematic of the sound-induced flash experiment stimulus and its corresponding illusory percept.

1.7.2.1. Bayesian Causal Inference Explanation of the Sound-Induced Flash Illusion. It has been argued that the perception of illusory visual flashes in the sound-induced flash experiment is best explained by the theory of Bayesian causal inference (Hirst et al., 2020). This model proposes that the single presented visual flash stimulus is perceptually integrated with the multiple concurrently presented auditory beep stimuli due to an inference of common causal structure (Shams, 2012; Shams et al., 2005). The discrepancy in the number of stimuli presented across the two senses is resolved through the perception of multiple visual flashes.

More than one visual flash is perceived because audition confers more reliable timing and numerosity information than vision (Metcalfe et al., 1981; Repp & Penel, 2002). It follows that the multiple presented auditory beep stimuli confer greater relative reliability weighting in terms of numerosity than the single presented visual stimulus (Shams, 2012; Shams et al., 2005). Perception of the sound-induced flash illusion therefore reflects the relative dominance of audition over vision in the integration of the stimuli. This form of auditory dominance contrasts with previously reviewed instances of visual dominance like the ventriloquism effect (Howard & Templeton, 1966) and the Colavita visual dominance effect (Colavita, 1974).

1.7.2.2. The Sound-Induced Flash Illusion after Early Monocular Enucleation. Susceptibility to the sound-induced flash illusion has been investigated in people who underwent early monocular enucleation compared to binocular and monocular viewing control participants (Moro & Steeves, 2018c). The stimuli used in the sound-induced flash experiment were an auditory pure tone that was beeped and a white visual ring that was flashed against a black background as illustrated in Figure 1.8. An illusory set of trials was presented in which a single flash was paired with zero to four rapidly successive beeps (Moro & Steeves, 2018c). Participants were then tasked with quantifying the number of flashes they perceived.

Participants that reported more than one flash in the illusory trials were susceptible to the sound-induced flash illusion since they perceived illusory flashes (Moro & Steeves, 2018c). Binocular viewing control participants were, as expected (Shams, 2012; Shams et al., 2005), susceptible to the illusion according to this criterion (Moro & Steeves, 2018c). However, people who underwent early monocular enucleation were not susceptible to the illusion and instead perceived a comparable number of flashes regardless of the number of auditory beeps presented alongside the single presented visual flash (Moro & Steeves, 2018c). Monocular viewing control participants perceived illusory flashes, albeit less than binocular viewing control participants. Monocular viewing control participants therefore demonstrated intermediate susceptibility to the sound-induced flash illusion compared to binocular viewing control participants and people who underwent early monocular enucleation.

No correlation was found between temporal binding window width and illusory flash perception across the three tested groups (Moro & Steeves, 2018c). This contrasts with previous research of binocular viewing participants which correlated narrower temporal binding window widths with reduced illusory flash perception (Stevenson et al., 2012). This correlation is consistent with narrower temporal binding windows conferring greater acuity in discriminating between asynchronously presented beep and flash stimuli (see Figure 1.7), which make the stimuli less likely to be integrated (Stevenson & Wallace, 2013).

The absence of this correlation (Stevenson et al., 2012) in people who underwent early monocular enucleation suggests that their reduced susceptibility to the sound-induced flash illusion cannot be attributed to differences in the temporal integration of auditory and visual stimuli (Moro & Steeves, 2018c). Instead, the findings suggest unique audiovisual processing mechanisms in the completion of this experiment (Moro & Steeves, 2018c). The altered processing of stimuli results

in altered audiovisual integration, which leads to more veridical perception in this context. This is because the asynchronously presented auditory and visual stimuli in this experiment are not erroneously integrated.

Recall that the perception of illusory flashes reflects a form of auditory dominance through the greater relative reliability weighting of auditory stimuli compared to visual stimuli (Shams, 2012; Shams et al., 2005). The reduced susceptibility to the sound-induced flash illusion therefore suggests altered sensory dominance, and more balanced processing of low-level auditory and visual stimuli, after early monocular enucleation (Moro & Steeves, 2018c). This is also consistent with evidence from other measures in this group like absence of the Colavita effect (Moro & Steeves, 2012, 2013) and more balanced processing of stimuli in person identification (Moro et al., 2019). The balanced processing of sensory stimuli is possibly due to altered audiovisual development experienced after early monocular enucleation which coincides with several critical periods for disruption (Moro & Steeves, 2018c).

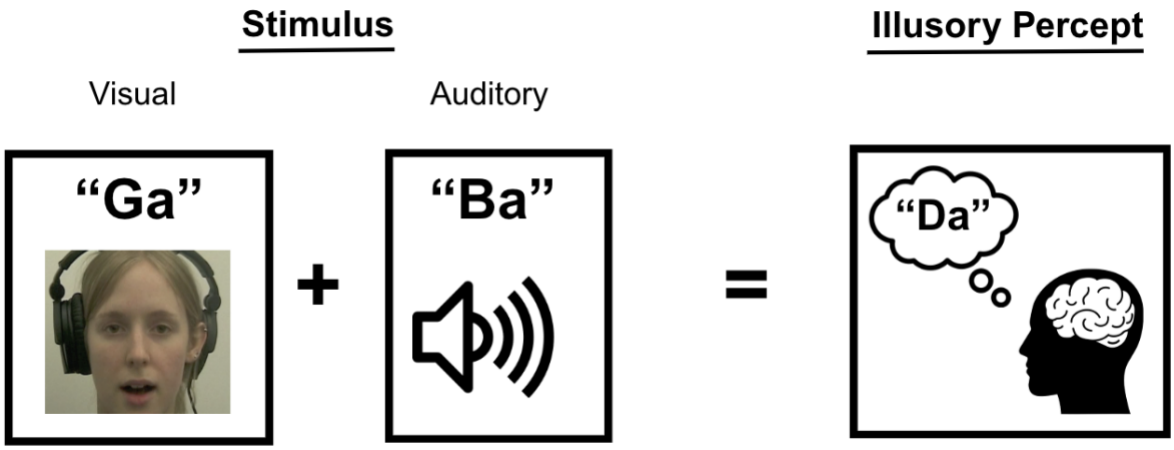
1.7.3. The McGurk Effect

The McGurk experiment (McGurk & Macdonald, 1976) is a commonly used tool for studying the unconscious integration of high-level auditory and visual stimuli (reviewed in Alsius et al., 2018; Marques et al., 2016). This experiment involves the presentation of incongruently paired facial stimulus and vocal speech stimulus that cannot be concurrently produced by a single speaker due to articulatory constraints (Green & Norrix, 1997). For example, the production of the consonant “b”, as in the syllable “ba”, requires bilabial closure, which closes the mouth. This prevents the same speaker from simultaneously producing the consonant “g”, as in the syllable “ga”, which requires an open mouth. In a McGurk experiment, the syllable “ba” can be presented as an auditory vocal stimulus, alongside the syllable “ga” as a visual facial stimulus (McGurk &

Macdonald, 1976). Participants often perceive an illusory syllable, known as the McGurk effect, which approximates to the syllable “da” with an auditory “ba” and visual “ga” syllable pair (see Figure 1.9). This audiovisual illusion has also been demonstrated through different syllable pairings, like the illusory perception of the syllable “ta” resulting from the auditory “pa” and visual “ka” syllable pair (McGurk & Macdonald, 1976).

Figure 1.9

McGurk Syllable Stimulus and Illusory Percept



Note. A schematic of the incongruent syllables presented in the McGurk stimulus and its accompanying illusory syllable percept, known as the McGurk effect.

1.7.3.1. Bayesian Causal Inference Explanation of the McGurk Effect. The McGurk effect is perceived due to audiovisual processing mechanisms in the brain that resolve the presented conflicting syllables by forming a fused illusory percept (Tiippana, 2014). Bayesian causal inference models of this illusion (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017) have been argued to provide the best explanation for its perception (Lindborg & Andersen, 2021;

Magnotti et al., 2020; Meijer & Noppeney, 2023). First, the incongruent auditory and visual speech stimuli presented in a McGurk experiment are inferred to originate from the same speaker (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). The resultant, illusory, McGurk effect percept is an integrated audiovisual fusion of the incongruent stimuli presented across the two senses. This audiovisual percept is influenced by the relative reliability weighting of the senses.

The illusory syllable “da” results from balanced sensory weighting of the auditory syllable “ba” and the visual syllable “ga” (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). This is because Bayesian causal inference models consider the syllable “da” as perceptually intermediate to the syllables “ba” and “ga”. The perception of non-illusory syllables can reflect sensory dominance and a altered integration of the presented auditory and visual stimuli. The perception of the syllable “ba” can suggest auditory dominance, since it was presented as a vocal stimulus, where there is greater relative reliability weighting of auditory stimuli. The perception of the syllable “ga” can suggest visual dominance, since it was presented as a facial stimulus, where there is greater relative weighting of visual stimuli.

The perception of McGurk effect has also been interpreted as a form of visual dominance instead of reflecting balanced sensory weighting (Hirst, Stacey, et al., 2018; Lüttke et al., 2016). This interpretation is consistent with definitions that describe the effect as a visually driven illusion where a visual stimulus alters an auditory percept (Hirst, Stacey, et al., 2018; Lüttke et al., 2016; Stacey et al., 2020; Tiippana, 2014). This interpretation can also be explained through a reliability weighting model of audiovisual integration like Bayesian causal inference as follows (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). Speech perception (reviewed in Rosenblum, 2008) is primarily facilitated through auditory speech stimuli (Easton & Basala, 1982), although

it can be improved with the integration of visual speech stimuli (Ross et al., 2007). The relative reliability weighting of auditory speech stimuli is therefore typically greater than visual speech stimuli (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). The McGurk effect is perceived only when the relative reliability weighting of a presented visual speech stimulus is sufficiently high to alter the perception of a presented auditory speech stimulus.

The interpretation of the McGurk effect reflecting a form of visual dominance is further supported by statistical predictions based on Bayesian causal inference models for this illusion in binocular viewing participants (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). Importantly, the predictions of these models are supported and confirmed by behavioural evidence that was also collected by the investigators. Approximately half of participants are predicted to not integrate the presented auditory and visual stimuli. These participants instead perceive the auditory syllable “ba”, but not the visual syllable “ga”, which reflects an auditory bias in speech perception. The other approximately half of participants are predicted to integrate the presented auditory and visual stimuli. The resultant audiovisual percept is the illusory syllable “da”, the McGurk effect. This is a visually influenced percept compared to the auditory syllable “ba”, which was likely to have been otherwise perceived if the stimuli were not integrated.

1.7.3.2. The McGurk Effect after Early Monocular Enucleation. The McGurk effect has been investigated in people who underwent early monocular enucleation compared to monocular and binocular viewing control participants (Moro & Steeves, 2018a). This study used an experiment with an incongruent audiovisual McGurk condition in which the auditory syllable “ba” was presented simultaneously with the visual stimulus “ga” (see Figure 1.9). Participants were instructed to report their perceived syllable in each trial from among three potential syllable options, “ba”, “ga”, or the illusory McGurk syllable “da”.

Accuracy in the McGurk condition differed across the three tested groups (Moro & Steeves, 2018a). Binocular viewing control participants perceived the illusory syllable “da” significantly more than people who underwent early monocular enucleation. Binocular viewing control participants also perceived the illusory syllable “da” significantly more than the two other syllable options. In contrast, people who underwent early monocular enucleation did not preferentially perceive the illusory syllable “da” over any other syllable and instead perceived all three syllable options comparably. These findings collectively suggest reduced susceptibility to the McGurk effect in people who underwent early monocular enucleation.

The monocular viewing control participants exhibited intermediate susceptibility relative to the two other tested groups (Moro & Steeves, 2018a). Namely, this group perceived the illusory syllable “da” significantly more than the syllable “ga” but comparably to the syllable “ba”. There was also a non-significant trend for the monocular viewing control participants to perceive the illusory syllable “da” less than the binocular viewing control participants. Together, the results suggest that monocular viewing control participants are more susceptible to the McGurk effect than people who underwent early monocular enucleation, but less than binocular viewing control participants.

The reduced susceptibility to the McGurk effect in people who underwent early monocular enucleation is indicative of altered audiovisual integration (Moro & Steeves, 2018a). This finding could have suggested less balanced processing of sensory stimuli according to the understanding that the McGurk effect is perceived when there is balanced weighting of auditory and visual stimuli (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). However, this group did not preferentially perceive the auditory syllable “ba” or the visual syllable “ga” that comprised the McGurk condition (Moro & Steeves, 2018a). The greater perception of either syllable would have

suggested greater relative weighting toward its corresponding sense (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017).

Instead, the participants perceived the three syllable options comparably, which was interpreted as evidence of less audiovisual integration due to more balanced processing of audiovisual stimuli after early monocular enucleation (Moro & Steeves, 2018a). This finding aligns with other evidence of altered sensory dominance in people who underwent early monocular enucleation. Specifically, their reduced susceptibility to the Colavita visual dominance effect (Moro & Steeves, 2012, 2013) and the sound-induced flash illusion (Moro & Steeves, 2018c), and more balanced processing of sensory stimuli in person identification (Moro et al., 2019).

1.8. Sensory Processing after Late Monocular Enucleation

The reviewed structural and behavioural evidence indicates that early monocular enucleation results in the altered morphology of the brain (Kelly et al., 2014, 2015), altered unisensory processing (reviewed in Kelly, Moro, et al., 2013; Steeves et al., 2008), and the more balanced, less sensory dominant, processing of audiovisual stimuli (Moro et al., 2019; Moro & Steeves, 2012, 2013, 2018c, 2018a). The structural (Beatty et al., 1982; Goldby, 1957; Horton, 1997; Kelly et al., 2014) and behavioural (Nicholas et al., 1996) consequences of late monocular enucleation have not been as extensively investigated and are therefore less clear. The existing evidence nonetheless suggests that both types of monocular enucleation are unique, warranting their investigation as distinct groups. Early monocular enucleation results in asymmetries of various structures of the visual system (Kelly et al., 2014, 2015) and auditory system (Kelly et al., 2015; Moro et al., 2015). Late monocular enucleation conversely results in bilateral and symmetric structural changes in visual areas (Beatty et al., 1982; Goldby, 1957; Horton, 1997; Kelly et al.,

2014). Behaviourally, early monocular enucleation also results in enhancements in contrast sensitivity which do not occur after late monocular enucleation (Nicholas et al., 1996).

