Integration of auditory and visual temporal rate in aging

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Abstract

In natural environments, accurate perception requires integration of related auditory and visual information into a coherent percept and segregation of unrelated information. One factor facilitating the binding of information across the senses is similarity in the rate of temporal modulations of light and sound. Whichever sensory modality specifies temporal rate more precisely, contributes more to the unified, audiovisual percept. Older adults may perceive audiovisual temporal rate differently to younger adults if there are age-related changes in integration ability or if audition and vision differ in their relative vulnerability to age-related decline.

This thesis aimed to investigate whether aging affects how audition and vision interact in the perception of temporal rate. A group of younger and older participants judged the temporal rate of an auditory temporal rate stimulus (a fluttering 500 Hz tone from a speaker) and/or a visual temporal rate stimulus (a green flickering LED).

Experiment 1A equated rate discrimination thresholds for auditory flutter to that of visual flicker on an individual basis by manipulating the modulation depth of auditory flutter. This required a greater modulation depth in older adults due to an age-related loss in sensitivity to amplitude modulation. This modulation depth was used in Experiments 1B and 1C to normalise for age-related auditory loss.

Experiment 1B investigated how the flutter rate subjectively equivalent to a 10 Hz reference shifted in the presence of an incongruent flicker rate, or vice versa, across a range of audiovisual rate disparities. There were no age-related differences in perceived rate, which suggests that aging does not affect the ability of older adults to integrate conflicting auditory and visual rates.

In Experiment 1C, temporal rate discrimination thresholds based on synchronous flicker and flutter were measured and found to be comparable across age groups. However, upon comparison to each individual’s flicker rate discrimination thresholds, the addition of flutter improved performance in line with statistically optimal inference only in the younger adult group. This indicates an age-related deficit in the interation of identical auditory and visual rates.

Experiment 2 measured the shift in perceived rate induced by audiovisual rate disparity when younger adults were presented with auditory flutter of the same modulation depth as the
average older adult in Experiment 1B. Younger adults weighted auditory temporal rate information more than visual for a modulation depth that balanced the relative contribution of audition and vision in older adults. This suggests that age-related differences in amplitude modulation sensitivity are sufficient to alter the percept of audiovisual rate.

The results of my study suggest that older adults will perceive audiovisual temporal rate differently to younger adults in everyday settings. When auditory and visual rates conflict, my results predict that older adults will compensate for the age-related decline in the precision of auditory rate estimates by weighting visual rate information more heavily through their intact ability to integrate. When auditory and visual rates are identical, older adults are expected to exhibit impaired audiovisual rate perception due to the combined effects of an age-related deficit in integration and auditory rate discriminability.
Declaration

This is to certify that:

i) The thesis comprises only my original work towards the Masters of Philosophy degree except where indicated in the preface;

ii) Due acknowledgement has been made in the text to all other material used; and

iii) The thesis is fewer than 40,000 words in length, exclusive of tables, maps, bibliographies and appendices

Cassandra Brooks
Preface

This MPhil was supported by an Australian Postgraduate Award. This research received funding from an Australian Research Council (ARC) grant FT0990930.

Professor Allison McKendrick conducted the programming of experimental tasks and assisted with some of the data collection.

The experiments outlined in this thesis have been published in the following peer reviewed journal article, included in an appendix:


and presented at the following conference:


As the primary author of the aforementioned publications, I contributed greater than 50% of the content and was responsible for the planning, execution and preparation of work for publication.
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Chapter 1: Literature review

Introduction

This thesis investigated whether physiological aging changes how audition and vision interact in temporal rate perception. Our environment is rich with information that stimulates multiple senses such as vision and hearing. Our eyes and ears encode separate visual and auditory accounts of the same object. At times, these two accounts complement each other by registering different aspects of an object. Other times, audition and vision register the same information. In the latter case, the brain achieves a coherent representation by integrating light and sound into a combined percept when both types of stimulation correspond to the same physical object. By definition, integration means that a statistically significant change in perception, behaviour or neural activity occurs when auditory and visual stimuli are presented together rather than separately (Stein et al. 2009). For example, integration can improve signal detection (Bolognini et al. 2005; Romei et al. 2011), discrimination (Romei et al. 2011), localisation (Charbonneau et al. 2013) and both manual and saccadic response times (Harrison et al. 2010; Hughes et al. 1994; Schröger & Widmann 1998), as well as help resolve perceptual ambiguity (Sekuler et al. 1997). Traditionally, it was believed that information from the different senses was processed independently by the brain before converging on higher order multisensory areas (Felleman & Van Essen 1991; Jones & Powell 1970). However, there is now a large body of evidence for earlier interactions between sensory modalities even at the level of the primary sensory cortices (Cappe et al. 2009; Driver & Noesselt 2008; Ghazanfar & Schroeder 2006; Kayser & Logothetis 2007; Macaluso & Driver 2005). Neuroimaging not only indicates functional connectivity between primary auditory and visual cortices (Eckert et al. 2008) but also suggests that the human brain may contain the same direct connections (Beer et al. 2011) found in primates (Falchier et al. 2010; Rockland & Ojima 2003). Thus, not just our perceptual experiences but also the cortical structures processing them are inherently multisensory in nature.

Temporal modulation rate is one aspect of objects in our environment that is registered by both audition and vision. For light (the visible portion of the electromagnetic spectrum) and sound (vibrations causing audible variation in air pressure), the term amplitude refers to distinct physical properties specified in different units. However, when the amplitude of either light or sound changes over time through a cycle of high and low extremes, both stimuli may
be described by their temporal rate. This property is specified in units of cycles per second or Hertz (Hz). Light and sound modulated at a regular rate over time feature in both our auditory and visual experiences as basic constituents of more complex objects in our environment (Attias & Schreiner 1997; Dong & Atick 1995). These auditory and visual amplitude modulations often occur in combination – from simple stimuli, like the flashing lights and ringing of a police or ambulance siren, to more complex stimuli, such as the shape of our mouths changing with the rise and fall of our syllables as we speak. The brain unifies these two accounts into a single audiovisual percept of temporal rate through the process of audiovisual integration. However, accurate interpretation of the world also requires segregation of light and sound into separate percepts if they relate to different objects. As temporal rate is one of the basic building blocks of more complex objects, understanding how auditory and visual rates are integrated and segregated is of ecological significance to perception. Accordingly, how audition and vision interact in temporal rate perception has been well-established in younger adults (Gebhard & Mowbray 1959; Recanzone 2003; Roach et al. 2006; Shipley 1964; Welch et al. 1986).

Just like younger adults, the perceptual experiences of older adults are multisensory. Yet in older adults, auditory and visual temporal rate perception has been only been studied for each sense in isolation, not in combination. The normal aging process degrades both auditory and visual temporal processing (Fitzgibbons & Gordon-Salant 1996; Owsley 2011). From a visual perspective, the poorer temporal perception that accompanies aging is associated with functional impairments in driving (Conlon & Herkes 2008; Wood 2002), balance (Freeman et al. 2008) and mobility (Kuyk & Elliott 1999). From an auditory perspective, poorer temporal resolution contributes to reduced speech comprehension in older adults (Lorenzi et al. 2006; Schneider 2002). However, visual and hearing impairments decrease functional status and quality of life collectively (Brennan et al. 2005; Chia et al. 2006). Therefore, considering age-related changes in audition and vision separately limits our understanding of how sensory decline contributes to any difficulties older adults may experience when completing everyday tasks.

In other contexts, the ability to integrate auditory and visual cues changes with older age; sometimes for better, sometimes for worse (for review see de Dieuleveult et al. 2017; Freiherr et al. 2013; Guerreiro et al. 2010; Mozolic et al. 2012). Many factors play a role in how we perceive multisensory objects, including attention, congruence of temporal, spatial and semantic features, and the saliency of each sensory stimulus (reviews include Alais et al. 2010;
Stanford & Stein 2007; Talsma et al. 2010). Consequently, age-related changes in these factors need to be distinguished from age-related changes in integration to understand how age-related differences in audiovisual perception arise. The question remains whether subtle age-related changes in the processing of auditory and visual temporal rate are sufficient to alter their integration and whether the process of integration itself for temporal rate is vulnerable to physiological aging.

Consequently, this literature review first addresses how temporal rate is perceived and processed when considering auditory and visual senses in isolation. This provides a framework for subsequent discussion of the integration of auditory and visual rates in younger adults. Next, an outline of how older age impairs auditory and visual temporal processing is provided, focusing on the perception of temporal rate. Finally, I summarise the findings on how aging affects integration, particularly for auditory and visual temporal information, and consider how age-related sensory loss might interact with the integration process. The chapter concludes with the aims and hypotheses of my thesis.

**Temporal rate perception**

**Auditory and visual rates**

*Definition and percept*

For audition, temporal rate describes how fast a series of discrete beeps repeat or how quickly cyclic changes occur in the amplitude of a continuous sound. In the latter case, an amplitude modulated sound consists of two temporal dimensions – the fine temporal structure (spectral frequencies) present in the carrier sound wave due to changes in air pressure, and the temporal envelope corresponding to the waveform that modulates the amplitude of the carrier over time (Joris et al. 2004). The cortical representation of sounds in humans consists of two co-occurring temporal profiles of neural activity, which explains our ability to decode acoustic information over these fast and slow timescales (Harms et al. 2005; Seifritz et al. 2002). A simple example of an amplitude modulated sound is sinusoidal amplitude modulation of a pure tone carrier, which consists of a single spectral frequency. A pure tone is created by sinusoidal variation in air pressure at a particular frequency and by itself, it is heard as a single pitch at a constant volume. However, when the pure tone is modulated by a sinusoid, this volume then changes over time at a regular rate (Joris et al. 2004; see Equation 1.1, Figure 1.1). Broadband carriers, which are composed of multiple spectral frequencies, may also be modulated in amplitude over time.
\[ s(t) = [1 + m \sin(2\pi f_m t)] \sin(2\pi f_c t) \]

Equation 1.1: Waveform \( s(t) \) for sinusoidal amplitude modulation (SAM) of a pure tone, where \( m \) = modulation depth, \( f_m \) = modulation frequency or rate and \( f_c \) = carrier frequency. \( \sin(2\pi f_c t) \) gives the waveform for the carrier, that of a pure tone (Joris et al. 2004).

The quality of the sound we perceive depends on the temporal rate of amplitude modulation. Slow rates up to about 10 Hz sound like they are fluctuating in intensity over time (Edwards & Chang 2013; Fastl 1982; Joris et al. 2004). At these low rates, the cycle of peaks and troughs in the modulating waveform can be individuated (Nourski & Brugge 2011). At around 10 Hz, the percept changes to flutter, where the listener can still appreciate intermittent amplitude variation (Edwards & Chang 2013; Joris et al. 2004; Nourski & Brugge 2011). For fluctuating or fluttering sounds, the perceived fluctuation strength increases with increasing sound level and modulation depth and varies with modulation rate in a bandpass manner with a peak at 4 Hz (Fastl 1982; Wojtczak & Viemeister 2008). At faster rates of approximately 25 Hz and above, amplitude modulation is heard as the fused percept of roughness (Edwards & Chang 2013; Joris et al. 2004). The critical flutter frequency, which is the maximum rate that can be distinguished from a continuous sound, is estimated at 45 to 100 Hz and varies with sound level (Besser 1967; Shipley 1964; Symmes et al. 1955).
Figure 1.1: The top panel shows a sinusoidal amplitude modulated (SAM) 500 Hz pure tone with a modulating frequency of 10 Hz. The square inset is magnified in the bottom panel, which compares the 500 Hz pure tone carrier with modulation (dark grey) and without modulation (light grey). At different time points in the cycle, the SAM waveform has greater, equal or reduced amplitude in comparison to the 500 Hz pure tone carrier.

For vision, temporal rate describes how fast a series of discrete flashes repeats or how quickly cyclic changes occur in the amplitude of a continuous light. Such a stimulus is created when the luminance of a uniform field is modulated over time at a regular rate, typically by a sinusoidal waveform (Schwartz 2004; see Equation 1.2, Figure 1.2). It may also be produced by modulating the contrast of a spatial frequency grating over time, where the contrast of the grating reverses twice per modulation cycle (Skottun & Skoyles 2008). This periodic luminance modulation gives rise to the percept of flicker. For slow rates, the alternating dark and bright periods can be individuated but above 10 Hz, flicker is perceived as a continuous fluctuation in brightness over time without individuation of dark periods (Van De Grind et al. 1973). The subjective contrast (i.e. amplitude modulation) of flicker with a fixed physical contrast level is a bandpass function of temporal rate (Magnussen & Björklund 1979). However, the decrease in subjective contrast with increasing rate diminishes as stimuli become more suprathreshold.
(Bowker 1983). The critical flicker frequency gives the temporal rate at which flicker can no longer be distinguished from steady illumination (Landis 1954). The rate at which this occurs increases with luminance, size and eccentric location in the visual field (Douthwaite et al. 1985; Hartmann et al. 1979; Landis 1954) and the greatest values reported are in the order of 80 Hz (Landis 1954).

\[ x(t) = I[1 + m \sin(2\pi ft)] \]

Equation 1.2: Waveform, \( x(t) \), describing change in luminance over time, \( t \), for sinusoidal flicker where \( I \) = average luminance, \( m \) = modulation depth and \( f \) = frequency or rate of modulation (Van De Grind et al. 1973).

Figure 1.2: Sinusoidal flicker. Luminance varies about an average luminance (I) in a sinusoidal fashion. The modulation depth (m) is the amplitude of the change in luminance. The temporal frequency or rate is the number of cycles (\( T=1/f \)) per second.

Sensitivity to amplitude modulation

One measure of sensitivity to temporal rate is the ability to detect the presence of temporal modulations in amplitude. This is given by the temporal modulation transfer function, which specifies the depth of modulation needed to detect temporal modulation as a function of the temporal modulation rate. For audition, the shape of the function depends on the carrier type. However, for low rates, sensitivity is consistent with the use of temporal cues (i.e. periodicity of amplitude changes) rather than spectral cues from the fine temporal structure of the carrier (Dau et al. 1997a). With a broadband carrier, thresholds hold constant up to 2-10 Hz (Dau et al. 1997a; Viemeister 1979) then decrease in a low pass function with a cut off around 50 Hz (Roß et al. 2000; Viemeister 1979). Unlike a broadband carrier, amplitude modulation of a pure tone
alters its spectrum (i.e. temporal fine structure). Thresholds are constant up to 100-130 Hz (Kohlrausch et al. 2000), largely invariant to carrier frequency (Eddins 1999), and then decrease up to a transition frequency (Kohlrausch et al. 2000). Beyond the transition frequency, additional spectral cues called sidebands become audible as separate tones and improve detection thresholds (Fassel & Kohlrausch 1996; Sek & Moore 1994).

For vision, the temporal modulation transfer function is bandpass in shape, peaking in sensitivity at approximately 10 Hz and declining at rates both higher and lower (De Lange 1958; Kelly 1961; Swanson et al. 1987). However, sensitivity to temporal modulation varies with the properties of the visual stimulus, such as luminance (De Lange 1958; Kelly 1961; Swanson et al. 1987), size (Mäkelä et al. 1994; Rovamo et al. 2000) and the presence of spatial frequency content (Kelly 1972). Sensitivity also varies with eccentricity, with greater sensitivity for high temporal rates and decreased sensitivity for low temporal rates in the periphery, relative to central vision (Allen & Hess 1992; Mäkelä et al. 1994; Seiple & Holopigian 1996; Tyler 1985).