Differences in the timing of enucleation likely account for the distinct consequences of early and late monocular enucleation. Consider the effect of age at enucleation observed in people who underwent early monocular enucleation. Enucleation at younger ages has been associated with greater improvements in contrast sensitivity (Nicholas et al., 1996) and may be associated with greater deficits in processing coherent motion (González et al., 2014). These findings indicate that the timing of enucleation is relevant for the altered function of sensory abilities, with earlier enucleation possibly leading to more extensive changes.

The timing of enucleation relative to critical periods for disruption is specifically relevant for the differences between early and late monocular enucleation (see 1.3.1.). Recall that early monocular enucleation coincides with the critical periods for disruption of many visual abilities (illustrated in Figure 1.2) which alters their typical developmental trajectories (reviewed Maurer & Lewis, 2013; Mitchell & Maurer, 2022). Late monocular enucleation occurs after most visual abilities have likely completed their periods of typical development and associated critical periods for disruption. It follows that disrupted visual development does not account for any structural or behavioural changes which may occur after late monocular enucleation. Instead, any such changes after late monocular enucleation would be the result of some mechanisms which occur after having completed typical visual development.

Late monocular enucleation may result in less extensive changes in sensory processing, if at all, compared to early monocular enucleation. In other words, sensory processing in people who underwent late monocular enucleation is likely comparable to people with binocularly intact vision because both groups ostensibly experienced typical visual development. Evidence for this comes

from research on contrast sensitivity after monocular enucleation (Nicholas et al., 1996). People who underwent early monocular enucleation exhibited enhancements in contrast sensitivity compared to binocularly intact control participants. Conversely, people who underwent late monocular enucleation exhibited fewer enhancements in contrast sensitivity and were mostly comparable to binocularly intact control participants.

In the described study, early monocular enucleation occurred before four years of age, whereas late monocular enucleation occurred between 11 and 13 years of age (Nicholas et al., 1996). Notably, the critical period for disruption of contrast sensitivity is completed at around eight years of age (Maurer et al., 2006). The removal of one eye therefore coincided with this critical period in people who underwent early, but not late, monocular enucleation in this study (Nicholas et al., 1996). It follows that the development of contrast sensitivity was altered after early, but minimally after late, monocular enucleation. The late monocular enucleation and binocularly intact control groups exhibited mostly comparable contrast sensitivity instead because they did not experience monocular deprivation during its critical period for disruption. These groups underwent the typical development of contrast sensitivity, which is completed by seven (Ellemberg et al., 1999) or 10 (Silvestre et al., 2020) years of age (Nicholas et al., 1996). These findings underscore the importance of investigating early and late monocular enucleation as distinct groups.

1.9. Objective & Hypotheses

Previous research has investigated audiovisual integration after early, but not late, monocular enucleation (Moro et al., 2019; Moro & Steeves, 2012, 2013, 2018c, 2018a, 2018b). The primary objective of my study was to fill this gap in research by investigating audiovisual integration after late monocular enucleation. This was done by testing susceptibility to the sound-induced flash illusion (Shams et al., 2000, 2002) and the McGurk effect (McGurk & Macdonald,

1976) in people who underwent late monocular enucleation and in binocular viewing control participants. Neither participant group experienced monocular deprivation during the critical periods for disruption in the development of many fundamental visual abilities (see Figure 1.2). It follows that both groups likely experienced typical visual development and may resultantly process then integrate auditory and visual stimuli similarly, unlike people who underwent early monocular enucleation (Moro et al., 2019; Moro & Steeves, 2012, 2013, 2018c, 2018a, 2018b). This rationale guided the following research questions and hypotheses.

1.9.1. Sound-Induced Flash Experiment

A sound-induced flash experiment (Shams et al., 2000, 2002) was used to investigate the integration of low-level auditory and visual stimuli. People who underwent early monocular enucleation are less susceptible to the sound-induced flash illusion (Moro & Steeves, 2018c) which suggests altered sensory dominance and more balanced processing of auditory and visual stimuli compared to binocular viewing control participants (Moro & Steeves, 2018c; Shams, 2012; Shams et al., 2005). I asked whether the loss of one eye later in life after late monocular enucleation also affects susceptibility to the sound-induced flash illusion. Namely, are people who underwent late monocular enucleation and binocular viewing control participants comparably susceptible to this illusion? Or does late monocular enucleation alter susceptibility to this illusion?

I hypothesized that people who underwent late monocular enucleation would be susceptible to the sound-induced flash illusion and perceive it comparably to binocular viewing control participants. This is because both groups experienced typical visual development without monocular deprivation during critical periods for disruption of visual abilities (Maurer & Lewis, 2013; Mitchell & Maurer, 2022). The predicted intact susceptibility to the sound-induced flash illusion after late monocular enucleation would be indicative of auditory dominance in the

integration of the low-level audiovisual stimuli presented in the experiment (Shams, 2012; Shams et al., 2005).

1.9.2. McGurk Experiment

A McGurk experiment (McGurk & Macdonald, 1976) was used to investigate the integration of high-level auditory and visual stimuli. People who underwent early monocular enucleation are less susceptible to the McGurk effect (Moro & Steeves, 2018a) which suggests altered sensory dominance and more balanced processing of auditory and visual stimuli compared to binocular viewing control participants (Magnotti & Beauchamp, 2017; Moro & Steeves, 2018a). I asked whether the loss of one eye later in life after late monocular enucleation also affects susceptibility to the McGurk effect. Namely, are people who underwent late monocular enucleation and binocular viewing control participants comparably susceptible to the McGurk effect? Or does late monocular enucleation alter susceptibility to this illusion?

I hypothesized that people who underwent late monocular enucleation would be susceptible to the McGurk effect and perceive it comparably to binocular viewing control participants. This is because both groups experienced typical visual development without monocular deprivation during critical periods for disruption of visual abilities (Maurer & Lewis, 2013; Mitchell & Maurer, 2022). The predicted intact susceptibility to the McGurk effect after late monocular enucleation would be indicative of visual dominance in the integration of the high-level audiovisual stimuli presented in the experiment (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017).

I also hypothesized that if susceptibility to these illusions is altered after late monocular enucleation, it would be less altered compared to after early monocular enucleation (Moro & Steeves, 2018c, 2018a). This prediction is based on previous evidence from people who underwent

late monocular enucleation who exhibited less extensive changes in sensory processing than people who underwent early monocular enucleation (Nicholas et al., 1996).

2. Methods

2.1. Participants

2.1.1. Late monocular enucleation participants (L-ME)

Six adult participants who underwent late monocular enucleation (L-ME) were recruited with a mean age of 49 years (SD = 12). L-ME was defined as the surgical removal of one eye at the age of 11 years and over (see 1.3.1). Participants were recruited through flyers in the office of a Toronto-based ocularist and through the monocular vision support groups on Facebook: Eyehesive, One Eye Fun and Support Group, and Monocular Vision Support Group. Five participants had one eye removed due to trauma and one participant had one eye removed due to ocular melanoma. Age at enucleation (AAE) varied from 12 to 52 years of age (mean AAE = 25 years, SD = 15) and years since enucleation varied from 1 to 45 years (mean years since enucleation = 25 years, SD = 19) (see Table 2.1).

Table 2.1

Demographics of Late Monocular Enucleation Participants

Participant #	Age (years)	Sex	AAE (years)	Time Since Enucleation (years)	Enucleation History
1	59	F	26	33	Ocular Melanoma
2	39	F	13	26	Trauma
3	31	F	30	1	Trauma
4	53	F	52	2	Trauma
5	56	M	12	45	Trauma
6	58	M	18	41	Trauma

Note. Late monocular enucleation participant demographics. Participant age, sex, age at enucleation (AAE), time since enucleation and reason for enucleation are reported.

2.1.2. Binocular viewing control participants (BV)

Ten adult age and sex-matched participants with intact binocular vision and a mean age of 42 years (SD = 15) served as controls for the study.

2.2. Online Experimentation

Due to COVID-19 restrictions during the pandemic, the experiments of this study were conducted remotely online using each participant's own desktop or laptop computers, using Google Chrome as their web browser. Previous research has found no differences in performance when comparing online versus in-lab delivery of the sound-induced flash experiment (Flanagan et

al., 2025) McGurk effect (Getz & Toscano, 2021; Magnotti et al., 2018). The experiments were programmed in PsychoPy (Peirce et al., 2019) to enable online testing as the lab was closed to in person testing during the COVID-19 pandemic. Stimuli were uploaded using the online experiment platform, Pavlovia. Prior to completing the experiments, participant consent and demographic information including age and clinical ophthalmology history were collected with a questionnaire using Qualtrics survey software (Qualtrics, Provo, UT).

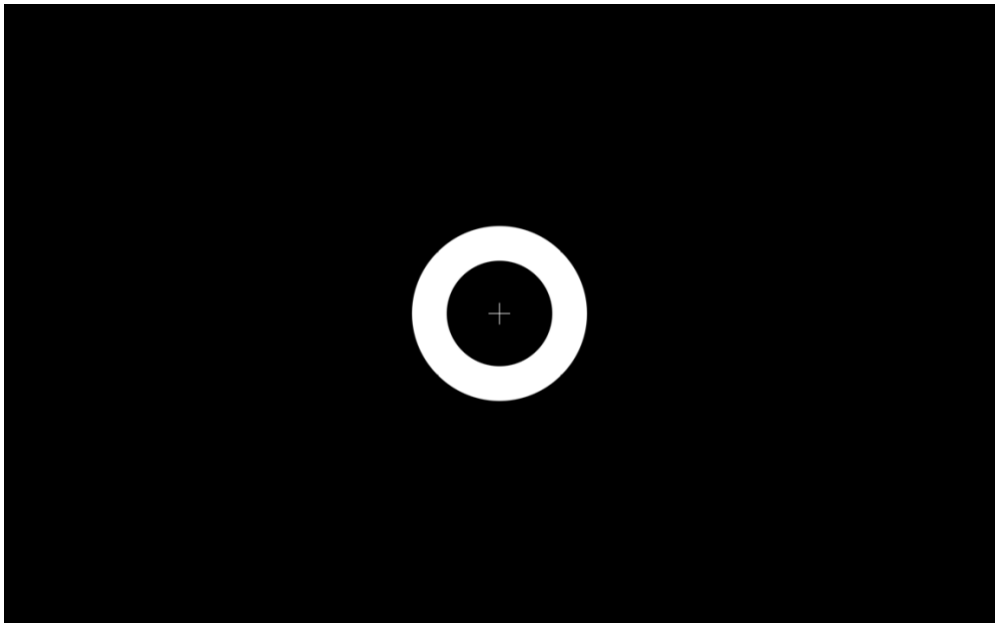
2.3. Stimuli

2.3.1. Sound-Induced Flash Experiment

The experimental stimuli were previously used in our lab (Moro & Steeves, 2018c). The visual stimulus consisted of an 8° white ring with a central fixation cross when sitting 60 cm from the computer screen (see Figure 2.1). This visual flash stimulus was one frame on a 60Hz display which is equivalent to approximately 17 ms. The auditory beep stimulus consisted of a 3500 Hz pure tone that was presented for 13 ms (see Figure 2.2).

Figure 2.1

Sound-Induced Flash Experiment Visual Stimulus



Note. The white 8° visual angle ring stimulus with fixation cross at the centre of the screen presented in the sound-induced flash experiment.

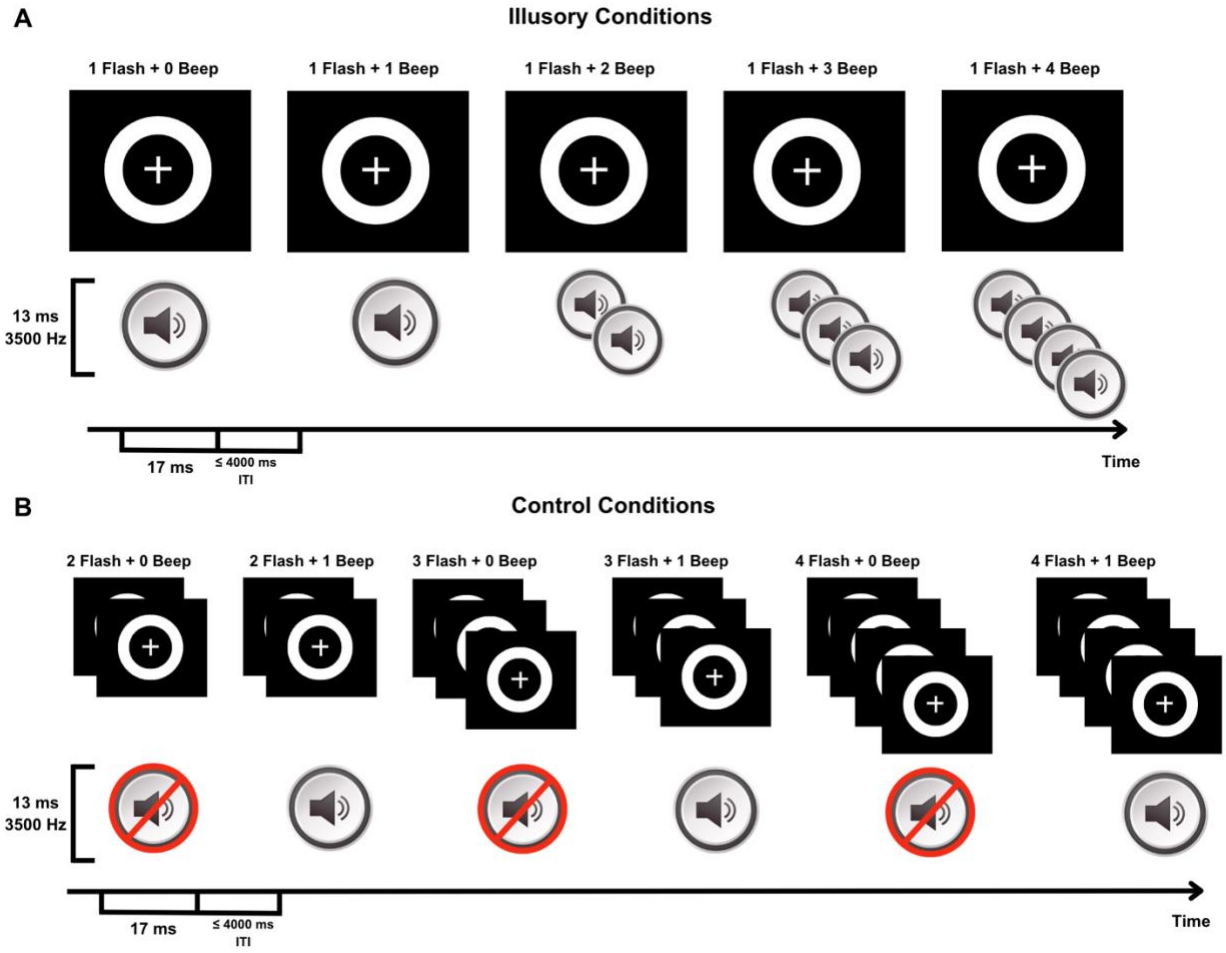
Five "illusory" conditions were presented where the white ring and fixation cross were flashed once, accompanied by 0, 1, 2, 3 or 4 3500 Hz pure tones. For the six control conditions, the visual stimuli were flashed 2, 3, or 4 times, paired with 0 or 1 3500 Hz pure tone. Participants were asked to use numbers 1 through 4 on their keyboard to indicate how many visual flashes they perceived. The intertrial interval (ITI) in both conditions was a blank screen of up to 4000 ms during which participants were able to respond. Once a participant responded, or if they failed to register any response within this period, the next trial commenced (see Figure 2.2). A 1000 ms blank screen preceded the presentation of stimuli in the next trial. This was a buffer period that

allowed the participant to return their attention to the screen after recording their response on the keyboard.

Five practice trials, which comprised a combination of illusory and control conditions, were presented to familiarize participants with how to indicate their response. Then, each of the 11 conditions were repeated 20 times in a randomized order, for a total of 220 trials excluding the five practice trials in the beginning.

Figure 2.2

Sound-Induced Flash Experiment Stimulus Conditions



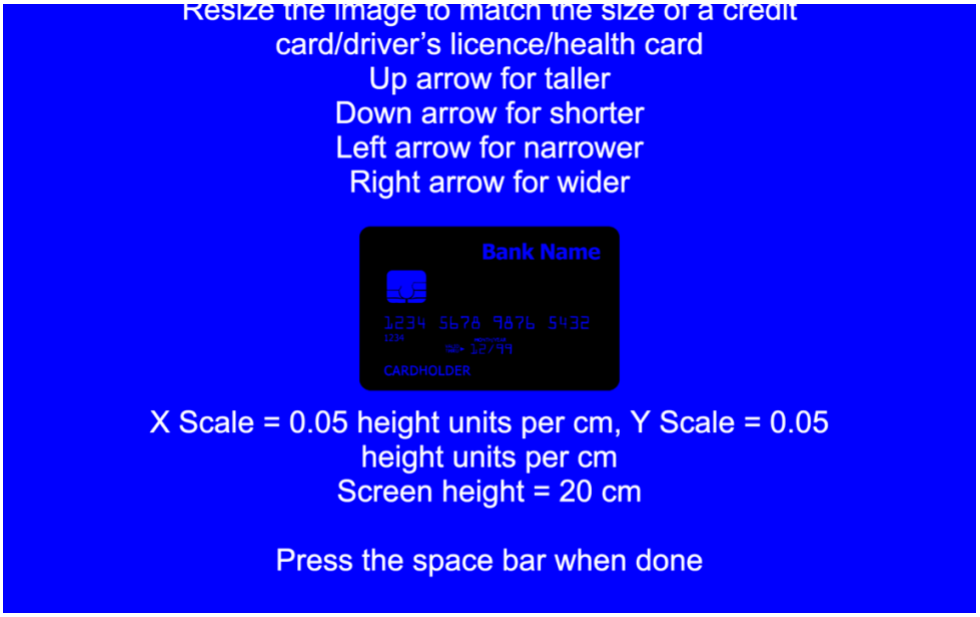
Note. Schematic diagram of the stimulus conditions presented in the sound-induced flash experiment. (A) The illusory conditions presented one visual flash stimulus accompanied by 0 to 4 auditory beeps. (B) The control conditions presented 2 to 4 visual flash stimuli accompanied by 0 or 1 auditory beep (ITI = intertrial interval). Adapted from "Normal temporal binding window but no sound-induced flash illusion in people with one eye" by S. S. Moro and J. K. E. Steeves, 2018, *Experimental Brain Research, 236*(6), p. 1828 (https://doi.org/10.1007/s00221-018-5263-x). Copyright 2018 by Springer Nature. Adapted with permission.

2.3.1.1. Visual and Auditory Calibration Tasks

Calibration tasks were presented at the start of the experiment to ensure the visual stimuli were the appropriate size and auditory stimuli were audible. Participants were asked to sit approximately 30 centimetres away from their monitor screen, described as roughly an arm's length. They were then instructed to match the size of a credit card to a box shown on their screen using the arrow keys to increase or decrease width and height, as shown in Figure 2.3. The program then converted the user-entered height and width of the card from pixel units to centimetres, using the standard height and width of a credit card as a scale for the experiment. This ensured that the ring size was constant across participants regardless of the size and resolution of the screen being used since testing was done online. Instrumental music was played while participants were requested to adjust the tone to a comfortable hearing level to calibrate their speakers.

Figure 2.3

Screen Calibration Task



Note. Screen scaling instructions presented at the beginning of the sound-induced flash experiment.

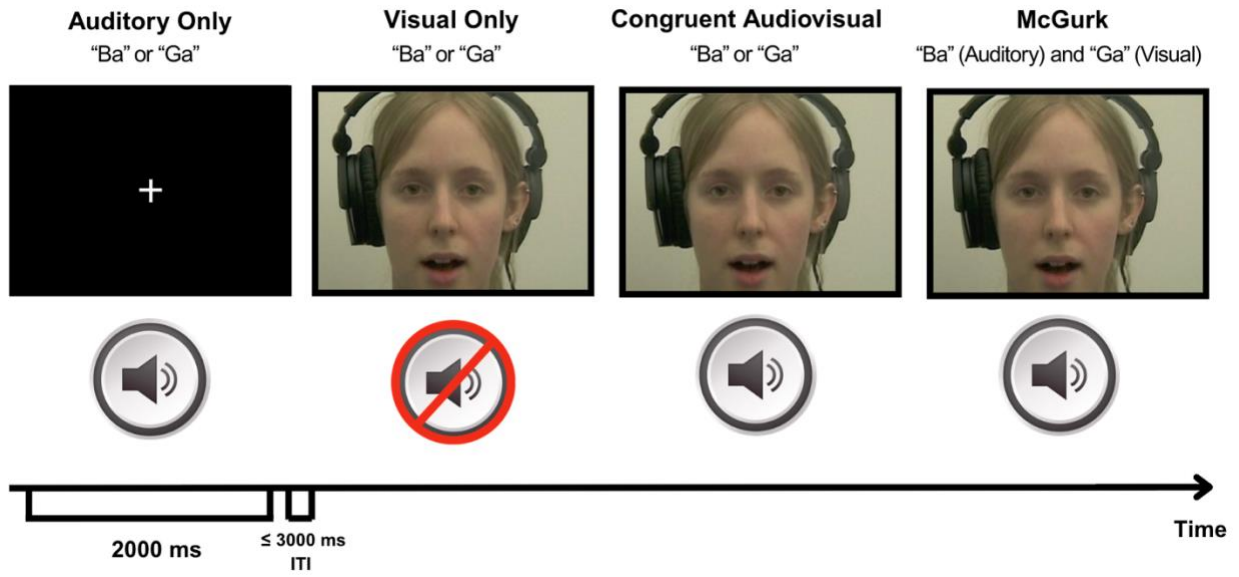
2.3.2. McGurk Experiment

The McGurk stimuli were used previously in our lab (Moro & Steeves, 2018a). Stimuli consisted of two 2-second videos of a female mouthing the syllables "ga" or "ba", alongside two 2-second audio clips of a female voice saying "ga" or "ba".

Four stimulus categories were created: auditory only, visual only, congruent audiovisual, and McGurk condition. The McGurk condition consisted of incongruently paired audiovisual stimuli of the "ba" auditory and "ga" visual stimuli. Overall, there were seven unique stimuli: two stimulus versions for each of the visual only, auditory only, congruent audiovisual categories, and one version for the McGurk condition (see Figure 2.4).

Figure 2.4

McGurk Experiment Stimulus Condition

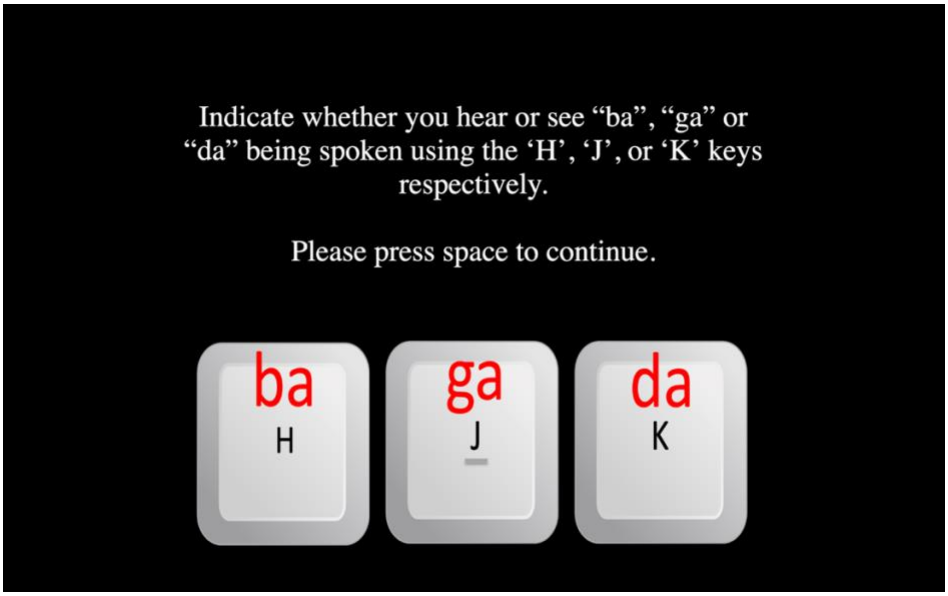


Note. Schematic diagram of the presented stimulus conditions in the McGurk experiment (ITI = intertrial interval). Adapted from "Perception of the McGurk effect in people with one eye depends on whether the eye is removed during infancy or adulthood" by S. S. Moro, F. A. Qureshi and J. K. E. Steeves, 2023, *Frontiers in Neuroscience, 17,* p. 4 (https://doi.org/10.3389/fnins.2023.1217831). CC BY 4.0.

Participants were asked to record their responses using the "H", "J" and "K" keys, where each key represents "ba", "ga" or "da", respectively. This was instructed through a prompt screen shown at start of the experiment and repeated every 10 trials to remind participants which syllables each key represents (see Figure 2.5).

Figure 2.5

McGurk Experiment Response Key Instructions



Note. Instructions prompt for completing the McGurk experiment. This prompt is repeated 7 times during the experiment to remind participants which keys correspond to the perceived syllable.

The ITI consisted of up to 3000 ms of silence and a fixation cross at the centre of the screen during which participants were to indicate their response. The next trial commenced immediately after a participant response, or if they failed to submit a response within 3000 ms (see Figure 2.4). There were brief delays in the start of the relevant facial stimuli in the presented videos and vocal stimuli in the presented audio clips which provided participants with adequate time to return their attention to the screen after recording their response. The mouthing of the syllable "ga" in its video started after 30 ms and the mouthing of the syllable "ba" in its video started after 50 ms. The vocal stimulus in the "ga" audio clip started after 50 ms and the vocal stimulus in the "ba" audio clip started after 65 ms. These delays eliminated the need to add an additional buffer period before the

presentation of the next trial, as was done in the sound-induced flash experiment (see 2.3.1. Sound-Induced Flash Experiment).

At the beginning of the experiment, participants were asked to adjust their speaker levels to a comfortable level while instrumental music was played to calibrate their speakers. This was followed by five practice trials to familiarize the participant with how to indicate their response. The seven unique conditions were repeated 20 times each in a randomized order for 140 trials total excluding the five practice trials in the beginning.