**Temporal rate discrimination**

Another measure of sensitivity to temporal rate is the ability to discriminate between different rates of visual flicker and between different rates of auditory flutter. For audition, temporal rate discrimination thresholds for broadband and pure tone carriers are comparable (Lemańska et al. 2002), although the frequency of the pure tone carrier affects rate discrimination thresholds for modulation rates greater than 320 Hz (Lee 1994). The just noticeable change in temporal rate is less than 1 Hz for a modulation rate of 10 Hz and increases thereafter with increasing temporal rate (Formby 1985; Füllgrabe et al. 2005; Hanna 1992; Lee 1994). Auditory rate discrimination thresholds are approximately 3-10% of the temporal rate (Lee 1994; Yost et al. 1989).

For vision, temporal rate discrimination thresholds vary in a bandpass manner with increasing rate, rising from approximately 0.2 Hz for 1 Hz flicker to 6 Hz for 40 Hz flicker before declining again when viewed foveally (Hammett & Smith 1992; Mandler 1984; Waugh & Hess 1994). Relative to foveal thresholds, peripheral rate discrimination thresholds are worse at mid temporal rates and better at high temporal rates but within a factor of two from values for foveal viewing (Waugh & Hess 1994).

For the same temporal rate, rate discrimination thresholds are lower for audition compared to vision (Gebhard & Mowbray 1959; Recanzone 2003) up until 25 Hz, where the situation
reverses due to the decline in auditory temporal rate discrimination with increasing rate (Gebhard & Mowbray 1959). For both vision and audition, temporal rate discrimination is poorer for modulations in amplitude closer to threshold (Roach et al., 2006; Waugh & Hess, 1994) and is therefore intertwined with an observer’s sensitivity to amplitude modulation (Formby 1985). However, discrimination at low flutter rates is likely also limited by periodicity encoding (Patterson et al. 1978) and at high modulation depths, flicker rate discrimination is limited by central noise rather than modulation depth (Bowne 1990).

Ecological significance of temporal rate

Auditory and visual temporal modulations are of ecological significance to perception. Slow amplitude modulations at a regular rate are a key constituent of our dynamic auditory environment (Attias & Schreiner 1997), found for example in natural scenes (Chandrasekaran et al. 2010) and human speech (Chandrasekaran et al. 2009). Perceptually, the temporal envelope of a sound contributes to the grouping of acoustic information into distinct objects (Griffiths & Warren 2004). For example, sequences of sounds can be segregated into distinct streams based solely on differences in their temporal rate for sinusoidal modulation of both broadband noise and pure tone carriers (Dolležal et al. 2012; Grimault et al. 2002; Szalárdy et al. 2013).

Likewise, the temporal structure of natural visual scenes includes repetitive modulation of luminance or contrast (Dong & Atick 1995), including human speech as the mouth opens and closes (Chandrasekaran et al. 2009). Perceptually, luminance modulation is a cue that facilitates the grouping of related input into a global percept, in an analogous role to that of temporal structure in auditory perception. For example, differences in temporal rate facilitate detection of a visual target embedded amongst distractors (Cass et al. 2011). Segregation of a target from its background occurs when they are oscillated at the same rate but out of phase from one another (Parton et al. 2006; Sekuler & Bennett 2001). In summary, temporal rate is an elementary stimulus dimension in visual and auditory perception. Within each sensory modality, temporal rate correspondence facilitates the grouping of related input while temporal rate differences facilitate the separation of unrelated input.

Comparison of the neural processing of auditory and visual rates

Temporal information is of greater ecological significance to hearing, since meaningful representation of acoustic information is primarily derived by analysis of how sounds evolve over time while many visual features such as spatial detail or colour can be resolved from a
snapshot of an object at the one time point (Seifritz et al. 2003). More broadly across temporal perception, audition outperforms vision for tasks such as duration discrimination (Ortega et al. 2014; Stauffer et al. 2012), temporal order judgement (Kanabus et al. 2002) and tapping in time with a rhythm (Iversen et al. 2015; Repp 2003; Repp & Penel 2002). Research suggests that visual awareness of time is cyclic, with temporal sampling occurring in cycles of approximately 7-13 Hz (VanRullen et al. 2014). It is unclear whether the auditory system is similarly cyclic, given that analysis of the spectral content of sound requires finer temporal resolution, or whether alternatively auditory perception of time is continuous (VanRullen et al. 2014). Differences in auditory and visual perception of time are consistent with processing via modality specific pathways as well as mechanisms common to both modalities (Merchant et al. 2008; Stauffer et al. 2012). Unlike visual signals, auditory signals pass through multiple subcortical sites which are capable of decoding basic features (King & Nelken 2009) and more complex features can then be extracted even in early auditory cortex (Nelken et al. 2003).

However, there are some similarities in temporal rate processing between the two modalities. Within audition, there are several channels selective to particular temporal rates of modulation (Bacon & Grantham 1989; Ewert & Dau 2000; Houtgast 1989). In fact, temporal rate perception is consistent with processing by a modulation filterbank consisting of multiple filters with bandpass tuning to modulation rate (Dau et al. 1997a; Dau et al. 1997b; Sek & Moore 2003). In this model, the temporal envelope of the sound is extracted by low pass filtering the output of the peripheral auditory filters that first decode the spectral frequencies present in a given sound, explaining the invariance of modulation sensitivity to tonal frequency at lower temporal modulation rates (Dau et al. 1997a; Dau et al. 1997b). For vision, multiple studies have shown that temporal rate perception is consistent with models of two or three independent temporal channels (depending on spatial frequency and eccentricity) that are tuned to a range of rates (Hammett & Smith 1992; Hess & Plant 1985; Horiguchi et al. 2009; Mandler & Makous 1984; Snowden et al. 1995; Watson & Robson 1981; Waugh & Hess 1994). Furthermore, perceived visual rate is found to shift in the opposite direction to a discrepant, auditory adaptor but only for small discrepancies, which suggests the presence of crossmodal channels tuned to a narrow range of temporal rates rather than modality-independent mechanisms of rate perception (Leflitan et al. 2015).

Neuroimaging in humans indicates that the auditory system is characterised by tuning to progressively lower temporal rates as the afferent signals ascend through the processing hierarchy (Brugge et al. 2009; Giraud et al. 2000; Harms & Melcher 2002; Nourski et al. 2013;
Overath et al. 2012). This progressive loss of temporal resolution occurs in the visual pathway also (Gauthier et al. 2012; McKeef et al. 2007; Mullen et al. 2010). However, the visual pathway is segregated subcortically into parvocellular and magnocellular pathways and cortically into ventral and dorsal streams, with the latter of each pair showing greater responses to high rates (Denison et al. 2014; Mullen et al. 2010). Furthermore, both auditory and visual neurons encode temporal information with spikes demonstrating millisecond precision, despite the different natural timescales of vision and hearing (Bair & Koch 1996; Kayser et al. 2010). This facilitates accurate encoding of dynamic auditory stimuli unfolding at fast timescales (Kayser et al. 2010), but also preserves information regarding the slower temporal structure of vision lost at coarser temporal representations (Butts et al. 2007).

**Conclusion**

Despite the differences between the senses, there is equivalency in the temporal information they provide. Flicker – visible fluctuations in light intensity – and flutter – audible fluctuations in sound amplitude – are analogous percepts registered by both senses over a common range of slow temporal rates. As a comparison, consider auditory amplitude modulation rate and visual spatial frequency. These two attributes provide complimentary information about the density of auditory and visual information across time and space and linearly correspond in rate/frequency when matched according to their perceived correspondence (Guzman-Martinez et al. 2012; Orchard-Mills et al. 2013; Sherman et al. 2013). The perceived correspondence between these frequency measures is nevertheless an associative link rather than a physical correlation since they are different object attributes specified in different units. Present theory posits that signals from different sensory modalities can be integrated by the brain when they supply the same type of information in the same unit (Ernst & Bülthoff 2004), as is the case for temporal rate. In the next section, the integration of auditory and visual amplitude modulations into a unified percept of audiovisual rate is reviewed.

**Audiovisual rate**

The brain’s challenge is to appropriately combine or separate the auditory and visual temporal rate information present in a busy environment into coherent representations of distinct objects. In a dynamic audiovisual scene, light and sound corresponding to the same object are likely to oscillate at similar rates. However, auditory and visual representations of the same object may not always agree since signals may be obscured by differing amounts of noise in a busy environment or momentary neural noise may impair the fidelity with which sensory
information is encoded (De Gelder & Bertelson 2003; Ernst & Bülthoff 2004). While synthesis of conflicting information accommodates slight differences in auditory and visual representations, achieving a coherent, unified percepts comes at the cost of veridical perception. Since differences in auditory and visual representations can naturally occur, experimentally inducing auditory and visual disparity is potentially a useful tool for understanding how the brain deals with natural audiovisual incongruence (De Gelder & Bertelson 2003).

In a process of crossmodal binding, the perceptual grouping of low level stimulus features registered by both audition and vision aids in the formation of audiovisual objects (Bizley et al. 2016b). Crossmodal binding is modulated by the perceived correspondence of auditory and visual stimuli, which is influenced not only by how closely they occur in space and time (Lewald & Guski 2003; Zampini et al. 2003) but also by whether their temporal structure is correlated (Denison et al. 2013; Vettel et al. 2008). Similarities in temporal rate is one stimulus feature exploited by our brains to group related sensory input into a global percepts. For example, when an irrelevant stimulus in one modality oscillates at the same rate as a stimulus in the target modality, this promotes segregation from distractors to enhance detection and reaction times (Kösem & Van Wassenhove 2012; Maddox et al. 2015). The advantage in integrating auditory and visual cues with congruent temporal structure has also been shown for other metrics. For example, temporal correspondence of auditory and visual patterns enhances neural activity in unisensory and multisensory cortex (Marchant et al. 2012; Noesselt et al. 2007). Temporal correspondence also improves spatial localisation (Parise et al. 2013), detection of changes in intensity (Marchant et al. 2012), response times (Marchant et al. 2012) and tapping in time to audiovisual cues (Mayer et al. 2009).

**Comparing temporal rate across audition and vision**

When measured for each sensory modality separately, the apparent auditory or visual temporal rate differs slightly from its true physical value (Fukuda 1977; Welch et al. 1986). In a comparative study using magnitude estimation, there was a 2 Hz difference between auditory and visual estimates of apparent rate (Welch et al. 1986). This was due to the tendency for apparent auditory rate to be perceived as slower and visual rate to be perceived as faster than the physical rate (Welch et al. 1986). Conversely, an earlier study reported that apparent flicker rate was lower than its physical rate of oscillation (Fukuda 1977). Differences between studies may be explained by the fact that apparent flicker rate varies with modulation depth and stimulus size (Bowker 1982; Fukuda 1977; Thompson & Stone 1997).
Although audition and vision both register temporal rate information physically present in our dynamic environment, the temporal rate subjectively equivalent to a reference deviates more from the true match when comparing rate crossmodally (i.e. the flutter rate judged equal to a reference flicker rate or vice versa) than within vision or audition alone (Gebhard & Mowbray 1959). However, other studies indicate that subjective auditory and visual rates can be accurately matched for slow physical rates below 12 Hz (Myers et al. 1981; Stockman et al. 2004). Indeed, auditory and visual rates are highly likely to be judged as equivalent when physically identical (Noesselt et al. 2005). As the physical disparity between auditory and visual rates increases, they are less likely to be perceived as oscillating at the same rate (Noesselt et al. 2005). On the other hand, the ability to match the phase (i.e. relative timing) of auditory and visual rates, or discriminate intersensory phase differences, is limited to slow rates below 2 to 3 Hz (Nishida & Fujisaki 2010; Stockman et al. 2004). Together, these studies suggest that precise temporal detail is not retained at the cortical locus of auditory and visual rate comparison.

**Integrating congruent and incongruent auditory and visual rates**

Historically, the modality appropriateness hypothesis proposed that multisensory perception was dominated by the sensory modality with the greatest acuity for the task (Welch & Warren 1980). In this model, vision dominates spatial perception and audition dominates temporal perception based on differences in their functional specialisation (Welch & Warren 1980). As such, temporal rate perception was thought to follow the auditory cue because auditory temporal resolution is superior to visual (Recanzone 2003; Welch et al. 1986). When auditory and visual rates are physically different, apparent flicker rate is driven towards the auditory cue to induce the perception of intersensory synchrony (Berger & Pelli 2001; Knox 1945; Regan & Spekreijse 1977; Shiplev 1964; Welch et al. 1986). However, these studies found that apparent flutter rate is not driven by visual flicker, thus finding no evidence of a visual influence on auditory rate perception (Knox 1945; Shiplev 1964; Welch et al. 1986).

Furthermore, flashes counted for a flickering stimulus are incorrect because they follow the discrepant rate at which auditory beeps are presented (Noesselt et al. 2008). When auditory and visual rates are physically equivalent, selective attention to either modality during a temporal rate discrimination task produced psychometric functions that resembled those for auditory rate discrimination when measured on its own (Recanzone 2003). Congruent auditory rate information also increases the critical flicker frequency, improving visual temporal resolution (Maier et al. 1961; Ogilvie 1956a; Ogilvie 1956b; Regan & Spekreijse 1977).
the above studies could be construed as providing support for the modality appropriateness hypothesis, as they show auditory dominance of temporal rate perception.

However, despite intersensory differences in sensitivity, a purely dichotomous view of vision analysing objects in space and audition analysing them in time is flawed, since both sensory systems encode spatiotemporal information about objects (Handel 1988a; Handel 1988b). Moreover, the relative accuracy of auditory and visual estimates of a stimulus attribute depends not just on sensory acuity but also stimulus and environmental conditions (Witten & Knudsen 2005). Accordingly, in more recent studies, evidence of visual effects on auditory temporal rate perception have emerged. When judging whether the temporal rate of an auditory stimulus is speeding up or slowing down over time, the perceived direction of the change in rate is dominated by the visual rate if the auditory rate is constant, hence providing an ambiguous cue (Wada et al. 2003). Detection of a deviant point in an otherwise regular auditory rhythm decreases when presented with a simultaneous visual rhythm without a deviant, more so when the visual and auditory rhythms are temporally congruent than when incongruent (Su 2014). Vision can also induce the perception of illusory beeps when the sound level is significantly reduced (Andersen et al. 2004). Therefore, the idea that auditory dominance was inherent in the multisensory processes underlying integration of temporal rate was countered as the understanding of multisensory processing advanced.

More recently, audiovisual rate perception has been explained by contemporary multisensory theory. When flicker and flutter rates are physically equivalent, integration permits more precise discrimination of temporal rate changes, in agreement with the maximum likelihood prediction (Koene et al. 2007). This prediction is derived from reliability-based weighting of the individual sensory estimates of a property (where reliability is defined as the estimate’s precision, as given by the inverse of its variance) to achieve a combined estimate with the smallest possible variance (Ernst & Bülthoff 2004; Fetsch et al. 2013; Witten & Knudsen 2005). Despite the superior facility of audition for discriminating temporal rate (Recanzone 2003), reducing auditory amplitude modulation to low levels can equate flicker and flutter rate discriminability, rendering each modality’s estimate of temporal rate equally reliable (Roach et al. 2006). Under these conditions, the flutter rate apparently equivalent to a 10 Hz reference is nonveridical when presented with a discrepant flicker rate (Roach et al. 2006), in contrast to earlier studies that showed no influence of vision on auditory rate perception (Knox 1945; Shipley 1964; Welch et al. 1986). As the discrepant rates were fused into a unitary percept, physical auditory rates faster than 10 Hz were required in the presence of slow visual rates to
match the 10 Hz audiovisual standard. Physical auditory rates slower than 10 Hz were required in the presence of fast visual rates (Roach et al. 2006). In the same manner, the auditory rate apparently equivalent to a 10 Hz reference is nonveridical when presented with a discrepant visual rate (Roach et al. 2006). As the degree of distortion in perceived rate is comparable for vision and audition, each sensory modality has the same capacity to influence perceived rate when auditory and visual information is equally reliable (Roach et al. 2006). Furthermore, when auditory rates are less discriminable than visual, vision influences perceived rate under audiovisual conditions to a greater degree whether selectively attending to audition or vision (Roach et al. 2006). Consequently, the degree of influence of each sensory modality on temporal rate perception is not hard-wired but rather determined by the relative reliability of the information each sense provides.

For small differences, the degree of rate distortion is consistent with partial integration between auditory and visual rates since it falls short of the maximum likelihood prediction, but for larger differences segregation occurs (Roach et al. 2006). This observation can be explained by a Bayesian model, which has been applied in other contexts to show that in addition to the relative reliability of sensory cues, multisensory integration is also governed by prior knowledge of the likelihood of two sensory events being related (Battaglia et al. 2003; Knill & Pouget 2004; Roach et al. 2006). Therefore, under a Bayesian model, the degree of integration declines for increasingly disparate rates as they are less likely to be related, resulting in smaller distortions in apparent rate, until rate perception becomes veridical due to the independent processing of considerably different rates (Roach et al. 2006).

Temporal rate perception may also benefit from audiovisual interactions even when integration does not occur. Temporal contrast thresholds for detection of luminance modulation are reduced by concurrent auditory noise at moderate sound levels but elevated for intense sound levels (Harper 1979; Lugo et al. 2008). Similarly, auditory noise enables detection of a train of flashes when flash intensity is sub-threshold (Manjarrez et al. 2007). This effect is attributed to stochastic resonance operating crossmodally, where the neural response to a visual signal is strengthened by auditory noise due to nonlineairities in visual processing (Lugo et al. 2008; Manjarrez et al. 2007).

Neural processing of audiovisual temporal rate

Though the studies detailed in the previous section indicate robust interactions between audition and vision in the perception of temporal rate, the underlying neural mechanisms of
these interactions have yet to be identified. Early studies showed no correlation between the frequency of visual evoked potentials and the change in perceived flicker rate by auditory flutter at a different rate (Regan & Spekreijse 1977). However, with the advent of neuroimaging, it was found that neural activity in auditory and visual cortices is altered by the temporal synchrony of simple and complex periodicities across modalities (Mossbridge et al. 2013; Noesselt et al. 2007; Nozaradan et al. 2012). Integration of temporal amplitude modulation could feasibly occur in early visual and auditory cortices, given similarities in neural encoding of modulation rates (Herrmann 2001, Bendor 2007). Alternatively, modulation of early sensory cortex may reflect feedback connections from multisensory areas of convergence within higher-order cortex, such as the superior temporal sulcus (STS; for review of it's role in integration see Beauchamp 2005).

While the neural substrate subserving audiovisual integration of the temporal rate of sinusoidal amplitude modulation has yet to be investigated, there is a body of literature detailing how the congruence of auditory and visual temporal structure influences neural activity. Temporal correspondence of a stream of flashes and beeps enhances activity in sensory specific cortex and STS (Marchant et al. 2012; Noesselt et al. 2007), while noncorresponding streams yield depression of neural responses, relative to response elicited by each stream presented in isolation (Noesselt et al. 2007). Analysis of functional connectivity suggests that neural activity in both primary sensory cortices in response to temporally correlated patterns of auditory and visual transients is influenced by feedback from STS (Noesselt et al. 2007). Regular, rather than random, timing of flashes and beeps also enhances activity in the inferior parietal cortex (Marchant et al. 2012). For incorrect flash counts due to a discrepant rate of beeps, event related potentials differ at parietal, frontal and occipital electrodes in comparison to correct counts (Noesselt et al. 2008).

These studies, however, employed transient stimuli rather than continuous, modulated ones. Comparison of responses for brief and sustained stimuli indicates that audiovisual stimulation enhances neural activity in low level sensory cortex in response to stimulus onset, while sinusoidal intensity modulation over time enhances neural activity in the STS (Werner & Noppeney 2011). As such, it is unclear how the results of studies employing transient stimuli such as flashes and beeps relate to the processing of continuous, temporally modulated stimuli. However, there are studies pairing amplitude modulated sounds with more complex visual temporal modulations, consisting of a shape modulated in size (Laing et al. 2015) or form (Jenkins III et al. 2011) over time at a regular rate. In one study, audiovisual rate
congruence increased neural activity in the right superior temporal gyrus and parietal cortex, and rate incongruence increased functional connectivity between auditory cortex, superior temporal sulcus and frontal cortex (Laing et al. 2015). In another study, differences in time locked neural activity between unimodal and bimodal stimulus presentations were suggestive of integration effects occurring in either the auditory or parietal cortex (Jenkins III et al. 2011). Consequently, it can be inferred from the literature that the neural processing of audiovisual temporal modulations is likely to recruit the primary auditory and visual cortices, the superior temporal sulcus and parietal and frontal cortices.

Conclusion

On the one hand, integration of identical auditory and visual rates facilitates perception, allowing more precise discrimination of rate changes (Koene et al. 2007; Recanzone 2003) to produce estimates of audiovisual rate with the smallest possible variance (Koene et al. 2007). On the other hand, integration of different auditory and visual rates into a single object distorts perception, skewing perceived rate away from the true physical rate to reconcile audiovisual incongruence (Berger & Pelli 2001; Knox 1945; Recanzone 2003; Regan & Spekreijse 1977; Roach et al. 2006; Shipley 1964; Welch et al. 1986), in a manner consistent with Bayesian inference (Roach et al. 2006). Therefore, an investigation of audiovisual interactions in temporal rate perception in older adults can explore the capacity of integration to both facilitate and distort perception in the context of contemporary multisensory theory.

Integration in older adults

There is a growing body of literature documenting age-related changes in perception and behaviour related to the combined presentation of auditory and visual stimuli. A well-researched example is the speeding of response times to audiovisual stimuli (Diederich et al. 2008; Hugenschmidt et al. 2009a; Hugenschmidt et al. 2009c; Laurienti et al. 2006; Peiffer et al. 2007; Ren et al. 2017). Audiovisual integration is said to occur when the speeding of response times exceeds the prediction from the sum of the cumulative distribution functions of response times to auditory and visual stimuli alone (Miller & Ulrich 2003). Older adults demonstrate greater multisensory facilitation of both manual and saccadic response times than their younger counterparts, which suggests an age-related enhancement in integration (Diederich et al. 2008; Hugenschmidt et al. 2009a; Hugenschmidt et al. 2009c; Laurienti et al. 2006; Peiffer et al. 2007; Ren et al. 2017). However, this section focuses on the integration of temporal information, since a comprehensive review of all perceptual tasks studied in older adults.
adults is outside the scope of this thesis. Though some changes in auditory (e.g. Grose et al. 2015), visual (e.g. Kim & Mayer 1994) and audiovisual (e.g. Alm & Behne 2013) temporal perception emerge in middle age, for the purposes of this review older adults are considered to be 60 years and older.

**Age-related changes in the perceived timing of auditory and visual cues**

When auditory and visual stimuli are temporally coincident, we perceive them to correspond and hence integrate them (Lewald et al. 2001; Lewald & Guski 2003; Romei et al. 2011; Wallace et al. 2004). However, non-coincident auditory and visual stimuli that fall within a temporal binding window will still be integrated due to tolerance for some incongruence in their relative timing (Donohue et al. 2011; Lewald et al. 2001; Lewald & Guski 2003; Schirillo 2011; Wallace et al. 2004).

When participants are asked to judge temporal asynchrony, the point of subjective simultaneity does not change with older age (Bedard & Barnett-Cowan 2016; Noel et al. 2016). However, one study found that older adults require wider temporal offsets between simple auditory and visual stimuli to correctly perceive them as asynchronous rather than simultaneous (Chan et al. 2014a) yet another did not (Bedard & Barnett-Cowan 2016). Differences in study outcomes may have arisen from the methodology, since only the study by Chan et al. (2014a) minimised criterion bias through a two-interval forced choice procedure (García-Pérez & Alcalá-Quintana 2011) and controlled for age-related sensory decline by normalising individual variation in the detectability of auditory and visual stimuli. Further indication of age-related difficulties in correctly identifying temporally offset auditory and visual cues comes from a cross sectional study, in which a significant widening of the perceived window of simultaneity occurred for participants 64 years and older (Noel et al. 2016).

Moreover, when judging audiovisual asynchrony, electroencephalographic recordings indicate greater audiovisual interactions in the frontal and parietal cortex in older compared to younger adults (Chan et al. 2017). In keeping with the trend for greater tolerance of audiovisual asynchrony in older age, there is a wider window of perceived simultaneity for audiovisual speech in older adults (Hay-Mccutcheon et al. 2009) and a wider window of integration on response time tasks (Diederich et al. 2008; Laurienti et al. 2006). However, there is an age-related impairment in recalibration of perceived synchrony (Chan et al. 2014b). Specifically, adaptation to a temporally asynchronous auditory and visual pair shifts the window of perceived synchrony towards the asynchrony of the adapting pair in younger adults (Fujisaki et al. 2004), but the effect is less in older adults (Chan et al. 2014b).
When participants are asked to judge temporal order, the point of subjective simultaneity also does not change with age (Bedard & Barnett-Cowan 2016; De Boer-Schellekens & Vroomen 2014). However, older adults require greater temporal offsets between auditory and visual stimuli to correctly identify the order (De Boer-Schellekens & Vroomen 2014; Virsu et al. 2003). Incongruously, one study reported similar thresholds despite using elderly participants 70 years and above (Fiacconi et al. 2013). Furthermore, older adults experience difficulties correctly identifying temporal order between auditory and visual stimuli when presented at large but not short temporal offsets, in line with a decrease in the neural response elicited by the second stimulus in the pair (Setti et al. 2011).

Considered together, age-related changes to performance on temporal order and asynchrony tasks suggest a general trend for physiological aging to increase the tolerance for audiovisual asynchrony, resulting in the binding of auditory and visual stimuli with greater temporal offsets in older adults. However, estimates of the temporal binding window from temporal order and asynchrony tasks are not correlated in older adults (Bedard & Barnett-Cowan 2016). This suggests that these tasks may not index the same perceptual processes (Love et al. 2013) but could also reflect differences in response strategy and decisional processes for the two tasks (García-Pérez & Alcalá-Quintana 2012; García-Pérez & Alcalá-Quintana 2015; Yarrow et al. 2014).

Age-related changes in the perceived timing of auditory and visual cues are also evident in a variant of the temporal ventriloquist effect. In this task, visual temporal order sensitivity for a sequence of two flashes improves when presented with a click before and after (Morein-Zamir et al. 2003). This is believed to reflect an apparent increase in flash onset asynchrony due to the binding and integration of disparate auditory and visual onsets (Chen & Vroomen 2013). Just noticeable differences in visual temporal order improve more in older than younger adults with the addition of auditory clicks, suggestive of greater multisensory facilitation in aging (De Boer-Schellekens & Vroomen 2014).

On balance, evidence suggests that older adults are more tolerant of asynchrony in the timing of auditory and visual stimuli. However, it seems unlikely that this effect would generalise to greater age-related tolerance for temporal rate disparity given that audiovisual enhancement of neural activity occurs in different cortical regions for transient compared to temporally modulated audiovisual stimuli (Werner & Noppeney 2011). In fact, whether or not dynamic
auditory and visual stimuli are fused into single object depends more on close correlation of their temporal structure than their temporal coincidence (Denison et al. 2013).

Age-related changes in the perception of temporal numerosity

When different numbers of flashes and beeps are physically present, the perceived number of flashes often follows the number of beeps in a phenomenon known as the sound-induced flash illusion. For example, two flashes are perceived when a solitary flash is presented with two beeps in an illusory fission effect (Shams et al. 2000). Signal detection analyses typically indicate that this illusion results from poorer discrimination between one and two flashes, which is attributed to multisensory integration (Knotts & Shams 2016; McCormick & Mamassian 2008; Pérez-Bellido et al. 2015; Rosenthal et al. 2009; Wozny et al. 2008). Some studies implicate a shift in the criterion measure, which indicates a sound-induced bias to report more flashes (McCormick & Mamassian 2005; McCormick & Mamassian 2008; Pérez-Bellido et al. 2015). However, the criterion measure does not differentiate between perceptual and decisional sources of bias for a discrimination task such as the sound-induced flash illusion (Witt et al. 2015; Witt et al. 2016).

Older adults more frequently report illusory flash doubling, indicating an age-related increase in susceptibility to the sound-induced flash illusion (De Loss et al. 2013; McGovern et al. 2014; Setti et al. 2011). Older adults also perceive the sound-induced flash illusion at larger temporal offsets between auditory and visual stimuli than younger adults (McGovern et al. 2014; Setti et al. 2011). This may relate to the widening of the temporal binding window with age (e.g. Chan et al. 2014a; Noel et al. 2016), since younger adults with wider temporal binding windows also experience illusory flashes more frequently (Stevenson et al. 2012).

In a related illusion known as flash fusion, two flashes accompanied by a single beep are perceived as one flash (Andersen et al. 2004). The sound-induced fusion of multiple flashes into one is age-invariant (McGovern et al. 2014). For illusory fusion, neural activity decreases in the primary visual cortex whereas the inverse (i.e. increased neural activity) occurs for illusory flashes, both in association with activity in the auditory cortex and the superior temporal sulcus (Mishra et al. 2008; Mishra et al. 2007; Watkins et al. 2007). The latency of event related potentials are also longer for illusory fusion, suggestive of distinct cortical mechanisms for each illusion type (Mishra et al. 2008). Therefore, it has been suggested that the mechanisms for flash fusion and fission could be differentially vulnerable to age-related effects (McGovern et al. 2014).
Additionally, the integration of flashes and beeps for their perceived number is sensitive to their relative discriminability (Andersen et al. 2005; Wozny et al. 2008), with individuals experiencing the illusion more frequently when beeps are more audible (Andersen et al. 2005) and when sensitivity to flash number is reduced due to decreased size or eccentric location (Kumpik et al. 2014). Since older adult perception of number is less veridical than in younger adults (Setti et al. 2011), greater susceptibility to the sound-induced flash illusion could also represent a relative loss in flash discriminability with age. However, individual variability in illusion frequency and the related modulation of neural activity in younger adults suggests that the innate tendency to integrate also plays a role (Balz et al. 2016; Mishra et al. 2008; Mishra et al. 2007).

In summary, older adults are more prone to perceiving illusory flashes than younger adults but equally prone to illusory flash fusion. However, the integration strategy for the percept of temporal rate is likely to be different from that of the percept of small numbers. Firstly, except at very slow rates, temporal rate stimuli will contain more peaks per stimulus duration than the small number of pulses (1-3) employed to elicit the sound-induced flash illusions. Neither audition nor vision can individuate pulses presented at rates faster than 10 Hz, giving rise to a percept of amplitude fluctuation rather than individual events to be counted (Edwards & Chang 2013; Joris et al. 2004; Nourski & Brugge 2011; Van De Grind et al. 1973). Consequently, for rates 10 Hz and above, perceived number is inaccurate except for small sets of 2 or 3 pulses in both vision (Cheatham & White 1952; Forsyth & Chapanis 1958) and audition (Cheatham & White 1954). Secondly, dual auditory and visual stimulation produces accurate estimates of number for small stimulus sets (Philippi et al. 2011). For stimulus sets larger than 3, estimates of audiovisual number are increased due to the use of a different, duration-based counting strategy (Philippi et al. 2011). However, auditory driving of perceived flicker rate is independent of stimulus duration, indicating that the effect lies in the percept of rate not the percept of number (Berger et al. 2003). Given the above considerations, age-effects for the sound-induced flash illusion are unlikely to translate directly to temporal rate tasks.