3. Results

3.1. Sound-Induced Flash Experiment

3.1.1. Response Time

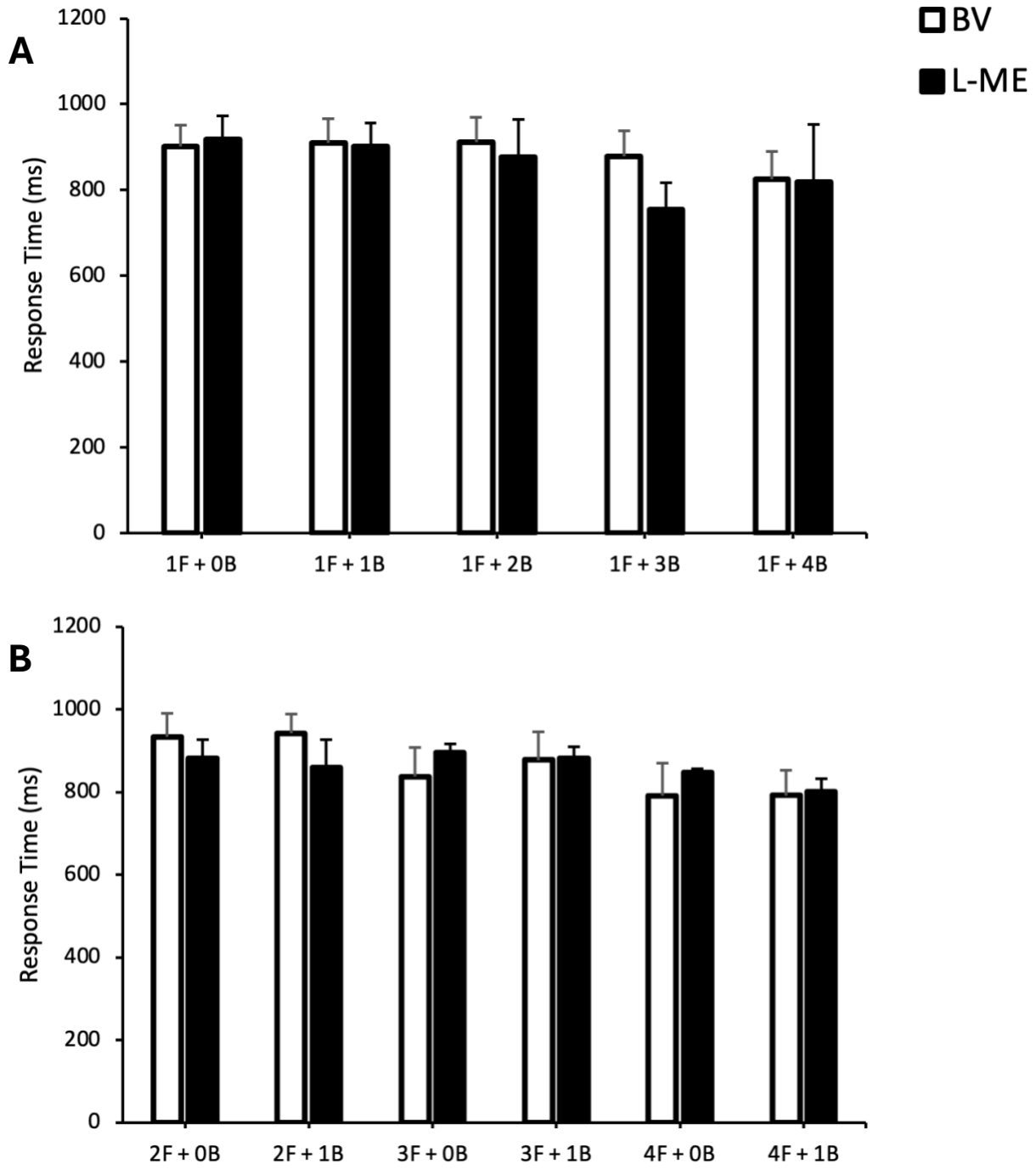
3.1.1.1. Illusory Conditions. Since the assumption for sphericity was not met a Greenhouse-Geisser corrected,5 × 2 Repeated Measures Analysis of Variance (ANOVA) was performed to compare Response Time for Group (L-ME vs BV) and sound-induced flash illusory conditions (1 flash + 0 beep, 1 flash + 1 beep, 1 flash + 2 beeps, 1 flash + 3 beeps, 1 flash + 4 beeps). There was no significant interaction $F(2.09, 25.03) = 1.47$, $p = .248$, $\eta^2_p = .109$ and no main effect of Group $F(1, 12) = 0.122$, $p = .732$, $\eta^2_p = .010$ but a significant main effect of illusory condition $F(2.09, 25.03) = 4.26$, $p = .024$, $\eta^2_p = .262$. Tukey corrected post hoc analysis revealed that collapsed across both groups, the 1 flash + 1 beep condition response time was significantly higher than the 1 flash + 3 beeps condition ($p = .020$). The response times did not differ across any conditions in either group. Figure 3.1A plots the response times for the illusory conditions in both groups.

3.1.1.2. Control Conditions. A Greenhouse-Geisser corrected 6 × 2 Repeated Measures ANOVA was performed to compare Response Time for Group (L-ME vs BV) and sound-induced flash control conditions (2 flash + 0 beep, 2 flash + 1 beep, 3 flash + 0 beep, 3 flash + 1 beep, 4 flash + 0 beep, 4 flash + 1 beep). This revealed no significant interaction $F(1.65, 19.82) = 1.56$, $p = .234$, $\eta^2_p = .115$ nor main effect of Group $F(1, 12) < 0.001$, $p = .989$, $\eta^2_p = .000$. There was, however, a significant main effect of control condition $F(1.65, 19.82) = 3.88$, $p = .045$, $\eta^2_p = .244$. Tukey corrected post hoc analysis indicate that collapsed across both groups, the 4 flash + 1 beep condition response time was significantly lower than the 2 flash + 0 beep ($p = .007$) and 3 flash + 1 beep ($p = .001$) conditions. The BV group response time for the 4 flash + 1 beep condition was

significantly lower than the 2 flash + 0 beep (p = .013) and 3 flash + 1 beep (p = .013) conditions. The L-ME group response time did not differ across any conditions. Figure 3.1B plots the response times for the control conditions in each group.

Figure 3.1

Sound-Induced Flash Experiment Response Times



Note. The response time (ms) for the late monocular enucleation (L-ME, black) and binocular viewing control (BV, white) participant groups in the sound-induced flash illusion experiment. (A)

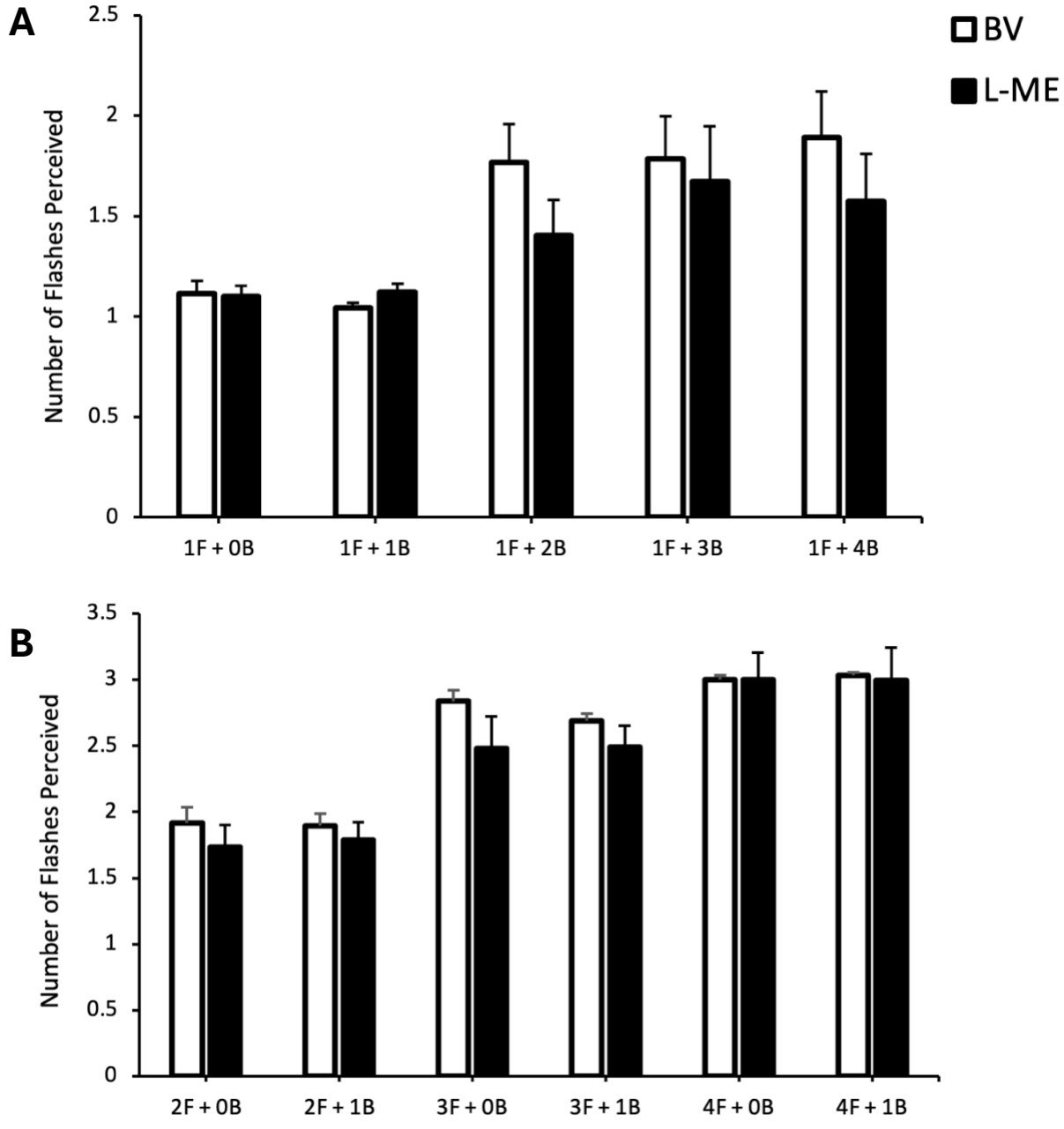
Experimental stimulus conditions where a single visual flash (1F) was paired with the presentation of 0-4 auditory beeps (0B, 1B, 2B, 3B, 4B). (B) Control stimulus conditions where 2-4 visual flashes (2F, 3F, 4F) were paired with 0 or 1 auditory beep (0B, 1B).

3.1.2. Perception of Visual Flashes

3.1.2.1. Perception of Sound-Induced Flash Illusion. A Greenhouse-Geisser corrected 5 × 2 Repeated Measures ANOVA was performed to compare Perception of Visual Flashes for Group (L-ME vs BV) and sound-induced flash illusory conditions (1 flash + 0 beep, 1 flash + 1 beep, 1 flash + 2 beeps, 1 flash + 3 beeps, 1 flash + 4 beeps). There was no significant interaction $F(1.25, 14.95) = 1.04$, $p = .343$, $\eta^2_p = .080$ and no significant main effect of Group $F(1, 12) = 0.515$, $p = .487$, $\eta^2_p = .041$ but a significant main effect of illusory condition $F(1.25, 14.95) = 12.43$, $p = .002$, $\eta^2_p = .509$. Tukey corrected post hoc analysis revealed that for the BV group, the perceived number of visual flashes compared to the 1 flash + 1 beep condition significantly increased when one visual flash was paired with two auditory beeps ($p = .019$) and four auditory beeps ($p = .029$) and there was a trend for increased visual flash perception when one visual flash was paired with four auditory beeps ($p = .054$). The number of visual flashes perceived by the L-ME group did not differ across the illusory conditions. Figure 3.2A plots the perceived number of visual flashes during the illusory conditions in each group.

Figure 3.2

Perception of Visual Flashes in the Sound-Induced Flash Experiment



Note. The perceived number of visual flashes for the late monocular enucleation (L-ME, black) and binocular viewing control (BV, white) participant groups in the sound-induced flash illusion experiment. (A) Illusory stimulus conditions where a single visual flash (1F) was paired with the

presentation of 0-4 auditory beeps (0B, 1B, 2B, 3B, 4B). (B) Control stimulus conditions where 2-4 visual flashes (2F, 3F, 4F) were paired with 0 or 1 auditory beep (0B, 1B).

3.1.2.2. Perception of Visual Flashes in Control Conditions. A Greenhouse-Geisser corrected 6 × 2 Repeated Measures ANOVA was performed to compare Perception of Visual Flashes for Group (LME vs BV) and sound-induced flash control conditions (2 flash + 0 beep, 2 flash + 1 beep, 3 flash + 0 beep, 3 flash + 1 beep, 4 flash + 0 beep, 4 flash + 1 beep). This revealed no significant interaction $F(2.81, 33.74) = 1.02$, $p = 0.393$, $\eta^2_p = 0.078$ nor significant main effect of Group $F(1, 12) = 1.27$, $p = 0.282$, $\eta^2_p = 0.096$. There was, however, a significant main effect of control condition $F(2.81, 33.74) = 87.88$, $p < 0.001$, $\eta^2_p = 0.880$. Tukey corrected post hoc analysis revealed that collapsed across both groups, the number of visual flashes perceived by each group increased with an increasing number of presented visual flashes, regardless of whether one or two auditory beeps were presented. Significantly more visual flashes were perceived in the 3 flash ($p < .001$) and 4 flash ($p < .001$) conditions (with 0 or 1 beep) compared to the 2 flash conditions (with 0 or 1 beep). The 4 flash + 0 beep condition was perceived more often than the 3 flash conditions (0 beep: $p = .001$, 1 beep: $p < .001$). The 4 flash + 1 beep condition was also perceived more than the 3 flash conditions (0 beep: $p = .001$, 1 beep: $p < .001$). A similar pattern was observed in each group.

In the BV group, more visual flashes were perceived in the 4 flash + 0 beep condition compared to the 3 flash + 1 beep ($p = .012$), 2 flash + 0 beep ($p < .001$), 2 flash + 1 beep ($p < .001$) conditions. More visual flashes were perceived in the 4 flash + 1 beep condition compared to the 3 flash + 1 beep ($p = .030$), 2 flash + 0 beep ($p < .001$), 2 flash + 1 ($p < .001$) beep conditions. More visual flashes were perceived in the 3 flash + 0 beep condition compared to the 2 flash + 0

beep (p = .005) and 2 flash + 1 beep (p = .003) conditions. More visual flashes were perceived in the 3 flash + 1 beep condition compared to the 2 flash + 0 beep (p = .007) and 2 flash + 1 beep (p = .003) conditions.

In the L-ME group, more visual flashes were perceived in the 4 flash + 0 beep condition compared to the 3 flash + 0 beep (p = .003), 3 flash + 1 beep (p = .011), 2 flash + 0 beep (p < .001), 2 flash + 1 beep (p < .001) conditions. More visual flashes were perceived in the 4 flash + 1 beep condition compared to the 3 flash + 0 beep (p = .009), 3 flash + 1 beep (p = .018), 2 flash + 0 beep (p < .001), 2 flash + 1 beep (p < .001) conditions .More visual flashes were perceived in the 3 flash + 0 beep condition compared to the 2 flash + 0 beep (p = .024) and 2 flash + 1 beep (p = .024) conditions. More visual flashes were perceived in the 3 flash + 1 beep condition compared to the 2 flash + 0 beep (p = .031) and 2 flash + 1 beep conditions (p = .002). Figure 3.2B plots the number of flashes perceived during the control conditions in each group.

3.1.3. Correlation Analysis

A Pearson correlation was performed to evaluate the relationship between the Number of Visual Flashes Perceived in the illusory conditions and Years Lived with Binocular Vision across the BV and L-ME groups. No statistically significant correlations were found between these two variables as depicted in Table 3.1.

Table 3.1

Descriptive Statistics and Correlations for the Number of Visual Flashes Perceived in Illusory Conditions and Years Lived with Binocular Vision in the BV and L-ME Groups

Variable	*M*	*SD*	1.	2.	3.	4.	5.	6.
1. Years BV	33.4	16.6	—					
2. 1F + 0B	1.11	0.165	-.124	—				
3. 1F + 1B	1.07	0.0910	-.420	.670**	—			
4. 1F + 2B	1.64	0.531	.319	.080	.216	—		
5. 1F + 3B	1.74	0.604	.221	.158	.363	.917***	—	
6. 1F + 4B	1.78	0.635	.254	.100	.248	.943***	.933***	—

Note. Descriptive statistics and Pearson correlations for the perceived number of visual flashes in illusory conditions by the BV and L-ME groups combined and their years lived with binocular vision. Years BV = The combined years that participants in the BV and L-ME groups lived with binocular vision, *M* = mean, *SD* = standard deviation.