**Age-related changes in the audiovisual bounce effect**

In younger adults, two discs moving towards and then past each other appear to either stream through one another or, less frequently, bounce at the moment they spatially coincide (Roudaia et al. 2013; Sekuler & Sekuler 1999). Bouncing is more frequently reported when a brief sound occurs as the discs overlap (Sekuler et al. 1997) but to a lesser degree in older adults (Roudaia et al. 2013). Multiple lines of evidence suggest that the effect results from
audiovisual integration (Bushara et al. 2003; Donohue et al. 2015; Fujisaki et al. 2004; Grassi & Casco 2009; Grove et al. 2012; Kawachi et al. 2014; Maniglia et al. 2012; Remijn et al. 2004). In fact, modelling demonstrates that the effect is not consistent with independent sensory processing but rather fits a model of integration with a vision-dominated weighted sum of cues (Zhou et al. 2007). While studies do not commonly find decreased integration in older adults, both a decrease in the likelihood of integration due to slower sensory processing (Diederich, Colonius et al. 2008) and a decrease in the amplitude of neural responses (Stephen, Knoefel et al. 2010, Setti, Finnigan et al. 2011) have been reported. The sound-induced bouncing also occurs over a wider temporal window in older adults (Bedard & Barnett-Cowan 2016). This indicates a greater tolerance for audiovisual asynchrony, in general agreement with findings from perceived simultaneity and temporal order tasks (Bedard & Barnett-Cowan 2016; Chan et al. 2014a; Setti et al. 2011; Virsu et al. 2003).

In addition to an age-related decrease in integration, age-related changes in decisional processes and sensory sensitivity could mediate the reduced audiovisual bounce effect in older adults. Control experiments suggested that gross differences in retinal illuminance or sound audibility were unlikely to be the source of the age-related reduction in sound-induced bouncing (Roudaia et al. 2013). However, this does not preclude an effect of age-related visual impairments specific to motion perception, such as attentional tracking (Sekuler et al. 2008) or temporal and spatial integration (Arena et al. 2012; Roudaia et al. 2010). Furthermore, in the study by Roudaia et al. (2013), older age was initially associated with an increase in bouncing responses in the absence of a sound but this age dependent difference was not reproducible when retested (Roudaia et al. 2013). Consequently, age-related differences in sound-induced bouncing could conceivably result from variable response bias, which would indicate a less consistent decision process or noisy sensory encoding (Cabrera et al. 2015). While many studies implicate perceptual processes in the audiovisual bounce effect (Dufour et al. 2008; Sanabria et al. 2004; Watanabe & Shimojo 2001), others indicate a role for inference (Grove et al. 2016; Zeljko & Grove 2016). Currently, this evidence cannot be reconciled and therefore the role of age-related changes in decisional processes in perceived bouncing is uncertain. Further study may clarify to what extent, if any, factors other than integration contribute to the age-related decrease in the audiovisual bounce effect.

Regardless, perceived rate and perceived motion are different aspects of temporal perception. For temporal rate, auditory and visual cues provide redundant information in the same units, which is considered a prerequisite for integration to occur (Ernst & Bülthoff 2004). On the
other hand, auditory and visual cues in the streaming/bouncing display are not commensurate (Zhou et al. 2007). When auditory and visual relative reliability are matched, both contribute equally to the combined temporal rate percept (Roach et al. 2006) but vision still dominates the audiovisual bounce effect (Zhou et al. 2007). Given these differences in the integration process, age-related effects on integration ability may differ between the audiovisual bounce effect and audiovisual rate perception.

Age-related changes in audiovisual speech perception

Speech studies provide further insight into the role of temporal factors in integration in aging. As we articulate speech, the changing distance between our lips temporally corresponds to the auditory amplitude envelope, predominately at slow modulation rates between 2 and 7 Hz (Chandrasekaran et al. 2009). The temporal coherence of mouth movements with the acoustic envelope of speech facilitates the detection (Alsious & Munhall 2013; Grant & Seitz 2000), recognition (Jaekl et al. 2015) and neural representation of auditory speech (Crosse et al. 2015; Crosse et al. 2016; Golumbic et al. 2013; Park et al. 2016). As such, studies investigating audiovisual speech perception in older adults are relevant to the general question of whether aging alters the integration of temporal information. However, auditory speech contains temporal modulations in spectral frequency in addition to modulations in amplitude (Singh & Theunissen 2003). Furthermore, it should also be noted that the perception and neural processing of audiovisual speech is influenced not just by the spectrotemporal structure of the auditory cue but also awareness of its linguistic meaning (Eskelund et al. 2011; Lee & Noppeney 2011; Stekenburg & Vroomen 2012; Tuomainen et al. 2005).

There is a large body of literature that has looked at speech perception in older adults when auditory and visual modalities supply congruent information. Older adults are less able to detect audiovisual speech and exhibit less crossmodal enhancement when detecting speech than younger adults (Tye-Murray et al. 2011). In contrast, the ability to integrate auditory and visual cues for the recognition of speech is retained in older age (Ballingham & Cienkowski 2004; Gordon & Allen 2009; Huyse et al. 2014; Legault et al. 2010; Smayda et al. 2016; Sommers & Phelps 2016; Sommers et al. 2005; Spehar et al. 2008; Tye-Murray et al. 2010; Winneke & Phillips 2011). Despite age-equivalent perceptual measures of integration for speech recognition, the integration process may be more efficient in older adults, as there is an age-related increase in the multisensory facilitation of neural responses to speech (Winneke & Phillips 2011). However, physiological aging does result in impaired recognition of audiovisual speech (Dey & Sommers 2015; Gordon & Allen 2009; Sommers et al. 2005; Stevenson et al.

However, there is an interaction between physiological aging and clarity in the integration of auditory and visual speech. Unlike younger adults, older adults do not display crossmodal enhancement in the detection of auditory speech when visual speech cues are degraded (Tye-Murray et al. 2011). Audiovisual speech recognition is also more adversely affected in older than in younger adults by degrading the quality of auditory and visual cues (Tye-Murray et al. 2008). While lipreading is equally impaired by blur in both age groups (Legault et al. 2010; Tye-Murray et al. 2016), age differences in the degree of integration that are absent under easy listening conditions (Legault et al. 2010) emerge when the auditory cue is degraded by greater levels of background noise (Gordon & Allen 2009). Older adults also demonstrate lower levels of integration (Huyse et al. 2014; Tye-Murray et al. 2010) and greater weighting of auditory cues (Huyse et al. 2014) when the contrast of visual speech is reduced. As for auditory clarity, multisensory gains in speech recognition are selectively reduced in older adults at low signal to noise ratios for auditory words (Stevenson et al. 2015).

The body of literature on audiovisual speech perception in aging also considers incongruent cues. When conflicting auditory and visual syllables are paired together, observers may perceive the auditory or visual option but often, in the McGurk effect, experience a fused percept that matches neither cue. For example, perception of the spoken syllable "ba" is distorted by the incongruent sight of lip movement corresponding to "ga" to give the resulting audiovisual percept of "da" (McGurk & Macdonald, 1976). In one study, older adults were more susceptible to the McGurk effect for syllables even when age-related differences in the intelligibility of auditory speech were normalised at the group level (Sekiyama et al. 2014). In another study, older adults also more frequently reported fused responses to incongruent auditory and visual words that were equally identifiable at the group level when presented on their own (Setti et al. 2013). In contrast, the age-related increase in susceptibility to the
McGurk effect was not reproduced in other studies (Ballingham & Cienkowski 2004; Cienkowski & Carney 2002; Huyse et al. 2014; Stothart & Kazanina 2016), three of which accounted for age-differences in auditory speech intelligibility at the individual level by adjusting signal to noise ratios (Ballingham & Cienkowski 2004; Huyse et al. 2014) or scaling to the listener’s hearing threshold level for speech (Stothart & Kazanina 2016). Incongruously, the amplitude of the neural signal to incongruent audiovisual speech in the STS is slightly reduced in older adults (Baum & Beauchamp 2014), which is associated with less susceptibility to the illusion in younger adults (Nath & Beauchamp 2012).

These conflicting study outcomes may be reconciled by considering the substantial individual variability in the McGurk effect, which suggests that the mean frequency of fused responses between age groups may be an inadequate measure of age-related changes in the tendency to integrate incongruous auditory and visual speech (Basu Mallick et al. 2015). In younger adults, individual differences in the temporal binding window (Stevenson et al. 2012), sensitivity to audiovisual disparity and internal noise of disparity encoding (Magnotti & Beauchamp 2015), individual ability to lipread and correctly distinguish congruent and incongruent speech (Strand et al. 2014) and time spent gazing at the speaker’s mouth (Buchan & Munhall 2011; Gurler et al. 2015) all contribute to variability in susceptibility to the McGurk effect. Additionally, visual modulation of the auditory syllable percept may occur even if the participant ultimately decides that the syllable they perceive is most consistent with the auditory-alone component (Brancazio & Miller 2005). Consequently, limiting analysis to the frequency of McGurk responses may underestimate the frequency of audiovisual interactions (Brancazio & Miller 2005).

Overwhelmingly, most studies on audiovisual speech perception suggest no age-related changes in integration occur (Ballingham & Cienkowski 2004; Cienkowski & Carney 2002; Gordon & Allen 2009; Huyse et al. 2014; Legault et al. 2010; Smayda et al. 2016; Sommers & Phelps 2016; Sommers et al. 2005; Spehar et al. 2008; Stothart & Kazanina 2016; Tye-Murray et al. 2010; Winneke & Phillips 2011) unless auditory or visual clarity is greatly reduced, which decreases integration in older adults (Gordon & Allen 2009; Huyse et al. 2014; Stevenson et al. 2015; Tye-Murray et al. 2010; Tye-Murray et al. 2011). However, despite the contribution of temporal correspondence between auditory and visual cues in audiovisual speech perception (Alsius & Munhall 2013; Golumbic et al. 2013; Grant & Seitz 2000; Jaekl et al. 2015), the higher order processes that play a role in speech perception also interact with age. Age-related differences in the integration of audiovisual speech are influenced by semantic content.
(Maguinness et al. 2011; Smayda et al. 2016) and lexical difficulty (Dey & Sommers 2015). There are also age-related differences in listening effort (Gosselin & Gagné 2011; Sommers & Phelps 2016) and inhibitory control (Dey & Sommers 2015; Kuchinsky et al. 2012) for audiovisual speech. Furthermore, correlation between audiovisual speech recognition for syllables, words and sentences is low, suggestive of different underlying mechanisms of integration (Sommers et al. 2005). These may be differentially affected by the aging process, as multisensory facilitation of speech perception is selectively reduced for whole words but not their constituent syllables at low signal to noise ratios (Stevenson et al. 2015). Consequently, the likely impact of older age on audiovisual temporal rate perception cannot be clearly extrapolated from studies on audiovisual speech.

Conclusion

In summary, integration is decreased for the audiovisual bounce affect (Roudaia et al. 2013) and speech detection (Tye-Murray et al. 2011) in older adults. However, conversely, older adults exhibit increased integration for sound-induced flash fission (De Loss et al. 2013; McGovern et al. 2014; Setti et al. 2011), the temporal ventriloquist effect (De Boer-Schellekens & Vroomen 2014) and the tolerance of audiovisual asynchrony (Chan et al. 2014a; De Boer-Schellekens & Vroomen 2014; Hay-Mccutcheon et al. 2009; McGovern et al. 2014; Noel et al. 2016; Setti et al. 2011; Virsu et al. 2003). Moreover, integration is maintained for speech recognition (Ballingham & Cienkowski 2004; Gordon & Allen 2009; Huyse et al. 2014; Legault et al. 2010; Smayda et al. 2016; Sommers & Phelps 2016; Sommers et al. 2005; Spehar et al. 2008; Tye-Murray et al. 2010; Winneke & Phillips 2011), the McGurk effect (Ballingham & Cienkowski 2004; Cienkowski & Carney 2002; Huyse et al. 2014; Stothart & Kazanina 2016) and sound-induced flash fusion (McGovern et al. 2014) in aging. This suggests that age-related changes in the integration of temporal information do not occur via a common universal mechanism, consistent with task-specific rather than global age-related effects on audiovisual perception. In the face of these conflicting findings, it is difficult to predict whether older age is likely to increase, decrease or have no effect on the ability to integrate auditory and visual rates.
Age-related sensory loss

Defining normal vision and hearing

Age-related changes to the auditory and visual pathways extend from the sensory periphery to the cerebral cortex. Within the ear, spiral ganglion cell loss (Felix et al. 2001; Makary et al. 2011; Viana et al. 2015) and synaptic degeneration (Viana et al. 2015) occurs in the human cochlea even in older adults with normal hearing and/or normal hair cell counts. Within the eye, older age affects both optical factors – such as decreased pupil size (Hennelly et al. 1998; Winn et al. 1994), increased lens density and thickness (Alió et al. 2005; Sample et al. 1988; Xu et al. 1997) and increased light scatter (Hennelly et al. 1998; Martínez-Roda et al. 2016; Siik et al. 1992) – and also causes loss of cell number and integrity within the retina, affecting the retinal pigment epithelium, photoreceptors and ganglion cells (Bonilha 2008; Gao & Hollyfield 1992; Harman et al. 2000; Shelley et al. 2009). Altogether, the quality of the sensory input encoded by the aging eye and ear is degraded. Structural and functional changes also occur within the auditory subcortex (Konrad-Martin et al. 2012; Lutz et al. 2007). Centrally, age-related changes in structure and integrity occur within both the visual (Chang et al. 2015) and auditory cortex (Lutz et al. 2007; Profant et al. 2014). Since the earliest sites of intersensory interaction are the subcortex or sensory cortex (Driver & Noesselt 2008; Ghazanfar & Schroeder 2006), age-related changes in the preliminary processing of auditory and visual input occur before integration is possible.

Unfortunately, the definition of what constitutes normal hearing and vision is not consistent and the boundary between age-related and pathological changes is at times indistinct (Owsley 2011; Owsley et al. 2016), complicating comparison between different studies. Underutilisation of health care services (Bylsma et al. 2004; McGwin et al. 2010; Müller et al. 2006; Wang et al. 1999) and increased prevalence of hearing loss and eye disease with age (Cruickshanks et al. 2003; Wang et al. 2000) may cause unnoticed mild dysfunction (Attebo et al. 1996; Bylsma et al. 2004; Fong et al. 2009; Klein et al. 1999; Müller et al. 2006; Sindhusake et al. 2001; Uchida et al. 2000). As a result, self-report is likely an unreliable indicator of sensory status (El-Gasim et al. 2012; Kamil et al. 2015; Scudder et al. 2003). However, the basic screening measures of visual acuity and audiometric thresholds, which tend to be reduced in older age even when within normal ranges (Elliott et al. 1995; Gates et al. 2008; Gordon-Salant 2005; Jay et al. 1987; Lindenberger & Baltes 1994; Owsley et al. 1983; Pitts 1982), are poor indicators of other aspects of auditory function (Plack et al. 2014) and visual function,
particularly under conditions of low luminance or contrast (Haegerstrom-Portnoy et al. 1999; Haegerstrom-Portnoy et al. 2000). A gamut of sensory changes occur in healthy aging (for review see Faubert 2002; Fitzgibbons & Gordon-Salant 1996; Owsley 2011; Stach et al. 2009), affecting the perception of basic properties of an audiovisual stimulus such as spectral and temporal content (Fitzgibbons & Gordon-Salant 1996; Gordon-Salant 2005), luminance, colour and contrast (Faubert 2002; Haegerstrom-Portnoy et al. 2000).

Presenting the same physical stimuli to a sample of younger and older adults that passed a basic sensory screening is representative of audiovisual experience in an older adult population, but doesn’t elucidate any potential role of subtle age-related sensory loss. Consequently, for a given experiment, task-specific measures will be more sensitive to the mild sensory changes that may affect how older adults perceive suprathreshold experimental stimuli. The subtle changes that occur in auditory and visual temporal perception are discussed in detail below, followed by a discussion of the potential implications of age-related sensory loss on the way auditory and visual stimuli are integrated by older adults.

Auditory temporal perception in aging

Age-related decline in spectrotemporal processing is evident even in older adults with normal audiometric thresholds. Difference limens for discriminating between pure tones with different frequencies are elevated in older adults (Clinard et al. 2010; He et al. 1998; Moore & Peters 1992). Older age also degrades the neural encoding of spectral information, as indicated by a decrease in the amplitude and phase coherence of the frequency-following response, an auditory evoked potential sensitive to the temporal fine structure of a sound (Clinard et al. 2010), though the effect is less at low frequencies (Grose & Mamo 2012). Differences in phase between the left and right ear are also less discriminable to older adults, with a corresponding decrease in the auditory evoked potentials they elicit (Clinard et al. 2010; Grose & Mamo 2010; Ross et al. 2007a). Thresholds for detecting frequency modulation of a pure tone are also elevated in older adults, particularly for a 500 Hz carrier (He et al. 2007). Additionally, older adults are poorer at discriminating changes in the frequency and intensity of a pure tone, more so at 500 Hz than higher frequencies, even when pure tone detection thresholds are comparable across age groups (He et al. 1998). Together, these studies indicate impaired processing of temporal fine structure in aging.

Age-related deficits are also evident at the slower timescale of the envelope of a modulated sound. In older adults with normal hearing, sensitivity to sinusoidal amplitude modulation of a
pure tone is decreased (He et al. 2008; Wallaert et al. 2016). Likewise, sensitivity to sinusoidal amplitude modulation of a broadband or white noise carrier is also decreased in older adults (Ajith Kumar & Sangamanatha 2011; Takahashi & Bacon 1992). The impaired sensitivity to auditory amplitude modulation is more pronounced at high modulation rates (Ajith Kumar & Sangamanatha 2011; He et al. 2008) and impaired sensitivity for high rates emerges earlier in the lifespan than for low rates (Ajith Kumar & Sangamanatha 2011). Furthermore, auditory evoked potentials show that the senescent auditory system has a reduced ability to follow amplitude modulation of higher temporal rates (Grose et al. 2009; Leigh-Paffenroth & Fowler 2006). Detection of broadband modulation becomes bandpass in older adults as thresholds are elevated at 2 Hz, rather than constant between 2 and 8 Hz (Takahashi & Bacon 1992). Older adults are also poorer at detecting gaps between stimuli with modulated amplitude envelopes (Schneider et al. 1998). Older adults also have elevated thresholds for discriminating changes in sound intensity (He et al. 1998), which is related to both the detectability and perceived fluctuation strength of amplitude modulation (Dietz et al. 2013; Wojtczak & Viemeister 1999; Wojtczak & Viemeister 2008).

Other aspects of auditory temporal perception are detrimentally affected in aging. Older adults exhibit impairments in duration discrimination (Ajith Kumar & Sangamanatha 2011; Fitzgibbons & Gordon-Salant 1994; Gordon-Salant & Fitzgibbons 1999; Grose et al. 2006; Ostroff et al. 2003), detection and discrimination of gaps between successive sounds (Ajith Kumar & Sangamanatha 2011; He et al. 1999; Heinrich & Schneider 2006; Humes et al. 2009; Snell 1997; Strouse et al. 1998) and temporal order judgements (Fitzgibbons & Gordon-Salant 1998; Gordon-Salant & Fitzgibbons 1999). Age-related impairments in temporal processing also affect other aspects of auditory perception. For example, poorer spatial perception in older adults is related to the reduced ability to use interaural timing differences to localise sounds (Babkoff et al. 2002; Freigang et al. 2015; Herman et al. 1977). Additionally, reduced speech recognition in older adults is likely mediated by age-related deficits in temporal processing (Fitzgibbons & Gordon-Salant 1996; Füllgrabe et al. 2014).

Visual temporal perception in aging

In healthy adults, older age impairs many aspects of visual temporal perception. The amplitude of the temporal impulse response to a flash of light is decreased in older adults (Shinomori & Werner 2003) with a corresponding decrease in the amplitude of the retinal response recorded with multifocal electroretinography (Gerth et al. 2002). The critical flicker frequency is lower in older compared to younger adults, indicating a loss in temporal resolution (Misiak
In fact, there is a progressive decline in critical flicker frequency with advancing age (Lachenmayr et al. 1994; McFarland et al. 1958; Misiak 1951; Wolf & Schraffa 1964). Comparison of the temporal modulation functions of younger and older adults reveals an age-related reduction in flicker sensitivity (Kim & Mayer 1994; Kuyk & Wesson 1991; Mayer et al. 1988; Tyler 1989), particularly for high flicker rates (Casson et al. 1993; Mayer et al. 1988; Tyler 1989). From middle age, there is a gradual decline in flicker sensitivity with increasing age, with decreased sensitivity for high rates occurring earlier in the lifespan than for low rates (Kim & Mayer 1994). The age-related decline in flicker sensitivity is also greater in the periphery (Casson et al. 1993). Older adult responses are consistent with age-related losses in sensitivity to temporal amplitude modulation rather than temporal resolution or age-related losses in retinal illumination (Kim & Mayer 1994; Kuyk & Wesson 1991; Mayer et al. 1988). Losses in spatiotemporal contrast sensitivity also occur with increasing age, with elevated amplitude modulation thresholds at all temporal rates for stimuli with spatial frequency content (Clark et al. 2010). Additionally, temporally modulating a spatial grating causes decrements in sensitivity to spatial contrast sensitivity in older adults (Clark et al. 2010; Elliott et al. 1990; Tulunay-Keesey et al. 1988; Wright & Drasdo 1985).

As found for audition, the perception of more complex temporal visual stimuli is detrimentally affected by healthy aging. For example, older adults have a reduced capacity to perceive moving visual stimuli (Habak & Faubert 2000; Snowden & Kavanagh 2006). Thresholds for discriminating a gap in time between successive visual stimuli are also elevated in older adults (Humes et al. 2009; Poggel et al. 2008). In temporal order judgement tasks, older adults show a reduced ability to correctly identify the order of sequentially presented visual stimuli (Busey et al. 2010).

Conclusion

Of note is that older age impairs sensitivity to both auditory and visual temporal modulations in amplitude (He et al. 2008; Kim & Mayer 1994; Kuyk & Wesson 1991; Mayer et al. 1988; Tyler 1989; Wallaert et al. 2016). Therefore, older adults need greater modulation depth than younger adults to perceive the fluctuation present in a fluttering pure tone or flickering light. Consequently, the same physical amplitude modulation will be closer to threshold in older adults than it is younger adults. As discussed previously, temporal rate discrimination thresholds are elevated for amplitude modulations of light or sound closer to threshold (Roach...
et al. 2006; Waugh & Hess 1994). As a result, the decreased modulation sensitivity of older age could act to elevate temporal rate discrimination thresholds in older adults, impairing their ability to identify different rates of suprathreshold amplitude changes of light or sound. If this is the case, then the ability of healthy older adults to correctly integrate or segregate auditory and visual stimuli according to rate similarity could be compromised.

**Interaction between age-related sensory loss and integration mechanisms**

*Inversely effective auditory and visual cues in older adults*

Absolute differences in how older and younger adults perceive the auditory and visual components of an audiovisual stimulus may affect how they are perceived in combination. Multisensory theory posits that weaker component signals are inversely effective— that is, they show a greater proportionate change in neural activity upon integration than stronger signals (Meredith & Stein 1983). This has been demonstrated in animal studies evaluating the response of neurons in the superior colliculus receiving input from more than one sensory modality (Meredith & Stein 1986; Stanford et al. 2005). Complementary behavioural facilitation has been demonstrated for orientation, detection and localization tasks in animals and humans, all of which are tasks in which the superior colliculus plays a role (Stein et al. 1988). Imaging of the human cortex shows enhanced neural activity for multisensory stimulation, extending this finding to the cerebral cortex (Diederich & Colonius 2004; Noesselt et al. 2010; Senkowski et al. 2011). Recent work on the superior colliculus of the cat also indicates that the relative salience of auditory and visual stimuli affects the degree of multisensory enhancement, such that enhancement is greatest when saliency is balanced and decreases as it becomes more unbalanced (Miller et al. 2015).

Theoretically, apparently enhanced integration in older age may stem from the interaction of age-related sensory loss with the principle of inverse effectiveness (Freiherr et al. 2013; Mozolic et al. 2012). In older adults, auditory and visual stimuli are likely to be less perceptible due to subtle age-related changes in sensory perception (for review see Faubert 2002; Fitzgibbons & Gordon-Salant 1996; Owsley 2011; Stach et al. 2009). Consequently, the same physical stimuli may be less effective for older relative to younger adults, thereby inducing greater integration effects in older adults. This possibility complicates the question of whether older age increases our capability to integrate. Firstly, this possibility is relevant to the design
of an experiment to specifically assess how aging affects the integration of auditory and visual rates. Flicker and flutter will be less salient to older adults due to the age-related decrease in sensitivity to temporal modulations in amplitude (He et al. 2008; Kim & Mayer 1994). In younger adults, the integration of auditory and visual temporal rhythms follows an inversely effective response pattern (Su, 2014). However, this was shown for a human point-light figure in motion coupled with an irregular auditory pattern and has not been investigated for amplitude modulation at a regular rate. Consequently, it is unclear whether the principle of inverse effectiveness applies to the integration of auditory and visual temporal rates.

Secondly, the possibility that age-related sensory loss may interact with the principle of inverse effectiveness is relevant to the interpretation of existing studies on audiovisual integration in aging. For example, in younger adults, audiovisual facilitation of response times is greater for less intense stimuli that produce slower response times on their own (Corneil et al. 2002; Diederich & Colonius 2004; Nidiffer et al. 2016; Rach et al. 2011; Senkowski et al. 2011). Most studies that found age-related differences in audiovisual gain also reported slower unimodal response times in their older adult participants (Diederich et al. 2008; Hugenschmidt et al. 2009a; Laurienti et al. 2006; Mahoney et al. 2011; Ren et al. 2017; Stephen et al. 2010). In theory, less salient auditory and visual stimuli may have provoked a greater proportionate change in response times in the older relative to younger adults. In keeping with this theory, a subset of older adults, who had fast response times to somatosensory stimuli alone, did not exhibit greater gains when somatosensory and visual stimuli were presented together (Mahoney et al. 2014). Moreover, in older adults, poor visual acuity and vibration sensitivity is associated with greater gains in response times when visual and somatosensory stimuli are presented together rather than separately (Dumas et al. 2016). It is plausible that age-related changes in sensory function may likewise influence audiovisual facilitation of response times in older adults.

However, it is worth noting that the principle of inverse effectiveness has been the subject of recent controversy regarding potential statistical artefacts arising from comparison of relative multisensory gain in different individuals sorted post-hoc according to sensory ability (Holmes & Holmes 2007; Holmes 2009). Furthermore, inverse effectiveness may not universally apply to all aspects of multisensory perception. It has also been identified that multisensory enhancement of performance may be greatest at intermediate stimulus levels, thereby maximising multisensory gains conferred from integration at what may be a more behaviourally relevant level for suprathreshold perceptual tasks such as speech and
localisation (Charbonneau et al. 2013; Ross et al. 2007b). Therefore, the effect of stimulus saliency on the degree of integration is still worthy of consideration as a possible cause of age-related differences, even without the assumption of inverse effectiveness.

Age-related changes in the relative reliability of auditory and visual stimuli

It was once proposed that age related changes in sensory and cognitive function were underpinned by the same generalised changes in cortical structure and function in what is known as the “common cause hypothesis” (Lindenberger & Baltes 1994). Subsequent research suggests that the aetiology of sensory decline in healthy aging within each sensory modality largely results from independent processes since correlation between age-related impairments in audition and vision is generally poor (Hofer et al. 2003; Humes et al. 2009; Lindenberger & Ghisletta 2009). Even within the same modality, different aspects of perception are not related (Cappe et al. 2014; Kidd et al. 2007). Consequently, auditory and visual systems are not expected to be equally vulnerable to age-related physiological deterioration. Note, however, that age-related ocular pathology and hearing loss are associated, though it is unclear whether this reflects shared vulnerability or environmental factors (Klein et al. 2001; Klein et al. 1998; Liew et al. 2007; Schneck et al. 2012).

The direct comparison of complimentary auditory and visual tasks in the same group of older adults often reveals age-related changes that are uneven across the senses. Duration judgement (Lustig & Meck 2011) and speeded detection tasks (Diaconescu et al. 2013) deteriorate more in vision than audition with age. However, older adults are more susceptible to visual distractors during an auditory task than vice versa (Guerreiro et al. 2013; Guerreiro & Van Gerven 2011). With older age, increasing presentation rate reduces fMRI blood oxygen level dependent signals for vision but not audition (Cliff et al. 2013) and event-related potentials are reduced at earlier latencies for visual than auditory stimuli (Čeponienė et al. 2008). It is therefore clear that functional decline differs across many aspects of auditory and visual perception. However, the scarcity of direct comparisons of older adult performance on auditory and visual tasks in the literature makes it difficult to generalize the results of the studies mentioned above to other perceptual tasks. Regardless, the consistent finding of differences between auditory and visual modalities precludes any assumption of equivalent age-effects on other perceptual tasks.

As a result, uneven age-related losses in auditory and visual perception need to be addressed on a task-specific basis to determine what role, if any, such differences play in how older adults
weight sensory input during integration. The quality of information each sensory modality provides varies with their functional specialisation and naturally fluctuates due to sensory and neural noise. As outlined earlier, current theory holds that the brain weights a pair of sensory cues according to their relative reliability to derive the most precise representation as possible of a multisensory object from the information available (Ernst & Bültzhooff 2004; Fetsch et al. 2013; Witten & Knudsen 2005). Much of the research to date on multisensory integration in aging has looked at the collective benefit of auditory and visual information on perception and behaviour under audiovisual conditions, failing to separate the effects of individual sensory modalities on the degree of multisensory integration. If aging differentially affects temporal rate discrimination thresholds (and therefore the precision of temporal rate estimates) in vision and audition, changes in audiovisual perceived rate are possible even if the underlying ability to integrate is unaffected by aging.

Conclusion

Apparent changes in integration with older age may result from the interaction of age-related sensory loss with the innate neural mechanisms of integration, rather than any age-related changes in integrative ability. Physiological aging has the potential to reduce the saliency of auditory and visual cues. According to the principle of inverse effectiveness, if auditory and visual cues are less salient, there will be a greater proportionate change in perception upon their integration. Additionally, on a particular task, older age may degrade the saliency of auditory cues more than visual or vice versa, altering the contribution of audition and vision to the unified, audiovisual percept.
Aims & hypotheses

The main aim of my thesis was to determine whether older age alters how vision and audition interact in the perception of temporal rate. My review of the literature raises several questions about how older age might affect audiovisual rate perception.