**$p < .01$, ***$p < .001$.

3.1.4. Power Analysis

An a priori power analysis was conducted with an 80% level of power for visual flash perception in the illusory conditions which indicated a total sample size of at least 22 participants, or 11 participants in each group. However, the sound-induced flash experiment was completed by 5 L-ME participants and 9 BV controls, for a total sample size of 14.

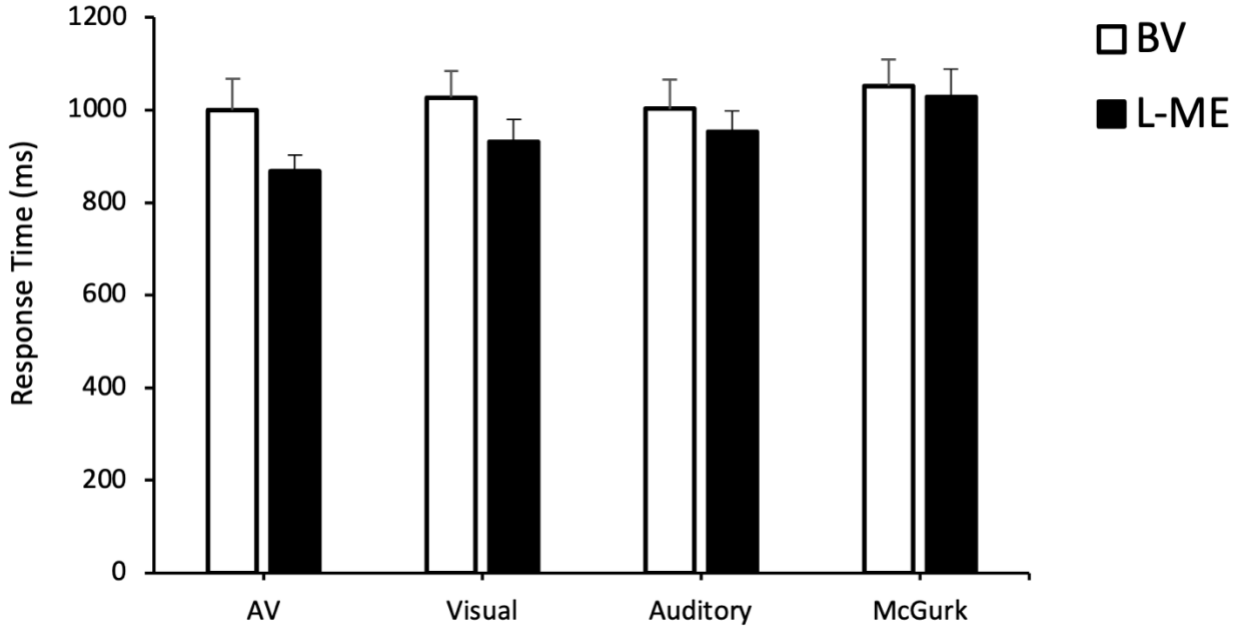
3.2. McGurk Experiment

3.2.1. Response time

A 4 × 2 Repeated Measures ANOVA was performed to compare Response Time for Group (L-ME vs BV) and condition (auditory only, visual only, audiovisual, McGurk). There was no significant interaction $F(3, 42) = 1.37$, $p = .266$, $\eta^2_p = .089$ and no main effect of participant group $F(1, 14) = 0.886$, $p = .363$, $\eta^2_p = .059$ but a significant main effect of condition $F(3, 42) = 4.54$, $p = .008$, $\eta^2_p = .245$. Tukey corrected post hoc analysis revealed that collapsed across both participant groups, the AV condition had a lower response time than the McGurk condition ($p = .015$). The response times did not differ across any conditions in either group. In the L-ME group, however, there was a trend for a lower response time in the AV condition compared to the McGurk condition ($p = .066$). Figure 3.3 plots the response times for each group in each condition.

Figure 3.3

McGurk Experiment Response Times



Note. Response time (ms) for each stimulus condition in the McGurk experiment. Audiovisual (AV), visual only, auditory only and McGurk stimulus. The late monocular enucleation participant group (L-ME) is presented in black bars, and the binocular viewing control group (BV) is presented in white bars.

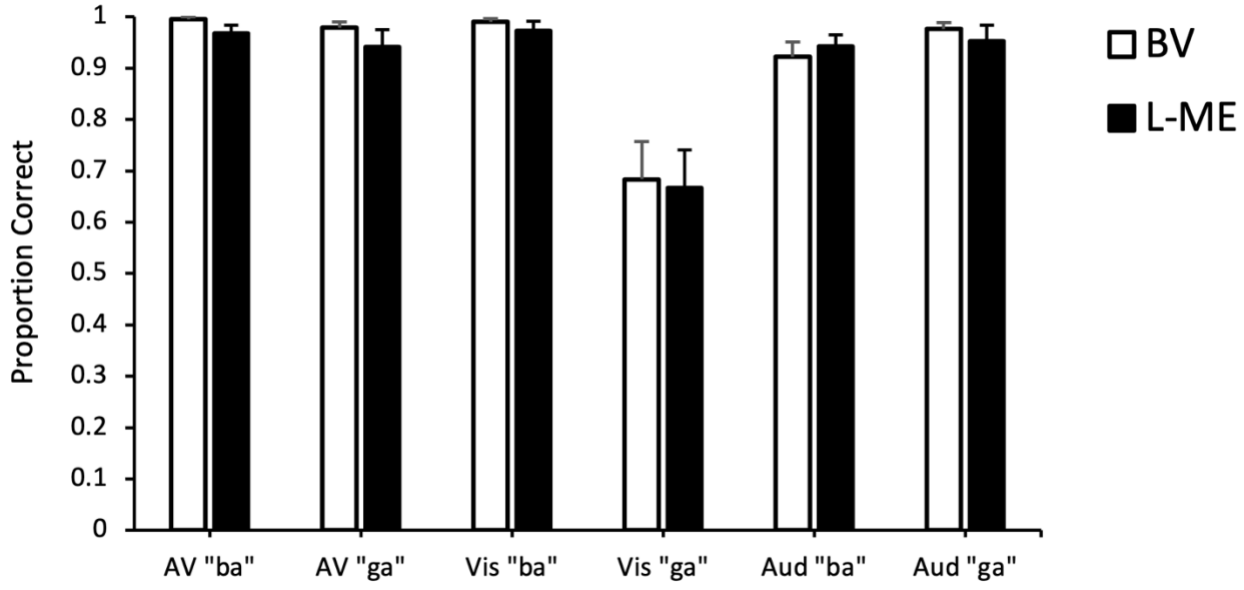
3.2.2. Non-McGurk Stimulus Accuracy

A Greenhouse-Geisser corrected 6 × 2 Repeated Measures ANOVA was performed to compare Accuracy in Task Performance for Group (L-ME vs BV) and non-McGurk stimulus condition (auditory only "ba", auditory only "ga", visual only "ba", visual only "ga", audiovisual "ba" and audiovisual "ga"). There was no significant interaction $F(1.41, 19.79) = 0.150$, $p = .787$, $\eta^2_p = .011$ and no main effect of group $F(1, 14) = 0.587$, $p = .456$, $\eta^2_p = .040$ but a significant main

effect of condition $F(1.41, 19.79) = 21.680$, $p < 0.001$, $\eta^2_p = .608$. Tukey corrected post hoc analysis revealed that collapsed across both groups, the visual "ga" condition was perceived less accurately than all other conditions (AV "ba": $p = .001$, AV "ga": $p < .001$, Vis "ba": $p < .001$, Aud "ba": $p = .016$, Aud "ga": $p = .001$). In the BV group, the visual "ga" condition was perceived significantly less accurately than the audiovisual "ba" ($p = .020$), audiovisual "ga" ($p = .010$), visual "ba" ($p = .017$), and auditory "ga" ($p = .018$) conditions. The L-ME group did not significantly differ in accuracy across the non-McGurk stimulus conditions. Figure 3.4 plots the accuracy of the non-McGurk stimulus conditions for each group.

Figure 3.4

Accuracy in Perception of Non-McGurk Stimuli



Note. Accuracy, presented as proportion correct, for the non-McGurk conditions. Audiovisual (AV), visual only (Vis), auditory only (Aud). The late monocular enucleation participant group (L-

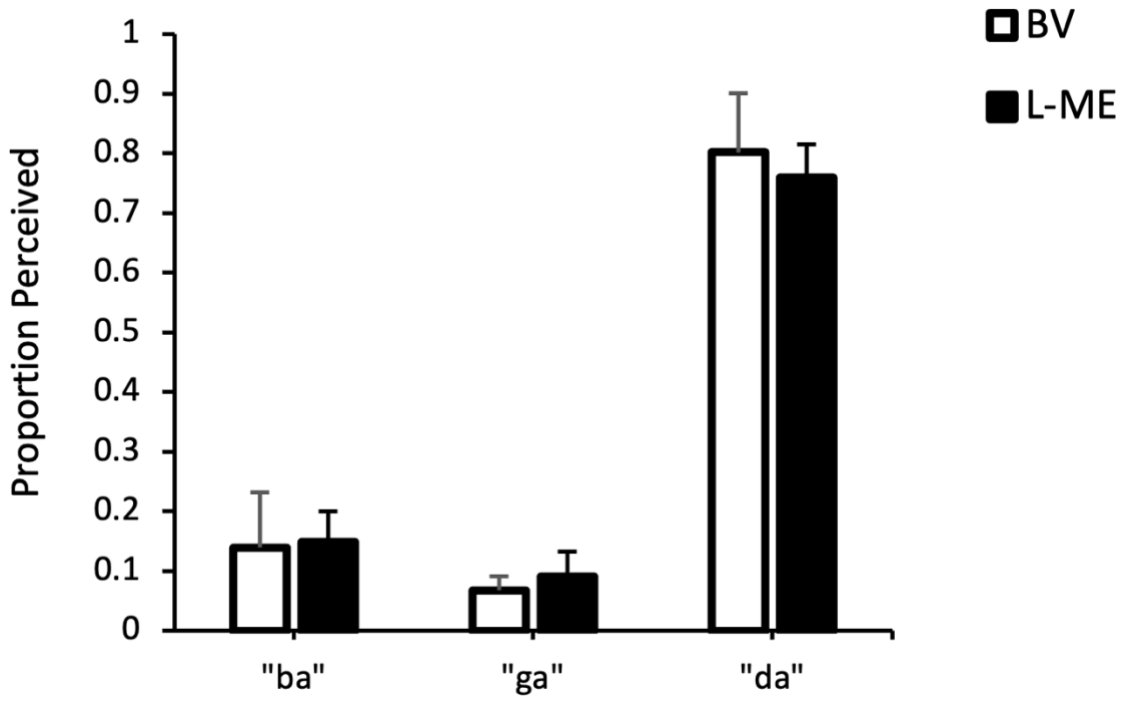
ME) is presented in black bars, and the binocular viewing control group (BV) is presented in white bars.

3.2.3. Perception of McGurk Effect

A Greenhouse-Geisser corrected 3 × 2 Repeated Measures ANOVA was performed to compare the Perception of the McGurk Stimulus for Group (L-ME vs BV) and syllable ("ba" vs "ga" vs "da"). There was no significant interaction $F(1.15, 16.06) = 0.00771$, $p = .836$, $\eta^2_p = .005$ an no main effect of group $F(1, 14) = 0.715$, $p = .412$, $\eta^2_p = .049$ but a significant main effect of syllable $F(1.15, 16.06) = 32.6689$, $p < 0.001$, $\eta^2_p = 0.700$. Tukey corrected post hoc analysis revealed that collapsed across groups, the illusory McGurk syllable "da" was perceived significantly more than the syllables "ba" ($p < .001$) and "ga" ($p < .001$). The BV group perceived the illusory McGurk syllable "da" significantly more than the syllables "ba" ($p = .010$) and "ga" ($p < .001$). The L-ME group perceived the McGurk syllable "da" significantly more than the syllable "ga" ($p = .002$), but not the syllable "ba" ($p = .086$). Figure 3.5 plots syllable perception in the McGurk stimulus condition for each group.

Figure 3.5

Accuracy in Perception of McGurk Stimulus



Note. Proportion of syllables percieved in the McGurk condition of "ba" being the auditory stimulus, "ga" being the visual stimulus and "ga" is the illusory McGurk effect syllable. The late monocular enucleation participant group (L-ME) is presented in black bars, and the binocular viewing control group (BV) is presented in white bars.

3.2.4. Correlation Analysis

A Pearson correlation was conducted to evaluate the relationship between the proportion of syllables perceived in the McGurk condition and years lived with binocular vision across the BV and L-ME groups. No statistically significant correlations were found between these two variables as depicted in Table 3.2.

Table 3.2

Descriptive Statistics and Correlations for Proportion of Syllables Perceived in the McGurk Condition and Years Lived with Binocular Vision in the BV and L-ME Groups

Variable	*M*	*SD*	1.	2.	3.	4.
1. Years BV [a]	35.7	16.7	—			
2. “ba”	.143	.238	.279	—		
3. “ga”	.0761	.0852	-.081	.270	—	
4. “da”	.786	.256	-.201	-.945***	-.567*	—

Note. Descriptive statistics and Pearson correlations for the proportion of syllables perceived in the McGurk conditions by the BV and L-ME groups combined and their years lived with binocular vision. Years BV = The combined years that participants in the BV and L-ME groups lived with binocular vision, *M* = mean, *SD* = standard deviation.

*$p < .05$, ***$p < .001$.

3.2.5. Power Analysis

An a priori power analysis was conducted with an 80% level of power for syllable perception in the McGurk condition which indicated a total sample size of 18 participants, or 9 participants in each group. However, the McGurk experiment was completed by 6 L-ME participants and 10 BV controls in this study, for a total sample size of 16.

4. Discussion

The purpose of this study was to investigate whether late monocular enucleation alters the integration of audiovisual stimuli. Susceptibility to the sound-induced flash illusion (Shams et al., 2000, 2002) and the McGurk effect (McGurk & Macdonald, 1976) were used as behavioural measures of low-level and high-level audiovisual integration, respectively, in people who underwent late monocular enucleation and binocular viewing control participants. People who underwent late monocular enucleation exhibited reduced susceptibility to the sound-induced flash illusion but intact susceptibility to the McGurk effect. In contrast, binocular viewing control participants were susceptible to both audiovisual illusions. These findings indicate that the integration of low-level, but not high-level, audiovisual stimuli is altered after late monocular enucleation.