Accounting for age-related sensory loss

Aim 1:

To normalise any age-related differences in relative auditory and visual temporal rate discriminability by equating each participant’s precision when discriminating between different flutter rates and when discriminating between different flicker rates

Hypothesis 1:

a) Older adults will have elevated temporal rate discrimination thresholds compared to younger adults
b) Older age will affect temporal rate discriminability in vision and audition unequally

Temporal rate discrimination is poorer for amplitude modulation depths closer to the threshold for detecting the presence of modulation (Roach et al. 2006; Waugh & Hess 1994). In addition to individual variability, healthy older adults require greater modulation depth than younger adults to perceive the fluctuation inherent in a fluttering pure tone or flickering light (He et al. 2008; Kim & Mayer 1994). Therefore, a reasonable hypothesis is that older adults’ reduced modulation sensitivity may be sufficient to impair sensitivity to the rate of suprathreshold amplitude changes in one or both modalities. Post-hoc comparison of mean temporal rate discrimination thresholds under auditory or visual-alone conditions would indicate whether there were significant sensory differences at the group level. However, this thesis aims to explicitly state the role, if any, of low-level sensory factors on how older adults integrate auditory and visual stimuli. Therefore, consideration of individual variability is more instructive. This can be achieved by a priori modulation of the saliency of auditory and visual stimuli at the individual level to remove age-differences.
When auditory and visual rates disagree, distortions in apparent rate occur as a function of both rate discrepancy and relative cue reliability, in accordance with a Bayesian model of integration (Roach et al., 2006). Critically, for a given incongruous rate in one modality, the degree of distortion in perceived rate in the task modality is the same whether the task modality is vision or audition only when auditory and visual reliability is balanced (Roach et al., 2006). Therefore, as an index of integration, rate distortion may be confounded by age-related sensory loss.

When auditory and visual rates agree, facilitation of rate discrimination agrees with the maximum likelihood prediction, which is based on the performance in visual and auditory alone presentations (Koene et al. 2007). Furthermore, the effectiveness of sensory cues in inducing multisensory facilitation is often inversely related to their reliability (Diederich & Colonius 2004; Meredith & Stein 1983; Meredith & Stein 1986; Noesselt et al. 2010; Senkowski et al. 2011; Stanford et al. 2005). Theoretically, this could produce an apparent age-related enhancement in multisensory facilitation of rate discrimination that in fact arose from the interaction of age-related sensory loss with unchanged mechanisms of integration. Therefore, as index of integration, rate discrimination may also be confounded by age-related sensory loss.

The precision of temporal rate discrimination can be equated across audition and vision by varying flutter rate discriminability through the manipulation of auditory amplitude modulation (Roach et al., 2006). Few studies directly compare auditory and visual performance in the same group of older adults, but these studies invariably find that aging asymmetrically affects function in these sensory modalities, although the most adversely affected modality varies by task (Čeponienė et al. 2008; Cliff et al. 2013; Diaconescu et al. 2013; Guerreiro et al. 2013; Guerreiro & Van Gerven 2011; Lustig & Meck 2011). As tasks comparable to those investigated in this thesis have yet to be studied, the literature provides insufficient information to predict whether auditory or visual temporal rate discrimination is likely to be more adversely affected by aging. If visual function declines to a greater extent, then older adults can be expected to require a lower auditory amplitude modulation depth than younger adults to equate rate discriminability across the senses. On the other hand, if auditory function declines to a greater extent, then older adults can be expected to require a greater auditory amplitude modulation depth than younger adults.
Exploring the integration of auditory and visual rates when congruent and incongruent

Aim 2:
To investigate whether older age alters the degree to which asynchronous auditory and visual temporal rates are integrated, irrespective of the effects of age-related sensory decline.

Hypothesis 2:
Older and younger adults will integrate asynchronous auditory and visual rates to the same degree under conditions of normalised auditory and visual rate discriminability

Aim 3:
To investigate whether older age alters the integration of synchronous auditory and visual temporal rate under conditions of normalised auditory and visual rate discriminability

Hypothesis 3:
a) Discrimination of a change in temporal rate based on synchronous flicker and flutter will be equally precise in younger and older adults under conditions of normalised auditory and visual rate discriminability
b) The relative improvement in discrimination precision will be the consistent with statistically optimal integration in both age groups

Furthermore, any investigation of audiovisual rate perception in older adults should explore both congruent and incongruent conditions to more completely characterise and distinguish any potential effects of age. In younger adults, interactions between auditory and visual temporal rate vary depending on whether they provide complimentary or conflicting information. The integration of physically identical auditory and visual rates advantageously increases the precision of temporal rate discrimination (Koene et al. 2007; Recanzone 2003) but resolution of conflicting rates disadvantageously prevents veridical perception of the
auditory and visual rates physically present (Knox 1945; Recanzone 2003; Roach et al. 2006; Shipley 1964).

In other aspects of temporal perception, decreased integration of congruent auditory and visual cues (Roudaia et al. 2013; Tye-Murray et al. 2011) but increased integration of incongruent cues (Bedard & Barnett-Cowan 2016; Chan et al. 2014a; De Loss et al. 2013; McGovern et al. 2014; Setti et al. 2013; Setti et al. 2011) has been reported in aging. However, integration may also be unchanged under both conditions in older adults (Ballingham & Cienkowski 2004; Cienkowski & Carney 2002; Gordon & Allen 2009; Huyse et al. 2014; Legault et al. 2010; McGovern et al. 2014; Smayda et al. 2016; Sommers & Phelps 2016; Sommers et al. 2005; Spehar et al. 2008; Tye-Murray et al. 2010; Winneke & Phillips 2011). This belies a universal effect of aging on audiovisual integration. Since the disparate tasks investigated in aging so far are not related to temporal rate perception, there is no a priori reason to theorise that older adults will be better or worse at integrating auditory and visual temporal rates. Furthermore, the underlying cause of reported differences between younger and older adults is not always clear. Instances of age-related changes in audiovisual perception may simply reflect the interaction of age-related sensory loss with the innate properties of integration mechanisms, such as inverse effectiveness and weighting according to sensory reliability. On the other hand, reports of altered audiovisual perception in older adults may reflect genuine changes in the ability to integrate auditory and visual cues. Consequently, whether age-related changes occur in the integration of auditory and visual temporal rates is an open question.

Conclusion

In summary, my principal hypothesis was that older adults would perceive combined auditory and visual temporal rates differently to younger adults due to age-related changes in audition, vision and possibly the integration process itself. The next chapter details the development of an experimental paradigm for testing this hypothesis.
Chapter 2: Experimental design and method

Introduction

This chapter outlines the method used in Experiment 1 (Chapter 3), which aimed to investigate whether aging altered the perception of audiovisual temporal rate. In accordance with the three aims, this experiment was broken into three parts: first to normalise the precision of auditory and visual temporal rate estimates, second to measure distortions in perceived rate under conditions of audiovisual temporal rate asynchrony and lastly, to measure improvements in rate discrimination under conditions of audiovisual temporal rate synchrony.

Experimental set up

Experimental equipment

The experiment was conducted in a quiet room with dim illumination. Auditory stimuli were presented by speaker (Acoustimass Cube, BOSE, Framingham, MA). Visual stimuli were displayed using a green light emitting diode (LED) that was 1 cm in diameter, subtending 0.7° at the testing distance of 80 cm. The LED sat on top of the speaker, surrounded by a black panel so that spatial cues facilitated the percept of a unified audiovisual object. A chin rest stabilised head position and incorporated appropriate lenses to ensure clear vision if the participants own spectacle correction was inadequate. Participants were instructed to fixate on the LED at all times. A computer keyboard was used to collect responses. This experimental set up is depicted in Figure 2.1.

The experiment used auditory and visual stimuli with a temporal profile of changing amplitude over time at a regular rate. A computer soundcard (SoundBlaster Live: Version 5.12, Creative Technology Ltd, Singapore) drove both the LED and speaker. The soundcard’s digital to analogue converter channels rendered the computer’s digital representation of sound dB level and LED luminance into analogue form as an electric voltage. This was then used to drive the LED and speaker to produce the desired auditory and visual stimuli as cued by the software. This set up enabled the timing of visual and auditory stimuli to be precisely matched since both were governed by the soundcard and therefore set to the computer’s clock. This was an important element of the experimental design as similarities in the timing of sensory cues is
one of the factors that determines whether integration occurs (Lewald et al. 2001; Meredith et al. 1987; Noesselt et al. 2007; Senkowski et al. 2007).

However, soundcards include a high pass filter to block unwanted, heating direct current signals while still reproducing the audible spectrum. As a consequence, this design blocks the comparatively lower temporal rates to which the visual system is sensitive. The soundcard therefore needed to be adapted for use in visual psychophysics. This was achieved using an electric circuit as proposed by Puts et al. (2005). Their approach has been successfully implemented in a number of visual psychophysics experiments (Cao et al. 2006; Cao et al. 2007; Dimitrov et al. 2008; Smithson et al. 2009). LED luminance was specified using a carrier waveform of 2000 Hz, which was within the range of the sound card. The carrier was then amplitude modulated at the desired temporal rate and inputted into the sound card. The soundcard’s output was demodulated to generate the desired temporal rate and the carrier was removed by a low pass filter (Figure 2.2). Software to generate the appropriate waveforms was custom written in Matlab (Matlab R2008a, Mathworks, Natick, MA, USA) and run on a Dell desktop computer.

Figure 2.1: Experimental set up. The observer sits at a distance of 80 cm from a black panel with an LED and speaker at its centre.
Figure 2.2: Schematic diagram of voltage input and output at different stages in the electric circuit. The low pass filter of the sound card is circumvented by encoding the signal to drive the LED as a high frequency carrier amplitude modulated by the desired temporal rate (A). This signal is then amplified (B). The signal required to drive the LED (C) is generated by the demodulator and low pass filter.

Calibration

The incorporation of the demodulator into the experimental circuit results in a nonlinear relationship between input voltage to the LED and output luminance. The equipment was therefore further adjusted to ensure that the desired luminance was being generated for the voltage input.

The LED luminance for various input voltages was measured using a PR-650 SpectraScan photometer (Photoresearch, Chatsworth, CA, USA). The photometer was mounted on a tripod for stability and adjusted so it was horizontally aligned with the LED. Measurements were taken at 30 points across the input voltage range. A minimum of two measurements were taken for each input voltage and then averaged. As shown in Figure 2.3, the relationship between input voltage and luminance output deviated from linearity only at high and low values. This was accounted for by interpolating between plotted points (Figure 2.3) using a Piecewise Cubic Hermite Interpolating Polynomial (PCHIP) with a resolution of 0.001 cd/m² in Matlab (Mathworks, Natick, MA, USA). Using this information, a one dimensional look up table with 256 values was created by calculating the input voltage required to produce a particular luminance output across the entire luminance (Figure 2.4). During experimental runs, the signal sent to the digital-to-analogue converters in the sound card to produce the desired LED luminance was determined by finding the closest value in the look up table.
Experimental stimuli

The auditory temporal rate stimulus (a fluttering sound) was produced by sinusoidally amplitude modulating a 65 dB 500 Hz pure tone (Figure 2.5). Note, this differed from the stimulus used by Roach et al. (2006), which consisted of a white noise carrier modulated by a square waveform. A low frequency pure tone was used as a carrier to avoid the effects of age-related hearing loss, which typically manifests at much higher frequencies, in the order of 4000 Hz and above (Gordon-Salant 2005). Since human sensitivity to pure tones varies with frequency, the measurement of sound pressure level was A-weighted to assess the risk of
noise-induced hearing loss (Brown 2002). At the testing distance, the auditory stimulus was 65dB and therefore noise exposure in the course of the experiment was below levels that can damage hearing (Lawton 2003).

**Figure 2.5:** 10 Hz sinusoidal flutter, created by amplitude modulating a 500 Hz pure tone carrier at a rate of 10 Hz and a modulation depth of 0.15.

The visual temporal rate stimulus was a flickering light that sinusoidally varied in luminance over time to a maximum 876 cd/m² (Figure 2.6). This corresponded to a highly salient stimulus, for which the fluctuations in luminance were readily perceptible.

**Figure 2.6:** 10 Hz sinusoidal flicker, created by modulating the luminance of a uniform field at a rate of 10 Hz and a modulation depth of 1.
A standard temporal rate of 10 Hz was used, in accordance with the study by Roach et al. (2006). Using this rate minimised differences in the perceptual quality of flicker and flutter for the temporal rates used in the experiment. This result arises from the fact that 10 Hz corresponds to visual modulation sensitivity near peak performance where the relationship between temporal rate and sensitivity is flattest (Mandler 1984; Waugh & Hess 1994) and also lies in a region of constant sensitivity for auditory modulation sensitivity (He et al. 2008).

### Experimental method

#### Participants

**Recruitment**

Participants were recruited in two groups, which consisted of younger or older adults within the age range 20 to 35 and 60 to 75, respectively. Younger adults were recruited from the University of Melbourne through flyers posted around campus (Parkville, Victoria) and advertisements in the staff newsletter. Previous participants of the lab were contacted if they had expressed an interest in participating in other experiments. Recruitment of older adults followed the same process with the addition of an advertisement also placed in the “The Senior” newspaper (Fairfax Media, Australia) in the January 2012 edition to recruit older adults from the general population. Previous participants recruited in this way by our lab have been active and engaged members of the community.

**Sample size determination**

Though sample size is typically determined by power analysis, there was little information available to inform the choice of an appropriate effect size. Aging effects on integration had not previously been assessed in the area of temporal rate perception. The experimental protocol was based on previous work that consisted of detailed observations on only a small number of observers without regard to their age. Consequently, a power analysis was likely to be inaccurate as there was no reasonable basis for electing a particular effect size. However, age related differences in visual, auditory and audiovisual function have been demonstrated with subject groups of approximately 8-15 participants (De Loss et al. 2013; He et al. 2008; Roudaia et al. 2013; Setti et al. 2013; Weymouth & McKendrick 2012). Therefore, the number of participants recruited was within this range.
Screening procedure

A phone interview screened prospective participants for their suitability for the study. Individuals that reported a history of loud noise exposure, hearing aid use and diseases or medications known to affect vision or hearing on questioning were ineligible to proceed. Eligible participants then attended a first session for further screening to confirm that they met study inclusion criteria. First, a registered optometrist performed an eye examination. Spectacle refraction ensured best corrected vision, which was required to be 6/7.5 or better in both eyes. High refractive error, defined as a spectacle prescription of more than +/- 5.00 D spherical error and -2.00 D astigmatism, was also grounds for exclusion. Appropriate spectacle correction during the experiment was achieved using either the participant’s own glasses or the results of the refraction. For older adults, this included a near addition tailored to the testing distance of 80 cm. Eye disease was excluded by slit lamp biomicroscopy and ophthalmoscopy, which assess anterior and posterior eye health, respectively. Cortical or nuclear changes in the intraocular lens greater than Grade 1 on the lens opacities classification system III scale (Chylack et al. 1993) were grounds for exclusion. Goldmann applanation tonometry was also performed to exclude those with ocular hypertension, defined as intraocular pressure greater than 21 mmHg, due to reduced sensitivity to temporal modulation in these individuals (Breton et al. 1991; Tyler 1981).

Secondly, digital audiometry was performed to exclude prospective participants with hearing loss. A qualified audiologist provided training on how to administer audiometry. Testing was conducted in a room with low ambient noise in which experimental trials were also run. Consistent with epidemiological research, normal hearing was defined as a pure tone average of the thresholds measured for 500, 1000, 2000 and 4000 Hz that was less than or equal to 25 dB (Cruickshanks et al. 2003).

I aimed to exclude individuals with any age-abnormal changes in peripheral sensory processing with this detailed screening and excluded three prospective participants on this basis. Of those that attended a first session, one younger adult was excluded due to a high spectacle refraction. Two older adults were excluded as one was a glaucoma suspect and the other failed the hearing screening. The resulting suitable participants recruited for the study were 11 younger adults (mean 26, range 22-32) and 10 older adults (mean 68, range 60 – 74). Participants typically completed all experimental tasks over three sessions, each of no more than two hours in duration. If experimental tasks were not completed within this time frame, participants attended a fourth session to complete the remaining trials.
Ethics

This research had ethics approval from the University of Melbourne Human Research Ethics Committee, approval number HREC 1034933. All participants gave both verbal and written informed consent after receiving an explanation of the nature and purpose of the experiment. Please see Appendices A and B for copies of the plain language statement and consent form.

Overview

The experimental protocol for this thesis was based on the studies by Roach et al. (2006) and Koene et al. (2007). A series of psychophysical tasks were performed in 3 stages, as summarised in the flowchart (Figure 2.7). Task order was counterbalanced across participants with unimodal tasks preceding audiovisual ones as per the experimental design. Since the precision of auditory and visual rate estimates plays a role in the degree of integration that occurs (Koene et al. 2007; Roach et al. 2006), the first part of the experiment normalised the precision of auditory and visual rate estimates to disentangle age-related sensory loss from age-related changes in integration. A pilot experiment was performed to adapt the approach of Roach et al. (2006) for use on a greater number of participants. The second part of the experiment measured distortions in the auditory temporal rate subjectively equivalent to a standard induced by a conflicting visual rate and vice versa. This was based on the temporal rate judgement task originally developed by Roach et al. (2006). The third part measured bimodal improvements in temporal rate discrimination over unimodal conditions when auditory and visual rates were identical, as in the experiment by Koene et al. (2007).

All tasks were two-interval forced choice with a standard and test interval presented in randomised order. Both stimulus duration and interstimulus interval were 500 ms. Tasks used a method of constant stimuli with seven stimulus levels, each presented 20 times. Presentations were divided into four blocks of five presentations to minimise participant fatigue. Participants responded to each trial at their own pace and were provided with rest breaks between blocks as needed. Practice trials were provided to ensure that subjects understood the task and to aid the determination of the appropriate stimulus range.
Experiment 1A: Equating auditory and visual temporal rate discriminability

<table>
<thead>
<tr>
<th>Vision</th>
<th>Audition</th>
<th>Audition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flicker rate discrimination Threshold: standard deviation (σ)</td>
<td>Amplitude modulation detection Threshold: mean (μ)</td>
<td>Flutter rate discrimination Threshold: standard deviation (σ)</td>
</tr>
</tbody>
</table>

Experiment 1B: Integration of asynchronous flicker and flutter rates

<table>
<thead>
<tr>
<th>Audiovisual- attend audition</th>
<th>Audiovisual- attend vision</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flutter rate discrimination Threshold: point of subjective equality (μ)</td>
<td>Flicker rate discrimination threshold: point of subjective equality (μ)</td>
</tr>
</tbody>
</table>

Experiment 1C: Integration of synchronous flicker and flutter rates

<table>
<thead>
<tr>
<th>Vision</th>
<th>Audiovisual- attend both</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flicker rate discrimination Threshold: standard deviation (σ)</td>
<td>Flicker-flutter rate discrimination Threshold: standard deviation (σ)</td>
</tr>
</tbody>
</table>

Figure 2.7: Flowchart of experiment tasks. Experiment 1A equates the participants’ flutter rate discrimination threshold, measured at various multiples of the participant’s amplitude modulation detection threshold, to their flicker rate discrimination threshold for a visual standard of fixed modulation. In Experiment 1B, the subjective equivalent to a reference temporal rate is determined when judgments are based solely on vision or audition. In Experiment 1C, the temporal rate discrimination threshold for combined flicker and flutter is determined, for comparison to flicker rate discrimination measured in 1A.

Participant thresholds were calculated by fitting a psychometric function to the data collected for each experimental task. The psychometric function was a cumulative Gaussian (Equation 2.1) with its parameters determined using maximum likelihood estimation.

\[
\Psi(x; \mu, \sigma) = \gamma + (1 - \gamma - \lambda) \frac{1}{\sigma \sqrt{2\pi}} \int_{-\infty}^{x} e^{-\frac{(x-\mu)^2}{2\sigma^2}} \, dx
\]

Equation 2.1: The psychometric function \(\Psi\) with guessing rate (γ), lapsing rate \((1 - \lambda)\) and cumulative Gaussian distribution of mean (μ) and standard deviation (σ) (Treutwein, 1995).
Experiment 1A: Equating auditory and visual temporal rate discriminability

Aim:

To normalise any age-related differences in relative auditory and visual temporal rate discriminability by equating each participant’s precision when discriminating between different flutter rates and when discriminating between different flicker rates.

Hypotheses:

a) Older adults will have elevated temporal rate discrimination thresholds compared to younger adults.

b) Older age will affect temporal rate discriminability in vision and audition unequally.

This thesis aimed to measure age-related differences in the integration of auditory and visual temporal rates after accounting for any age-related differences in unimodal sensitivity. Although participants underwent screening tests, basic measures such as visual acuity and audiometric thresholds don’t screen for deficits in temporal processing in older adults (Haegerstrom-Portnoy et al. 1999; Haegerstrom-Portnoy et al. 2000; Plack et al. 2014) since different aspects of perception are largely unrelated (Cappe et al. 2014; Kidd et al. 2007). In light of this, the purpose of Experiment 1A was to approximate the unique amplitude modulation for each participant that equated temporal rate discriminability for 10 Hz flicker and flutter. This amplitude modulation was used in all subsequent audiovisual tasks to allow investigation of integrative ability without the confound of individual differences in auditory and visual sensitivity. The experiment relied on the fact that thresholds for the discrimination of auditory temporal rate vary systematically with modulation depth, permitting indirect manipulation of flutter rate discriminability (Roach et al. 2006). Experiment 1A consisted of two parts: a series of visual and auditory alone tasks (Figure 2.7) and calculation of the desired modulation depth.

Experimental tasks

Flicker rate discrimination

This task determined the threshold for discriminating a change in the temporal rate of 10 Hz flicker. The standard interval contained 10 Hz flicker. In the test interval, flicker rate was varied.
about 10 Hz in seven steps using a method of constant stimuli, with each of the seven rates presented twenty times. The standard and test interval were presented in randomised order. Participants judged whether the first or second interval contained flicker oscillating at a faster rate. The proportion of responses for which the test interval was perceived as oscillating faster was plotted for each of the test interval rates and a psychometric function fit to the data. The flicker rate discrimination threshold was given by the standard deviation of the psychometric function (Figure 2.8B).

Detection of auditory amplitude modulation
Since equivalent discriminability for flicker and flutter requires a low auditory modulation depth (Roach et al. 2006), it was necessary to determine the smallest modulation in amplitude that gave rise to the percept of flutter. Individual participant modulation detection thresholds could then be used to ensure that flutter rate discrimination was measured at suprathreshold amplitude modulations.

In this task, the standard interval contained an unmodulated tone. The test interval contained 10 Hz flutter of variable modulation depth. The standard and test interval were presented in randomised order. Participants judged whether the first or second interval contained the fluttering sound. The proportion of correct responses was plotted for each of the test modulation depths and fitted with a psychometric function. The mean of the psychometric function specified the modulation detection threshold (Figure 2.8A).

Flutter rate discrimination
The flutter rate discrimination task was the auditory analogue of the flicker rate discrimination task. It followed the same format, consisting of a standard interval of 10 Hz flutter and a test interval of variable temporal rate, presented in randomised order. A psychometric function was fit to the data collected and the standard deviation gave the rate discrimination threshold (Figure 2.8B). Unlike the visual task, flutter rate discrimination was performed multiple times with flutter of different modulation depths, each a multiple of the individual participant’s modulation detection threshold.
Figure 2.8: Experimental procedure for Experiment 1A, which equated the temporal rate discriminability of flicker and flutter. All tasks followed a two-interval forced choice, method of constant stimuli format. Psychometric functions shown are from a sample participant data from the younger adult group. A) Detection of modulation in a tone. B) Discrimination of a change in temporal rate. The temporal rate stimulus was either auditory flutter or visual flicker.

*Pilot experiment: Calculating the desired auditory modulation depth*

Roach et al. (2006) modelled the relationship between modulation depth and flutter rate discriminability as a power function by measuring discrimination at seven different modulation depths. However, while appropriate for the 3 participant study by Roach et al. (2006), testing across such a broad range of modulation depths would be impractical for a study with greater participant numbers.

Pilot testing in a single participant confirmed that rate discrimination threshold could be modelled as a power function of modulation depth across a broad range of modulation depths.
(Figure 2.9), despite differences in the stimuli used for this study and that by Roach et al. (2006). Notably, inspection of Figure 2.9 suggests that the relationship could be satisfactorily modelled as a linear function over a more restricted range. Consequently, a pilot experiment was conducted using four additional participants not included in the main experiment in order to determine the viability of an alternate approach to equating rate discriminability using linear regression.

![Graph showing relationship between modulation and discrimination thresholds](image)

Figure 2.9: Relationship between the degree of flutter modulation when expressed as a multiple of the individual’s modulation detection threshold (filled circles) and flutter rate discrimination thresholds for a single pilot participant. The relationship could be described by a power function (solid line; \( y_1 \)) or a linear function over a shorter range (short dashed line; \( y_2 \)). The temporal rate discrimination threshold for 10 Hz flicker is shown (dashed line).

In these four participants, flutter rate discrimination was measured at three distinct modulation depths. The relationship between modulation depth and temporal rate discrimination thresholds was suitably linear in the four pilot subjects, 2 of whom were experienced psychophysical observers not naive to the purpose of the experiment (Figure 2.10). This pilot experiment confirmed that temporal rate discriminability can be similarly matched under the differing experimental conditions using a less time intensive method more suitable for greater subject numbers.
Figure 2.10: Relationship between the degree of flutter modulation when expressed as a multiple of the individual’s modulation detection threshold (filled circles) and the corresponding thresholds for discriminating a change in the temporal rate of 10 Hz flutter for four pilot participants A-D. Participants B & D were naïve observers. The relationship could be adequately approximated with a linear fit (solid line). The temporal rate discrimination threshold for 10 Hz flicker is shown for each participant (dashed line).

Two potential issues emerged from the pilot experiment. $R^2$ values were lower in the two participants naïve to the purpose of the experiment (Figure 2.10B & D). In light of this, the decision was made to measure flutter rate discrimination for an additional modulation depth in the main experiment. From inspection of Figure 2.10, it was also apparent that there was individual variation in the multiples of the modulation detection threshold that corresponded to flutter rate discrimination thresholds close in value to the flicker discrimination threshold. Consequently, one set of multiplying values could not be expected to be appropriate for all participants in the main experiment. On this basis, it was decided that multiplying values would be selected on an individual basis at the experimenter’s discretion. Though this
approach would preclude comparison of flutter rate discrimination between age groups in the main experiment, it served the primary purpose of balancing the relative saliency of the auditory and visual stimuli.

To summarise, in the main experiment, flutter rate discrimination thresholds were obtained for four different modulations. The modulations selected were multiples of each individual’s modulation detection threshold at values where rate discriminability was likely similar across vision and audition. Linear regression was then used to interpolate the desired auditory modulation depth at which flutter rate discriminability matched flicker rate discriminability.

Experiment 1B: Integration of asynchronous (non-identical) flicker and flutter rates

Aim:
To investigate whether older age alters the degree to which asynchronous auditory and visual temporal rates are integrated, irrespective of the effects of age-related sensory decline

Hypothesis:
Older and younger adults will integrate asynchronous auditory and visual rates to the same degree under conditions of normalised auditory and visual rate discriminability

Perceived auditory temporal rate shifts when a concurrent visual stimulus oscillates at a different, asynchronous rate. As a result, the subjective equivalent to a reference auditory rate is non-veridical. Likewise, shifts in perceived visual rate can be induced by asynchronous auditory rates, resulting in non-veridical matches to a reference visual rate (Roach et al. 2006). Experiment 1B measured distortions in the perceived temporal rate of a reference stimulus that physically oscillated at a rate of 10 Hz.

In a two-interval forced choice task, the standard interval contained the reference stimulus of synchronous 10 Hz auditory flutter and visual flicker presented in phase. For the auditory condition, the test interval contained an auditory flutter rate, which varied as a method of constant stimuli, and a fixed task-irrelevant visual flicker rate (Figure 2.11A). Participants indicated which interval fluttered faster, basing their judgments solely on what they heard.
This procedure was repeated for seven task-irrelevant rates (8, 9, 10, 11, 12, 14, and 16 Hz flicker), generating a total of seven psychometric functions. The mean of each psychometric function corresponded to the point of subjective equality, the physical test rate of flutter that was subjectively equivalent to the 10 Hz reference for a particular task-irrelevant rate (Roach et al. 2006). A visual condition was the reverse of the auditory condition, where participants based their judgements solely on a variable test rate of visual flicker in the presence of asynchronous auditory flutter (Figure 2.11B). This was repeated for the same range of task-irrelevant rates as the auditory condition (8, 9, 10, 11, 12, 14, and 16 Hz flutter). The mean of each psychometric function corresponded to the physical test rate of flicker that was perceptually equivalent to the 10 Hz reference. As demonstrated by Roach et al. (2006), a slow task-irrelevant rate results in a point of subjective equality faster than 10 Hz (Figure 2.11A) and a fast task-irrelevant rate results in a point of subjective equality slower than 10 Hz (Figure 2.11B).

A select range of task-irrelevant rates were chosen to capture the features of the relationship between audiovisual rate asynchrony and perceived rate revealed by the detailed testing of Roach et al. (2006). For task-irrelevant rates in the range 8 to 12 Hz, increasing distortion of perceived rate occurs with increasing rate asynchrony but in a manner consistent with partial audiovisual integration, rather than a model of maximum likelihood estimation (Roach et al. 2006). Experiment 1B aimed to contrast this characteristic in younger and older adults by testing densely in this range. However, for larger audiovisual discrepancies, increasing rate asynchrony results in a declining effect on the point of subjective equality, modelled as the influence of the likelihood that auditory and visual rates correspond (Roach et al. 2006). Since this characteristic is approximately symmetric for fast and slow task-irrelevant rates, Experiment 1B tested only one side with additional task-irrelevant rates at 14 and 16 Hz. The range of rates tested was restricted to minimize differences in the perceived depth of amplitude modulation with changing temporal rate (Mandler 1984; Marks 1970), and to avoid the fused perception of roughness (rather than flutter) that occurs at higher temporal rates for auditory stimuli (Fastl 1997).
Figure 2.11: A) Auditory asynchronous task: flutter discrimination in presence of task-irrelevant flicker rates of 10 Hz (black) and 8 Hz (grey). Vertical lines indicate the temporal rate subjectively equivalent to the 10 Hz flutter standard (the perceived match). B) Visual asynchronous task: Flicker discrimination in presence of task-irrelevant flutter rates of 10 Hz (black) and 12 Hz (grey). Vertical lines indicate the temporal rate subjectively equivalent to the 10 Hz flicker standard (the perceived match). Psychometric functions shown are from a sample participant in the younger adult group.
Experiment 1C: Integration of synchronous (identical) flicker and flutter rates

Aim:

To investigate whether older age alters the integration of synchronous auditory and visual temporal rate under conditions of normalised auditory and visual rate discriminability

Hypotheses:

a) Discrimination of a change in temporal rate based on synchronous flicker and flutter will be equally precise in younger and older adults under conditions of normalised auditory and visual rate discriminability

b) The relative improvement in discrimination precision will be the consistent with statistically optimal integration in both age groups

Integration of identical, equally reliable auditory and visual rates improves temporal rate discrimination over visual alone performance (Koene et al. 2007). The original experiment by Koene et al. (2007) manipulated cue reliability by adjusting signal to noise ratios. However, for consistency with Experiment 1B, Experiment 1C used the Roach et al. (2006) method of adjusting auditory amplitude modulation.