To my knowledge, this is the first study to administer the sound-induced flash and McGurk experiments to people who underwent late monocular enucleation. This is also the first study to administer these experiments online to people who underwent any type of monocular enucleation. The implications of the obtained findings are discussed in terms of how susceptibility to these illusions can reflect sensory dominance in the processing and subsequent integration of audiovisual stimuli.

4.1. Less Susceptibility to the Sound-Induced Flash Illusion Suggests Altered Audiovisual Integration for Low-Level Audiovisual Stimuli after Late Monocular Enucleation

People who underwent late monocular enucleation were not susceptible to the sound-induced flash illusion (see Figure 3.2). Binocular viewing control participants were, however, susceptible to this illusion, which is consistent with previous research in this group (Moro & Steeves, 2018a). This difference in susceptibility suggests that audiovisual integration of the low-

level audiovisual stimuli presented in the sound-induced flash experiment (Shams et al., 2000, 2002) is altered after late monocular enucleation. The theory of Bayesian causal inference applied to the perception of the sound-induced flash illusion (Shams, 2012; Shams et al., 2005) can be used to explain how audiovisual integration may be altered. According to this model, the illusion is perceived due to a form of auditory dominance in the processing and subsequent integration of the presented low-level audiovisual stimuli (see section 1.7.2.1). Reduced susceptibility to the illusion in people who underwent late monocular enucleation may therefore result from less auditory dominance, or greater visual dominance, compared to binocular viewing control participants.

As such, I propose that there may be an increase in visual dominance for processing low-level audiovisual stimuli after late monocular enucleation that accounts for their altered integration. This could be facilitated through an increase in the relative reliability weighting of visual stimuli. The proposed re-weighting of senses could nullify or reverse the previously outlined auditory dominance (see 1.7.2.1) that is necessary to perceive the sound-induced flash illusion (Shams, 2012; Shams et al., 2005). Support for this mechanism comes from research that has investigated the role of sensory weighting in susceptibility to the illusion. These studies demonstrate that susceptibility to the illusion is reduced when the relative reliability weighting of visual stimuli is increased.

4.1.1. Evidence of Reduced Susceptibility to the Sound-Induced Flash Illusion with Increased Relative Reliability Weighting of Visual Stimuli

4.1.1.1. Developmental Evidence. Evidence from developmental research suggests that an increase in visual dominance can reduce susceptibility to the sound-induced flash illusion (Shams et al., 2000, 2002). Children under 18 years of age are more susceptible to this illusion

compared to adults who are 18 years of age and older (Innes-Brown et al., 2011; Wang et al., 2025). Similarly, children between six and seven years of age are more susceptible to this illusion compared to children between nine and 12 years of age (Nava & Pavani, 2013). These findings collectively indicate that susceptibility to the sound-induced flash illusion is reduced during development (Innes-Brown et al., 2011; Nava & Pavani, 2013; Wang et al., 2025).

Investigators have proposed that this developmental reduction in susceptibility (Innes-Brown et al., 2011; Nava & Pavani, 2013; Wang et al., 2025) is the result of a shift from auditory dominance to visual dominance (Robinson & Sloutsky, 2004) in the processing of sensory stimuli during childhood (Nava & Pavani, 2013; Wang et al., 2025). Evidence for this comes from the absence of the Colavita visual dominance effect (Colavita, 1974) in children (Hirst, Cragg, et al., 2018) under seven years of age (Nava & Pavani, 2013). The onset of this visual dominance effect is at around seven years of age, extending into adulthood, which coincides with a reduction in susceptibility to the sound-induced flash illusion flash illusion (Nava & Pavani, 2013; Wang et al., 2025).

A recent study that compared the performance of children and adults in a sound-induced flash experiment directly examined the factors underlying the developmental reduction in susceptibility to this illusion (Wang et al., 2025) using a Bayesian causal inference model (Shams et al., 2005). The investigators concluded that binding tendency (see 1.7.1) (Körding et al., 2007; Quintero et al., 2022) remains stable across development and therefore cannot explain the observed reduction in susceptibility to the illusion (Wang et al., 2025). Instead, developmental enhancements in visual abilities increase the relative reliability weighting of visual stimuli resulting in a reduction in susceptibility to the illusion (Wang et al., 2025). This mechanism was proposed (Wang et al., 2025) to explain the observed developmental reduction in susceptibility the sound-induced flash

illusion with an increase in visual dominance (Innes-Brown et al., 2011; Nava & Pavani, 2013; Wang et al., 2025).

4.1.1.2. Evidence from Ageing in Adulthood. In contrast, susceptibility to the sound-induced flash illusion (Shams et al., 2000, 2002) progressively increases with age in adulthood according to evidence from research comparing different age groups (DeLoss et al., 2013; Hernández et al., 2019; Hirst et al., 2019; McGovern et al., 2014). Some of these studies have compared groups of younger adults around 20 years of age with older adults who were 65 years of age and above (DeLoss et al., 2013; McGovern et al., 2014). Similar findings have been reported in large-scale studies with more than 2000 adults who were 50 years of age and above (Hernández et al., 2019; Hirst et al., 2019).

The increasing susceptibility to the sound-induced flash illusion in ageing adults has been associated with age-related declines in visual acuity (Hirst et al., 2019) which have been widely observed in adults with healthy vision starting from around 50 years of age (Chapanis, 1950; Gittings & Fozard, 1986; Sjöstrand et al., 2011). These age-related declines in visual acuity decrease the relative reliability weighting of visual stimuli, thereby increasing susceptibility to the sound-induced flash illusion with age (Hirst et al., 2019). This pattern of findings is notably consistent with a Bayesian causal inference explanation of this illusion (Shams, 2012; Shams et al., 2005). The reviewed developmental (Innes-Brown et al., 2011; Nava & Pavani, 2013; Wang et al., 2025) and ageing (DeLoss et al., 2013; Hernández et al., 2019; Hirst et al., 2019; McGovern et al., 2014) evidence collectively indicate that changes in the relative reliability weighting of vision underlie the changes in susceptibility to the illusion across the lifespan. As such, there is precedent that the reduced susceptibility to the sound-induced flash illusion after late monocular enucleation may reflect an increase in visual dominance.

4.2. Intact Susceptibility to the McGurk Effect Suggests Unaltered Audiovisual Integration for High-Level Audiovisual Speech Stimuli after Late Monocular Enucleation

People who underwent late monocular enucleation were susceptible to the McGurk effect, as indicated by their perception of syllables in the McGurk stimulus condition (see Figure 3.5). The illusory syllable “da” was perceived significantly more than the syllable “ga” but comparably to the syllable “ba”. Binocular viewing control participants were also susceptible to the McGurk effect, although they perceived the illusory syllable “da” significantly more than the syllable “ga” and the syllable “ba”. This pattern of syllable perception is consistent with the results of the original McGurk experiments (Macdonald & McGurk, 1978; McGurk & Macdonald, 1976) and the binocular viewing control participants from the previous investigation of this illusion in people who underwent early monocular enucleation (Moro & Steeves, 2018a).

The comparable perception of the illusory syllable “da” and the syllable “ba” in the late monocular enucleation group may indicate reduced susceptibility to the McGurk effect relative to the binocular viewing control group. A similar pattern was exhibited by monocular viewing control participants in a previous study (see 1.7.2.2), who perceived the illusory syllable “da” less frequently than binocular viewing control participants (Moro & Steeves, 2018a). However, people who underwent late monocular enucleation in the present study perceived the illusory syllable “da” and the other syllable options comparably to the binocular viewing control participants. This suggests that the two groups are comparably susceptible to the McGurk effect.

Moreover, the apparent difference in the pattern of syllable perception may reflect the increased variance associated with the small sample size of this study rather than reduced susceptibility to the McGurk effect in people who underwent late monocular enucleation. There is also considerable evidence that binocular viewing participants usually exhibit a pattern of syllable

perception in which the illusory syllable “da” is perceived more than the syllable “ga” but comparably to the syllable “ba” (Alsius et al., 2018; Butera et al., 2023; Hirst, Stacey, et al., 2018). This pattern has also been predicted by Bayesian causal inference models of the McGurk effect for binocular viewing participants (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). For these reasons, the results of the present experiment are interpreted as comparable susceptibility to the McGurk effect in people who underwent late monocular enucleation and binocular viewing control participants.

The comparable susceptibility to the McGurk effect exhibited by the two groups in this experiment suggests that audiovisual integration for high-level audiovisual speech stimuli is not altered after late monocular enucleation. As reviewed earlier (see 1.7.3.1), visually dominant processing is required for the perception of the McGurk effect, consistent with Bayesian causal inference explanations of this illusion (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). Susceptibility to the McGurk effect can accordingly reflect visual dominance (Hirst, Stacey, et al., 2018; Lüttke et al., 2016). Based on this interpretation, I propose that the present findings indicate that visual dominance in the processing of high-level audiovisual speech stimuli is intact and not altered after late monocular enucleation.

If visual dominance were altered after late monocular enucleation, susceptibility to the McGurk effect would be expected to differ between groups (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). This is supported by evidence from research on the effect of sensory dominance, which can be altered through changes in the relative reliability weighting of sensory stimuli, on susceptibility to the McGurk effect that is discussed below. Increased visual dominance, through an increase in the relative reliability weighting of visual stimuli, results in greater susceptibility to the McGurk effect. It follows that decreased visual dominance, through a decrease

in the relative reliability weighting of visual stimuli, results in reduced susceptibility to the McGurk effect.

4.2.1. Evidence of Altered Susceptibility to the McGurk Effect with Changes in the Relative Reliability Weighting of Visual Stimuli

4.2.1.1. Developmental Evidence. Developmental evidence supports the described influence of visual dominance on susceptibility to the McGurk effect. Children under nine years of age demonstrate reduced susceptibility to the McGurk effect compared to adults between 19 years (Tremblay et al., 2007) and 35 years (Hirst, Stacey, et al., 2018) of age. Susceptibility to the McGurk effect increases to adult levels in children at approximately 10 years of age (Hirst, Stacey, et al., 2018; Tremblay et al., 2007). The increase in susceptibility to this illusion is attributed to greater visual dominance in adults compared to children under 10 years of age (Hirst, Stacey, et al., 2018). This interpretation is consistent with evidence for a developmental shift from auditory to visual dominance during childhood (Hirst, Cragg, et al., 2018; Robinson & Sloutsky, 2004). The previously reviewed evidence for this shift in sensory dominance comes from measures such as the Colavita visual dominance effect (Hirst, Cragg, et al., 2018; Nava & Pavani, 2013) and the sound-induced flash illusion (Innes-Brown et al., 2011; Nava & Pavani, 2013; Wang et al., 2025).

Further support comes from research on susceptibility to the McGurk effect in ageing adults. Adults around 60 years of age exhibit greater susceptibility to the McGurk effect compared to younger adults around 20 years of age (Sekiyama et al., 2014). This finding is consistent with the greater visual dominance exhibited by older adults compared to younger adults which likely reflect age-related declines in hearing (Chapanis, 1950; Gittings & Fozard, 1986; Sjöstrand et al., 2011). These declines in hearing may result in an increase in the relative reliability weighting of visual stimuli in older adults which facilitates more visually dominant processing of audiovisual

stimuli (Hirst et al., 2019). Greater susceptibility to the McGurk effect in older adults (Sekiyama et al., 2014) may therefore reflect increased visual dominance, caused by an increase in their relative reliability weighting of visual stimuli (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017).

4.2.1.2. Evidence from Visual Stimulus Blurring and Auditory Stimulus Noise. The influence of visual dominance on susceptibility to the McGurk effect has been directly investigated by manipulating the relative reliability weighting of sensory stimuli in the McGurk experiment. The perception of syllables in the McGurk experiment is influenced by the levels of noise in the presented auditory syllable “ba” and the extent of blurring in the presented visual syllable “ga”. Higher levels of auditory noise increase the perception of the illusory syllable “da” (Fixmer & Hawkins, 1998; Hirst, Stacey, et al., 2018; Sekiyama & Burnham, 2008; Stacey et al., 2020). This indicates that an increase in the relative reliability weighting of visual stimuli, facilitated by high levels of auditory noise, results in greater susceptibility to the McGurk effect. Higher levels of visual blurring decrease the perception of the illusory syllable “da” (Fixmer & Hawkins, 1998; Hirst, Stacey, et al., 2018; Stacey et al., 2020) and increase the perception of the auditory syllable “ba” (Stacey et al., 2020). This indicates that a decrease in the relative reliability weighting of visual stimuli, facilitated by high levels of visual blurring, results in reduced susceptibility to the McGurk effect. Changes in the relative reliability weighting of visual stimuli can therefore alter susceptibility to the McGurk effect (Fixmer & Hawkins, 1998; Hirst, Stacey, et al., 2018; Sekiyama & Burnham, 2008; Stacey et al., 2020).

The reviewed developmental (Hirst, Stacey, et al., 2018; Sekiyama et al., 2014; Tremblay et al., 2007) and behavioural (Fixmer & Hawkins, 1998; Hirst, Stacey, et al., 2018; Sekiyama & Burnham, 2008; Stacey et al., 2020) evidence supports the proposed interpretation of the McGurk

experiment findings through a Bayesian causal inference explanation of this illusion (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). Namely, that the visual dominance in processing high-level audiovisual speech stimuli is unaltered but intact after late monocular enucleation. If this processing were altered, then people who underwent late monocular enucleation are expected to have differed in their susceptibility to the illusion compared to the binocular viewing control participants.

4.3. The Possibly Altered Integration of Low-Level Audiovisual Stimuli After Late Monocular Enucleation was Unexpected

People who underwent late monocular enucleation and binocular viewing control participants were hypothesized to exhibit comparable audiovisual integration since both groups underwent typical visual development. As expected, people who underwent late monocular enucleation and binocular viewing control participants were comparably susceptible to the McGurk effect. However, the apparent reduction in susceptibility to the sound-induced flash illusion in people who underwent late monocular enucleation was unexpected. These findings indicate that the integration of low-level audiovisual stimuli may be altered after late monocular enucleation, but not that of high-level audiovisual speech stimuli. I proposed that there may be altered audiovisual processing for low-level audiovisual stimuli (see 4.1), and unaltered audiovisual processing for high-level audiovisual speech stimuli (see 4.2), after late monocular enucleation. I proposed that these mechanisms underly the observed findings based on Bayesian causal inference explanations for the perception of the sound-induced flash illusion (Shams, 2012; Shams et al., 2005) and the McGurk effect (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017).

The performance of monocular viewing control participants compared to binocular viewing control participants in previous behavioural studies provides precedent for altered sensory processing after late monocular enucleation. As reviewed earlier, monocular viewing control participants have exhibited improvements in sound localization (Hoover et al., 2012) and more balanced processing of auditory and visual stimuli in face-voice recognition (Moro et al., 2019). Importantly, monocular viewing control participants have also exhibited reduced susceptibility to both the sound-induced flash illusion (Moro & Steeves, 2018c) and the McGurk effect (Moro & Steeves, 2018a). These findings indicate that monocular deprivation in adulthood, even when transient and incomplete as with an eye patch, can alter sensory processing. Prolonged and complete monocular deprivation in adulthood, as experienced by people who underwent late monocular enucleation, may therefore lead to altered low-level audiovisual processing as exhibited by their reduced susceptibility to the sound-induced flash illusion.

The removal of one eye results in the permanent loss of half of the previously received visual input to the brain. It would therefore be reasonable to expect a decrease in the relative reliability weighting of vision, which constitutes an increase in the relative reliability of audition, after late monocular enucleation. More auditory dominant processing of audiovisual stimuli would likely result in greater susceptibility to the sound-induced flash illusion (Shams, 2012; Shams et al., 2005) and reduced susceptibility to the McGurk effect (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017) compared to binocular viewing control participants. People who underwent late monocular enucleation instead appear to exhibit less susceptibility to the sound-induced flash illusion and intact susceptibility to the McGurk effect compared to binocular viewing control participants. These findings are contrary to an outcome of greater auditory dominance in the processing of audiovisual stimuli. The altered audiovisual processing of low-level stimuli after late

monocular enucleation that is possibly suggested by the present findings may reflect adaptive changes which compensate for the loss of visual input from one eye.

4.4. Possible Reasons for the Altered Processing of Low-Level Audiovisual Stimuli after Late Monocular Enucleation

4.4.1. Increased Attention Directed Toward Vision After Late Monocular Enucleation

It is possible that people who underwent late monocular enucleation compensate for the loss of visual input from one eye by allocating additional attentional resources toward visual stimuli compared to people with intact binocular vision. This reallocation of attention could account for the audiovisual integration exhibited by this group. In other words, the present findings may reflect increased attention directed toward the visual input received from their remaining eye. This explanation is consistent with evidence of how visual attention can modulate susceptibility to the sound-induced flash illusion (Wahn et al., 2020; Zhang et al., 2018) and the McGurk effect (Buchan & Munhall, 2011; Tiippana et al., 2004).

4.4.1.2. Visual Attention and the Sound-Induced Flash Illusion. An increase in visual attention can contribute to a reduction in susceptibility to the sound-induced flash illusion. Evidence for this comes from a study that directed the attention of participants toward vision more than audition through a modified sound-induced flash experiment (Shams et al., 2000, 2002) that included three stimulus conditions: visual, auditory, and audiovisual (Zhang et al., 2018). The visual condition presented one visual flash, and the auditory condition presented one auditory beep (Zhang et al., 2018). The audiovisual condition corresponded to the sound-induced flash paradigm, presenting one visual flash accompanied by more than one auditory beep. These three stimulus conditions were randomized and presented multiple times. Participants were instructed to report the number of visual flashes they perceived. Investigators presented the visual condition three

times more frequently than the auditory and audiovisual conditions and described this manipulation as increasing visual attention. This increase in visual attention resulted in less illusory visual flashes being perceived in the audiovisual condition, which was interpreted as reduced susceptibility to the sound-induced flash illusion.

Visual attention was decreased in a study in which participants completed the sound-induced flash experiment (Shams et al., 2000, 2002) jointly with a confederate, another person, seated beside them (Wahn et al., 2020). Participants reported the number of visual flash stimuli they perceived, while the confederates reported the number of auditory beep stimuli they perceived (Wahn et al., 2020). Participants perceived more illusory visual flashes, reflecting greater susceptibility to the sound-induced flash illusion, when completing the task alongside a confederate compared to completing it alone.

However, susceptibility to the illusion was not greater when jointly completing the experiment (Shams et al., 2000, 2002) if an opaque physical barrier was placed between the participant and the confederate (Wahn et al., 2020). The investigators attributed this finding to a difference in the visual attention of participants during the experiment (Wahn et al., 2020). The placement of a barrier prevented the confederate from being visible in the participant's peripheral vision. The visible presence of the confederate without a barrier acted as a visual distractor that decreased the visual attention of participants and resulted greater susceptibility to the illusion.

4.4.1.2. Visual Attention and the McGurk Effect. Increased visual attention does not alter susceptibility to the McGurk effect. Evidence comes for this comes from a study in which participants were instructed to specifically attend to either the visual or auditory speech stimuli (Buchan & Munhall, 2011) while completing the McGurk experiment (McGurk & Macdonald,

1976). Neither increasing visual attention nor increasing auditory attention altered susceptibility to the McGurk effect (Buchan & Munhall, 2011).

A decrease in visual attention may, however, result in reduced susceptibility to this illusion. One study added a moving image of a leaf across the face of a speaker in the visual component of the McGurk stimulus (Tiippana et al., 2004). The moving leaf image did not obscure the speaker's mouth but acted as a visual distractor. This distraction decreased the visual attention of participants, which correspondingly reduced susceptibility to the McGurk effect compared to when it was completed without a distractor.

The reviewed findings indicate that visual attention modulates susceptibility to audiovisual illusions in distinct ways. An increase in visual attention may reduce susceptibility to the sound-induced flash illusion (Zhang et al., 2018), whereas a decrease in visual attention may result in greater susceptibility (Wahn et al., 2020). In contrast, increasing visual attention may not alter susceptibility to the McGurk effect (Buchan & Munhall, 2011), although decreasing visual attention may reduce susceptibility (Tiippana et al., 2004). The reduced susceptibility to the sound-induced flash illusion but intact susceptibility to the McGurk effect after late monocular enucleation is therefore consistent with an increase, but not a decrease, in visual attention. Collectively, these findings support the proposed mechanism whereby there is increased attention directed toward the remaining eye in people who underwent late monocular enucleation

4.4.2. Neuroplasticity after Late Monocular Enucleation

The present findings may reflect cortical reorganization facilitated by neuroplasticity in the brain which enables adaptations that compensate for the loss of visual input from one eye. Different cortical regions of the brain have been implicated in perceiving the sound-induced flash illusion (Shams et al., 2000, 2002) and McGurk effect (McGurk & Macdonald, 1976). Perception of the

sound-induced flash illusion, which entails the integration of low-level audiovisual stimuli (Shams, 2012; Shams et al., 2005), has primarily been attributed to early sensory cortical areas (Shams, 2012) like the primary visual cortex (Bolognini et al., 2016; Mishra et al., 2007; Watkins et al., 2006) and the primary auditory cortex (Mishra et al., 2007). For example, people with brain damage to the occipital cortex, which includes the primary visual cortex, are less likely to perceive the sound-induced flash illusion (Bolognini et al., 2016). This finding suggests that changes in the structure of early cortical areas like the primary visual cortex could alter the tendency to perceive this illusion, its susceptibility.

Perception of the McGurk effect (McGurk & Macdonald, 1976), which entails the integration of high-level audiovisual speech stimuli (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017), has been associated with the superior temporal sulcus in the left hemisphere of the brain (Nath & Beauchamp, 2012). This is a higher cortical area than the primary sensory cortices and has been implicated with audiovisual integration (Beauchamp et al., 2004) and other forms of multisensory integration (Beauchamp et al., 2008). Higher levels of activity in the left superior temporal sulcus have been associated with greater susceptibility to the McGurk effect (Nath & Beauchamp, 2012). As such, changes in the structure or functional activity of the described cortical regions could alter susceptibility to these audiovisual illusions.

4.4.2.1. Neuroplasticity after Monocular Eye Patching. Evidence of neuroplasticity in early cortical regions of the brain has been demonstrated after short-term monocular deprivation in monocular viewing participants. Patching one eye of binocularly intact participants for 150 minutes results in a shift in ocular dominance toward the patched eye (Lunghi et al., 2011). This shift lasts for approximately 90 minutes after restoring normal binocular vision by removing the

eye patch. Importantly, the described transient shift in ocular dominance has been associated with evidence of increased neuroplasticity in the primary visual cortex (Lunghi et al., 2015).

It is therefore possible that neuroplasticity could facilitate cortical reorganization that contributes to the reduced susceptibility to the sound-induced flash illusion (Moro & Steeves, 2018c) and McGurk effect (Moro & Steeves, 2018a) previously reported in monocular viewing control participants. This provides precedent for the possibility that longer periods of monocular deprivation, as experienced after late monocular enucleation, could result in more extensive cortical reorganization in the brain. These changes would likely be permanent, since the monocular deprivation experienced after late monocular enucleation is irreversible, unlike that induced by temporary monocular eye patching. Such neuroplasticity induced changes in the brain could therefore contribute to the reduced susceptibility to the sound-induced flash illusion observed in people who underwent late monocular enucleation.

4.4.2.2. Neuroplasticity after Early versus Late Monocular Enucleation. The findings of the present investigation indicate that late monocular enucleation may not alter audiovisual integration to the same extent as early monocular enucleation. Recall that people who underwent early monocular enucleation exhibit reduced susceptibility to the sound-induced flash illusion (Moro & Steeves, 2018c) and reduced susceptibility to the McGurk effect (Moro & Steeves, 2018a). This indicates altered audiovisual integration of low-level (Moro & Steeves, 2018c) and high-level (Moro & Steeves, 2018a) audiovisual stimuli, respectively, after early monocular enucleation.

In contrast, people who underwent late monocular enucleation exhibit less susceptibility to the sound-induced flash illusion but are susceptible to the McGurk effect. This indicates altered audiovisual integration of low-level, but not high-level, audiovisual stimuli after late monocular

enucleation, respectively. This finding is consistent with a previously reviewed study (see 1.4.1.1) in which people who underwent late monocular enucleation exhibited less extensive changes in contrast sensitivity than those who underwent early monocular enucleation (Nicholas et al., 1996). It is also consistent with structural differences in the visual pathways of people who underwent monocular enucleation where evidence of neuroplasticity exists after early but not late monocular enucleation (Kelly et al., 2014, 2015) (see 1.4.3).

Together, these findings indicate that late monocular enucleation may result in less extensive changes in audiovisual integration compared to early monocular enucleation. This may reflect different levels of neuroplasticity at the time of enucleation. As previously outlined (see 1.1.2), neuroplasticity is heightened during critical periods in the development of the visual system (reviewed in Mitchell & Maurer, 2022) which coincide with early monocular enucleation. Neuroplasticity in visual areas of the brain persists after visual development has been completed and extends into adulthood (reviewed in Castaldi et al., 2020), although it is reduced compared to during critical periods (Mitchell & Maurer, 2022). The described neuroplasticity could have therefore facilitated cortical reorganization after late monocular enucleation that is less extensive than after early monocular enucleation.

4.5. An Alternative Explanation for the Results

As discussed, I interpreted the findings from the two experiments in this study as evidence that people who underwent late monocular enucleation exhibit altered audiovisual integration of low-level but not high-level audiovisual stimuli compared to binocular viewing control participants. However, an alternative interpretation of the results is that the exhibited reduction in susceptibility to the sound-induced flash illusion (Shams et al., 2000, 2002), but intact susceptibility to the McGurk effect (McGurk & Macdonald, 1976), does not reflect the altered

processing of low-level audiovisual stimuli after late monocular enucleation. The present findings may instead relate to a negative correlation that has previously been reported between susceptibility to these illusions in binocular viewing participants (Butera et al., 2023; Stevenson et al., 2012). This inverse relationship indicates that people who are susceptible to the McGurk effect tend to be susceptible to the sound-induced flash illusion.

It follows that the differential susceptibility to the two audiovisual illusions in people who underwent late monocular enucleation may at least partly reflect factors that underlie the previously reported negative correlation (Butera et al., 2023; Stevenson et al., 2012). For instance, one proposed factor is individual differences in the temporal integration of audiovisual stimuli among binocularly intact participants (Stevenson et al., 2012), which has yet to be investigated in people who underwent late monocular enucleation. It is possible that there are changes to temporal integration, or other factors in audiovisual integration, which occur after late monocular enucleation that affect the processing of both low-level and high-level audiovisual stimuli.

4.6. Limitations

4.6.1. Low Sample Size

The low sample size of both experiments in the present study is a limitation that may have influenced the obtained findings and subsequent statistical analyses. Power analyses (reviewed in Serdar et al., 2021) were conducted to determine the sample size required to detect an effect of late monocular enucleation on the perception of each illusion with 80% power. This level of power corresponds to a 20% probability of Type II error, also known as false negatives, in which a real effect is incorrectly concluded to be absent (reviewed in Banerjee et al., 2009). For the sound-induced flash illusion, the power analysis suggested a total sample size of 22 participants, or 11

participants per group. For the McGurk effect, the power analysis suggested a total sample size of 18 participants, or 9 participants per group.

Neither experiment was completed by the suggested number of participants in the present study. Instead, the sound-induced flash experiment included a sample size of 14 participants, with 5 participants who underwent late monocular enucleation and 9 binocular viewing control participants. The McGurk experiment included a sample size of 16 participants, with 6 participants who underwent late monocular enucleation and 10 binocular viewing control participants. The low sample size of these experiments is therefore a limitation which reduces the statistical power of the present study below 80%. This reduction in power indicates an increased probability of Type II errors that exceeds 20%. This suggests that the results should be interpreted with caution.

The low sample size of participants in the present study was expected given the rare nature of late monocular enucleation (Moshfeghi et al., 2000). Extensive recruitment efforts were made to mitigate this expected limitation. Diverse modes of advertisement were employed, which included collaborations with online support groups for people with monocular vision, social media, email, word of mouth, and assistance from a Toronto area ocularist. The use of online experimentation (reviewed in Sauter et al., 2020) also likely facilitated the recruitment of more participants than would have been possible through in-person research. Online participation removed barriers such as travel distance and scheduling constraints, both of which could have deterred people from participating. Instead, participants were able to complete the study using their own computers at a location and time most convenient for them.

4.6.2. Online Experiments

The COVID-19 pandemic imposed unique challenges that affected scientific research efforts across several disciplines (reviewed Sohrabi et al., 2021). Participants in the present study

were tested remotely, with experiments that were completed online due to pandemic related restrictions on in-person research. Online experimentation confers advantages like facilitating participant recruitment but also introduces unique disadvantages compared to in-person research (reviewed in Latkovikj & Popovska, 2020).

4.6.2.1. Limitations of Online Experimentation. In-person testing of participants provides experimenters the opportunity to ensure optimal and uniform environmental testing conditions. In contrast, experimenters have less control over testing conditions in experiments completed online, since participants are responsible for the experimental setup. Monocular viewing control participants were not tested in this study for this reason. Specifically, it was logistically challenging to distribute eye patches to participants and ensure that they were worn appropriately during the experiments.

Differences in experimental setup across participants could have influenced susceptibility to audiovisual illusions. For instance, recall that the volume of auditory stimuli can alter susceptibility to the sound-induced flash illusion (Ito et al., 2023), and auditory noise can alter susceptibility to the McGurk effect (Fixmer & Hawkins, 1998; Hirst, Stacey, et al., 2018; Sekiyama & Burnham, 2008; Stacey et al., 2020). The position of presented visual stimuli relative to the visual field of a participant can also alter susceptibility to the sound-induced flash illusion (Chang et al., 2023; Chen et al., 2017; Kumpik et al., 2014; Shams et al., 2002; Tremblay et al., 2007). This position can be affected by the gaze of participants, which also alters susceptibility to the McGurk effect (Wahn et al., 2022).

Both experiments of the present study incorporated instructions and programmed calibration tasks to mitigate differences in environmental conditions and experimental setup across participants. The procedure of these steps is described in detail in the Methods section, and their

rationale is outlined here. The auditory calibration task (see 2.3.1.1) was designed to standardize sound levels across participants by controlling for variations in environmental noise and speaker volume. Participants were instructed to complete the experiment in a quiet environment, after which they adjust their speaker volume to a comfortable hearing level. The visual calibration task (see Figure 2.3) aimed to ensure consistent scaling and positioning of the visual stimuli presented across different monitor sizes and resolutions (see 2.3.1.1). Both experiments also presented a fixation cross at the centre of the screen between trials to re-centre the gaze of participants (see Figure 2.2 and Figure 2.3).

One limitation that was not controlled for was the possibility of smudges on monitor screens, which could have blurred the presented visual stimuli. This is noteworthy because the blurring of visual stimuli has been shown to alter susceptibility to the McGurk effect (Fixmer & Hawkins, 1998; Hirst, Stacey, et al., 2018; Stacey et al., 2020). Including an instruction for participants to clean their monitors before completing the experiments could have mitigated this limitation.

4.6.2.2. Limitations of Online Experiment Software. Certain technical limitations are inherent to online experimentation. Auditory and visual stimuli are presented with less precise timing when experiments are administered online compared to in-person (Bridges et al., 2020; Semmelmann & Weigelt, 2016). This precision refers to the variability in when stimuli are presented relative to the times specified in the experimental code. Experiments administered in-person typically exhibit an average variability of less than one millisecond, which means that stimuli are presented within one millisecond of the specified time (Bridges et al., 2020). In contrast, experiments administered online can have up to an average variability of 10 milliseconds, although this varies with different psychophysical experiment software. This relative imprecision has,

however, been described as minimal and unlikely to affect the results of experiments that do not require a high degree of precision in timing (Bridges et al., 2020; Semmelmann & Weigelt, 2016). Previous studies have accordingly demonstrated that participants perform comparably in online and in-person versions of both the sound-induced flash experiment (Flanagan et al., 2025) and the McGurk experiment (Getz & Toscano, 2021; Magnotti et al., 2018).

The experiments of the present study were designed in PsychoPy (Peirce et al., 2019), which provides superior precision in stimulus presentation for online experiments compared to other psychophysical experiment software (Bridges et al., 2020). PsychoPy exhibits an average variability of 3.5 milliseconds, whereas other software can vary by up to 10 milliseconds (Bridges et al., 2020). It follows that the use of PsychoPy has been reported to enable testing that is most comparable to in-person testing (Bridges et al., 2020; Peirce et al., 2019). The experiments were also designed to maximize accessibility for participants by making them compatible with the most widely used operating systems and internet browser. Specifically, they were optimized for completion on computers using Windows and MacOS operating systems and Google Chrome internet browser (Mohamed & Ismail, 2022).

4.7. Future Directions

Efforts to mitigate previously identified limitations should be made, wherever possible, to strengthen the findings of future studies and further advance research on monocular enucleation. In-person experimentation in a controlled laboratory setting may be preferable to online experimentation despite being potentially less accessible for participants. This would allow investigators to include monocular viewing control participants in their studies and ensure consistent testing environments and conditions for all participants. If future psychophysical testing must be conducted online, as with the current study, then additional steps may be taken to

counteract some of its associated challenges (see section 4.6.2). For instance, participants could be required to complete the study while on a video call with a researcher. This would enable the supervision of the experimental setup and procedure to ensure proper adherence to the instructions and the appropriate completion of the experiments.

Future research can further investigate the consequences of late monocular enucleation using behavioural measures that have previously been tested in people who underwent early monocular enucleation. The performance of both groups in these behavioural experiments can then be directly compared through statistical analyses. This would provide additional insight into how the timing of enucleation may affect the processing of sensory stimuli.

4.7.1. Auditory Processing after Late Monocular Enucleation

As previously reviewed, people with early blindness, who lost vision in both eyes during childhood, have exhibited improvements in sound localization compared to people with intact binocular vision (Battal et al., 2020; Lessard et al., 1998; Röder et al., 1999; Voss et al., 2004). People who underwent early monocular enucleation have exhibited similar improvements compared to binocularly intact control participants (Hoover et al., 2012). The loss of vision early in life, whether monocular (Hoover et al., 2012) or binocular (Battal et al., 2020; Lessard et al., 1998; Röder et al., 1999; Voss et al., 2004), can therefore alter auditory processing.

People with late blindness, who lost vision in both eyes after childhood and into adulthood, have also exhibited improvements in sound localization (Abel et al., 2002; Voss et al., 2004). This indicates that the loss of vision later in life can also alter auditory processing. These findings collectively provide a rationale for investigating sound localization in people who underwent late monocular enucleation. Such an investigation would determine whether late monocular enucleation also results in changes in auditory processes comparable to those observed after early

monocular enucleation (Hoover et al., 2012), or after early (Battal et al., 2020; Lessard et al., 1998; Röder et al., 1999; Voss et al., 2004) and late (Abel et al., 2002; Voss et al., 2004) binocular blindness.

4.7.2. Colavita Visual Dominance Effect after Late Monocular Enucleation

People who underwent early monocular enucleation have exhibited reduced susceptibility to the sound-induced flash illusion (Moro & Steeves, 2018c), the Colavita visual dominance effect (Moro & Steeves, 2012, 2013), and to the McGurk effect (Moro & Steeves, 2018a). These findings collectively indicate balanced processing of auditory and visual stimuli after early monocular enucleation. In contrast, people who underwent late monocular enucleation in the present study appear to exhibit less susceptibility to the sound-induced flash illusion (see Figure 3.2) but intact susceptibility to the McGurk effect (see Figure 3.5). As previously discussed, this pattern has been interpreted as evidence of altered audiovisual processing of low-level but not high-level audiovisual stimuli after late monocular enucleation.

Investigating the Colavita visual dominance effect (Colavita, 1974) in people who underwent late monocular enucleation could clarify how the processing of audiovisual stimuli may be altered after late monocular enucleation. Such an investigation would also enable researchers to compare the effects of early and late monocular enucleation. It would determine whether people who underwent late monocular enucleation exhibit balanced processing of audiovisual stimuli in the Colavita experiment, as observed after early monocular enucleation (Moro & Steeves, 2012, 2013). People who underwent early monocular enucleation were resistant to changes in the relative reliability of stimuli that investigators made to elicit a reversed Colavita visual dominance effect (Moro & Steeves, 2013) (see 1.6.3.1). Similar manipulations could be made when testing people

who underwent late monocular enucleation to determine whether they exhibit a tendency for sensory dominant processing that is resistant to changes in the relative reliability of stimuli.

4.7.3. Temporal Integration after Late Monocular Enucleation

Future research can also determine whether early and late monocular enucleation result in similar adaptations that account for their shared reduction in susceptibility to the sound-induced flash illusion. As reviewed earlier, the reduced susceptibility to this illusion in people who underwent early monocular enucleation was not due to differences in the temporal integration of audiovisual stimuli compared to binocular viewing control participants (Moro & Steeves, 2018c). This is notable because differences in temporal binding window widths have been correlated with differences in susceptibility to this illusion in people with binocularly intact vision (Stevenson et al., 2012).

Future studies can therefore investigate the temporal integration of people who underwent late monocular enucleation as it was previously investigated in people who underwent early monocular enucleation (Moro & Steeves, 2018c). This would provide insight into the underlying reasons for the reduced susceptibility to the sound-induced flash illusion after late monocular enucleation. One possibility is that this reduction in susceptibility is related to differences in temporal integration, as it can be in people with binocularly intact vision (Stevenson et al., 2012). Another possibility is that it reflects adaptations unrelated to temporal integration, like those proposed after early monocular enucleation (Moro & Steeves, 2018c).

4.7.4. Improved Categorization of Late Monocular Enucleation

4.7.4.1. Early versus Late Monocular Enucleation. Future research could benefit from improved definitions and categorization of the different types of monocular enucleation. The dichotomy of early and late monocular enucleation is likely an oversimplification that does not

fully account for the heterogeneity that likely exists in this group. As previously outlined, I have delineated early and late monocular enucleation with age of 11 years at enucleation in the present study (see 1.3.1). This age was selected because it is consistent with previous studies (Day, 1995; Kelly et al., 2015; Nicholas et al., 1996) and approximately aligns with the completion of the critical periods for disruption in the development of many fundamental visual abilities (see Figure 1.2) (reviewed in Maurer & Lewis, 2013; Mitchell & Maurer, 2022).

Recall that visual development comprises the development of several visual abilities which emerge through different trajectories and times (Daw, 2014). Monocular enucleation can therefore occur at any point during or after the critical periods for disruption of specific visual abilities. For example, consider the completion of the critical periods for disruption of global motion (Ellemberg et al., 2002), and letter acuity (Maurer & Lewis, 2001b, 2001a) by one and 10 years of age, respectively. The removal of one eye at six months of age and five years of age would both be classified as early monocular enucleation according to the definition used in the present study. The development of letter acuity in both cases would likely be altered. However, a participant who had one eye removed at five years of age would have ostensibly experienced typical development of global motion, unlike a participant who had one eye removed at six months of age. It follows that although both participants would be included in an early monocular enucleation group, they may differ in their processing of visual stimuli. This distinction suggests that these participants may warrant independent categorization.

An approach that specifies which visual abilities may have been affected based on the timing of their corresponding critical periods for disruption is likely preferable. This would result in a categorization where participants are stratified based on their ages at enucleation. A similar approach has been implemented by a previous study in which participants were categorized as

belonging to ‘very early’, ‘early’, and ‘late’ monocular enucleation groups based on their ages at enucleation (Nicholas et al., 1996). I propose a similar categorization, which stratifies participants based on their ages at enucleation relative to the critical periods for disruption in the development of specific visual abilities.

4.7.4.2. Time Between Visual Disruption and Monocular Enucleation. Another factor that can be considered in monocular enucleation research is the period between the onset of the visual disruption that necessitated the removal of one eye and the surgical intervention itself. This is particularly relevant for people who had one eye removed due to traumatic injury, which is the leading cause of monocular enucleation (Moshfeghi et al., 2000), and was the reason for monocular enucleation for all but one participant in the present study. A review of patients who sought medical attention for eye injuries at a major emergency eye trauma centre in the United States over an eight-year period provides relevant statistics (Gauthier et al., 2020). Nearly 70% of patients underwent monocular enucleation more than 24 hours after injury. The interim period between injury and eye removal ranged from two days to nearly 10 years, with a median of 34 days. During this time, most patients experienced severely impaired vision in the injured eye, with more than 80% unable to perceive light prior to eye removal.

Future research can consider the elapsed time from the onset of injury, or other visual disruptions which necessitate monocular enucleation such as ocular malignancies, to the surgical removal of the affected eye. This interval can be understood as a period of incomplete monocular deprivation. The brain receives aberrant visual input from the injured or otherwise impaired eye during this period, which may result in developmental consequences like amblyopia (Levi, 2021). Complete monocular deprivation is only experienced after monocular enucleation. As reviewed earlier, this removal of one eye has unique developmental consequences compared to incomplete

forms of monocular deprivation that result in amblyopia (reviewed in Kelly, Moro, et al., 2013; Steeves et al., 2008).

5. Conclusion

The findings of the sound-induced flash and McGurk experiments in this study may suggest increased or unaltered visual dominance after late monocular enucleation. This interpretation is based on evidence that the perception of both illusions may reflect a form of sensory dominance in the integration of audiovisual stimuli. Specifically, perceiving the sound-induced flash illusion reflects auditory dominance in the integration of the presented low-level audiovisual stimuli (Shams, 2012; Shams et al., 2005). In contrast, perceiving the McGurk effect reflects visual dominance in the integration of the presented high-level audiovisual speech stimuli (Lindborg & Andersen, 2021; Magnotti & Beauchamp, 2017). The tendency of both groups to perceive these illusions, their susceptibility, was accordingly interpreted as possibly reflecting their sensory dominance.

I interpreted the findings of this study to suggest that people who underwent late monocular enucleation may exhibit less susceptibility to the sound-induced flash illusion, but similar susceptibility to the McGurk effect compared to binocular viewing control participants. This interpretation may suggest altered audiovisual processing for low-level audiovisual stimuli, and unaltered audiovisual processing for high-level audiovisual speech stimuli after late monocular enucleation. Late monocular enucleation may also lead to less changes in audiovisual integration compared to people who underwent early monocular enucleation, who exhibit a tendency for more balanced processing of audiovisual stimuli (Moro & Steeves, 2012, 2013, 2018c, 2018a).

The present research is significant in that it works to fill a gap in research, namely audiovisual integration in people who lost one eye after the full development of their visual system.

The altered integration of audiovisual stimuli after late monocular enucleation may reflect compensatory adaptations for the loss of one eye. These could include the allocation of additional attentional resources toward visual input from the remaining eye, or cortical reorganization facilitated by neuroplasticity in the brain.

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