Experiment 1C consisted of a single audiovisual rate discrimination task. The standard interval contained 10 Hz flicker and flutter presented in phase as a reference. The test interval contained flicker and flutter, both oscillating at one of seven possible test rates using a method of constant stimuli. Participants indicated which interval contained the faster rate of fluctuation, basing their judgements on both what they heard and what they saw. The standard deviation of the psychometric function gave the audiovisual rate discrimination threshold (Figure 2.12). Audiovisual rate discrimination thresholds were then compared to each participant’s threshold for flicker rate discrimination, which was obtained in Experiment 1A.
Conclusion

Manipulating auditory amplitude modulation is a viable means of controlling the relative precision of auditory and visual temporal rate estimates (Experiment 1A). Once individual differences in sensory sensitivity are controlled in this way, the point of subjective equality in the asynchronous task (Experiment 1B) and change in temporal rate discrimination thresholds in the synchronous task (Experiment 1C) serve as quantitative measures of integration to contrast in younger and older adults. In the next chapter, the results of Experiment 1 are presented and discussed, to establish whether age-related changes in auditory, visual and integrative abilities influence how older adults perceive audiovisual temporal rate.
Chapter 3: Experiment 1

Introduction

To review, the main aim of my thesis was to determine whether older age alters how vision and audition interact in the perception of temporal rate. My principal hypothesis was that older adults would perceive combined auditory and visual temporal rates differently to younger adults due to age-related changes in audition, vision and possibly the integration process itself. Integration is known to change our perception of the rate of amplitude modulation of auditory flutter and visual flicker - altering the apparent rate of oscillation (Roach et al. 2006) and our ability to discriminate between different rates (Koene et al. 2007). The sensory modality that can discriminate rate with greater precision contributes more to the integrated percept of auditory and visual temporal rates (Roach et al. 2006). If sensory loss in healthy aging impairs sensitivity to the rate of suprathreshold amplitude changes to different extents in vision and audition, this is likely to alter the relative influence of audition and vision on temporal rate perception. Age-related changes in the degree of integration are also known to occur (Chan et al. 2014a; De Boer-Schellekens & Vroomen 2014; De Loss et al. 2013; McGovern et al. 2014; Noel et al. 2016; Sekiyama et al. 2014; Setti et al. 2013; Setti et al. 2011) (Roudaia et al. 2013; Tye-Murray et al. 2011). Therefore, changes in sensory reliability must be separated from any changes in the integration process itself in order to understand how older adults achieve a coherent percept of auditory and visual temporal rate information.

To test this hypothesis, I developed an experimental procedure based on the approach of Roach et al. (2006). As the previous chapter outlines, this entailed first testing vision and audition separately and then normalising any individual differences in sensitivity between the senses. Subsequent testing under normalised conditions then probed the underlying ability to integrate auditory and visual temporal rate (Roach et al. 2006). In this chapter, audiovisual temporal rate perception is compared in a group of younger and older adults using this experimental procedure. In this way, the effect of aging on vision, audition and integration ability are disentangled to arrive at an improved understanding of how audiovisual temporal rate perception changes with advancing age.
Experiment 1A: Equating auditory and visual temporal rate discriminability

Aim:
To normalise any age-related differences in relative auditory and visual temporal rate discriminability by equating each participant’s precision when discriminating between different flutter rates with their precision when discriminating between different flicker rates

Hypotheses:

a) Older adult will have elevated temporal rate discrimination thresholds compared to younger adults

b) Older age will affect temporal rate discriminability in vision and audition unequally

Task overview
The first auditory task was a modulation detection task. The measured threshold was used to enable the flutter rate discrimination tasks to be completed at four suprathreshold modulations. A single visual task determined discriminability of the flickering standard. Since pilot data demonstrated that flutter rate discriminability varies approximately linearly with auditory modulation depth over the restricted range used in this experiment (see Chapter 2), a linear regression was fit to the auditory data. The linear regression was then used to interpolate the auditory modulation depth that rendered changes in flutter temporal rate equally discriminable to changes in the flicker rate of the visual standard (Figure 3.1). The modulation depth determined for each participant was used in all subsequent audiovisual tasks to normalise individual differences in auditory and visual sensitivity. Further description of these experimental tasks can be found in Chapter 2, which details the full method for Experiments 1A, 1B and 1C.
Analysis

Statistical testing was carried out using SPSS (Version 22, IBM Inc., New York, NY, USA) and plots generated using SigmaPlot (Version 11, Systat Software, Inc. San Jose, CA, USA). Nonparametric statistical tests were employed where the data was not normally distributed, as determined by the results of the Shapiro-Wilk test and inspection of normal probability plots.

Results

Flicker rate discrimination

Figure 3.2 displays the thresholds for discriminating between different flicker rates in comparison to a reference rate of 10 Hz. There was no significant difference in mean flicker rate discrimination thresholds between age groups ($t(19)=1.2, p=0.25$). Older adults are therefore able to estimate the temporal rate of the 10 Hz visual standard as precisely as younger adults.
Detection of auditory amplitude modulation

As Figure 3.3A shows, the median modulation detection threshold was elevated in older adults, who generally required auditory amplitude modulation of greater depth to appreciate flutter (Mann Whitney, $U=17$, $p=0.008$).

Equating flicker and flutter rate discriminability

As Figure 3.3B shows, the median auditory modulation depth required to match the discriminability of flicker and flutter temporal rate changes was approximately twice as large as the younger adult median. Older adults tended to require greater auditory amplitude modulation (Mann-Whitney, $U=18$, $p=0.01$). The modulation for a match also appears differently distributed in each age group, with the younger adults mostly clustered at low modulations with a skew towards greater modulations (kurtosis: 4.6 skew: 1.9). In contrast, older adults displayed greater heterogeneity, and a few achieved a match at values more typical of a younger adult (kurtosis: -0.2 skew: -0.6). Given the differences in distribution shape across age groups, the Mann-Whitney test indicates that there was a difference in mean rank (having ranked the data from low to high values) for younger and older adults, but this cannot be used to infer a difference in group medians (Hart 2001).
Figure 3.3: Individual participant data (open circles) and box plots of A) modulation detection thresholds (%) for discriminating 10 Hz sinusoidal amplitude modulation of a 500 Hz pure tone from the unmodulated tone, B) modulation (%) required to match flicker and flutter temporal rate discriminability at the standard rate of 10 Hz, and C) modulation required for a match when expressed as a multiple of the participant’s modulation detection threshold. Median (central line), interquartile range (box) and 10th and 90th percentiles (whiskers) are shown in all box plots.
However, the data provides some evidence that older adults may not have required more modulated flutter due to a primary deficit in discriminating between different flutter rates. More older adults had modulations for a match similar to that of younger adults when the match was expressed as a multiple of each individual’s threshold, as Figure 3.3C demonstrates. Correspondingly, any differences between younger and older adult distributions of modulations for a match expressed in this way did not reach statistical significance (Mann-Whitney, $U=29, p=0.07$). While not definitive, this suggests that the relative impairment in auditory rate discriminability may stem from the age-related reduction in sensitivity to auditory amplitude modulation.

**Supplementary analysis**

The approach of approximating flicker and flutter rate discriminability using linear regression was based on initial exploration of suitable methods in younger adults (see Chapter 2). To supplement the above analysis, the relationship between modulation depth and flutter rate discrimination thresholds was compared across age groups by analysing the slope of the linear fits. As Figure 3.4 displays, the degree to which temporal rate discrimination thresholds improved for increasingly modulated auditory flutter was the same in younger and older adults (Mann-Whitney $U=36.5, p=0.21$).

![Figure 3.4](image)

Figure 3.4: Individual results (open circles) and box plot for the slope of the linear regression, specifying the change in temporal rate discrimination threshold per unit of percentage modulation.

**Summary**

Taken together, the results of Experiment 1A support the hypothesis that older age would affect temporal rate perception to different extents in the auditory and visual sensory modalities. Older adults retained the ability to discriminate temporal rate for the 10 Hz
flickering standard, but the age-related decline in sensitivity to auditory amplitude modulation impaired temporal rate discrimination for 10 Hz flutter.

Discussion

**Flicker rate discrimination**

The mean threshold for flicker rate discrimination for younger adults was similar to previous findings for stimuli with either uniform luminance or spatial frequency content modulated at 10 Hz (Hammett & Smith 1992; Mandler 1984; Waugh & Hess 1994). To my knowledge, the effect of older age on flicker rate discrimination has not been studied. The percept of flicker corresponds to amplitude modulation of the luminance of a visual stimulus. The age-related decrease in temporal contrast sensitivity renders this change in amplitude less visible to older adults (Wright 1985; Mayer et al. 1988; Kim and Mayer 1994). Contrary to expectations, this did not impede discrimination of the rate of amplitude change. It should be noted that the flickering visual standard was a bright, highly modulated LED. As such, reduced sensitivity to amplitude modulation may not have affected rate discriminability in older adults as contrast responses were likely saturated for a stimulus of such a high temporal contrast. Since flicker rate discriminability is poorer for flicker with temporal contrast closer to detection threshold (Hess & Plant 1985; Waugh & Hess 1994), it’s possible that older adults may show poorer discriminability than younger adults for less modulated flicker.

**Detection of auditory amplitude modulation**

Younger adult thresholds for detection of amplitude modulation are in general agreement with previously reported thresholds, which span ~2 – 5% when a pure tone carrier is modulated at rates near 10 Hz (Demany & Semal 1986; Zwicker 1962). Direct comparison is not possible as thresholds vary not only with modulation rate but also sound level and duration (Demany & Semal 1986; Zwicker 1962). For older adults, a decrease in sensitivity to sinusoidal amplitude modulation is typically reported for higher temporal modulation rates for both pure tone and white noise carriers (Ajith Kumar & Sangamanatha 2011; He et al. 2008). Auditory steady state responses, which provide an electrophysiological measure of neural entrainment to the rate of sinusoidal amplitude modulation, also highlight an impairment at high temporal rates (Grose et al. 2009; Purcell et al. 2004) that is absent at the moderate rate of 40 Hz (Boettcher et al. 2001).

However, the temporal modulation transfer function, which describes how sensitivity changes with temporal rate, does suggest that modulation detection thresholds for older adults begin
to diverge from younger adult levels for modulation rates greater than the 5 Hz for a 500 Hz carrier (He et al. 2008). For a 500 Hz carrier, greater amplitude modulation detection thresholds have also been reported for modulation rates of 2 and 20 Hz in older compared to younger adults (Wallaert et al. 2016). Direct comparison of modulation detectability for 10 Hz is not possible since neither He et al. (2008) or Wallaert et al. (2016) tested densely at low modulation frequencies. Results from Takahashi and Bacon (1992) suggest that the temporal modulation transfer function for sinusoidally modulated white noise becomes band pass in shape in older adults due to a loss in sensitivity at 2 Hz. In keeping with this, cross-sectional assessment of modulation sensitivity for white noise across different age ranges demonstrates a reduced sensitivity for low rates with advancing age (Ajith Kumar & Sangamanatha 2011). However, impaired sensitivity for high rates emerges earlier in physiological aging (Ajith Kumar & Sangamanatha 2011). As such, my finding of impaired sensitivity at 10 Hz for a 500 Hz carrier provides further evidence that deficits in modulation sensitivity do occur even for slow modulation rates in older adults.

Another consideration is the magnitude of amplitude modulation used in this experiment (mean 20% in older adults) since steady state amplitudes are increased for greater modulation depths (Boettcher et al. 2001). Therefore, the low temporal rate impairment found in older adults may reflect both the temporal modulation rate and depth of amplitude modulation since both were atypical of auditory aging research. Note, however, that both slight modulations in amplitude and slow modulation rates have ecological relevance since they feature in natural scenes and human speech (Attias & Schreiner 1997; Chandrasekaran et al. 2009; Nelken et al. 1999; Singh & Theunissen 2003).

*Relative temporal rate discriminability*

The physical auditory stimulus that equated flutter and flicker rate discrimination was more modulated in older adults. However, the auditory modulation depth required was comparably supratreshold (in relation to amplitude modulation detection) across age groups. By design, flutter rate discrimination was assessed at individually determined modulation depths and cannot be directly compared between age groups. Flutter rate discrimination, however, improved at the same pace per unit of increasing percentage modulation in younger and older adults. Altogether, this implies that poorer discrimination of flutter rate in older adults doesn’t result from difficulty identifying the rate of oscillation but rather because modulations in amplitude are less perceptible. This is consistent with findings at higher amplitude modulation
rates, where reduced sensitivity to amplitude modulation impairs temporal rate discrimination (Grant et al. 1998; Patterson et al. 1978).

Regardless, older age degraded how precisely temporal modulation rate was specified in audition but not vision, altering the relative reliability of these two sources of sensory information. This adds to the body of literature that highlights an unequal age-related decline in perception and neural processing across these sensory modalities (Čeponienė et al. 2008; Cliff et al. 2013; Guerreiro et al. 2013; Guerreiro & Van Gerven 2011; Lustig & Meck 2011). In the temporal domain, the only auditory stimulus used so far has been human speech, which also contains modulations in the frequency of the spectral content (Singh & Theunissen 2003). Cliff et al. (2013) looked at fMRI blood oxygen level dependent signals in older adults in response to increasing presentation rates of auditory (30 - 90 words spoken per minute) and visual stimuli (checkerboard with 2 - 8 Hz rate of reversal). While signals declined in older adults with increasing presentation rates of visual but not auditory stimuli, a cross-section of signal strength found that only auditory signals decreased as a function of increasing age. In contrast, word recognition is degraded by increasing the rate at which words are spoken but not by increasing the rate at which text is displayed (Humes et al. 2007). In my experiment, an age-related impairment specifically in auditory relative to visual rate perception was demonstrated using simple temporal stimuli.

Animal studies demonstrate deficits in the neural coding of temporal information within the visual system in the primary visual cortex (Zhang et al. 2008) and middle temporal area with age (Yuan et al. 2014). Within the auditory system, aging impairs temporal rate processing in the dorsal cochlear nucleus (Schatteman et al. 2008) and the inferior colliculus (Herrmann et al. 2017; Palombi et al. 2001; Walton et al. 2002). While temporal rate processing has not been investigated in the auditory cortex, there is evidence of age-related impairments in temporal processing speed (Mendelson & Lui 2004; Mendelson & Ricketts 2001). It has been noted that this auditory impairment in temporal rate processing is consistent with reduced glycinergic and GABAergic inhibition (Backoff et al. 1999; Caspary et al. 2002), which is a feature of aging throughout the auditory pathway (for review see Caspary et al. 2008). Though both audition and vision show impaired coding of temporal information in animal studies, the vulnerability of temporal rate processing to aging may differ across the senses.
Summary

Age-related sensory decline was evident in reduced auditory modulation sensitivity and impairment in auditory relative to visual temporal rate discrimination in the older adult participants. The implications of this finding are discussed further in Chapter 5. These results provided a foundation upon which to draw inferences about the effect of older age and age-related sensory decline on integration in the subsequent audiovisual tasks.

Experiment 1B: Integration of asynchronous (non-identical) flicker and flutter rates

Aim:

To investigate whether older age alters the degree to which asynchronous auditory and visual temporal rates are integrated, irrespective of the effects of age-related sensory decline

Hypothesis:

Older and younger adults will integrate asynchronous auditory and visual rates to the same degree under conditions of normalised auditory and visual rate discriminability

Task overview

This task measured the physical test rate of flutter (in the auditory condition) or flicker (in the visual condition) that was perceptually equivalent to a 10 Hz audiovisual reference for a series of task-irrelevant, asynchronous rates in the other sensory modality (see Chapter 2). This rate, known as the point of subjective equality, was given by the mean of the psychometric function. The experimental task is depicted in Figure 3.5 and further details may be found in Chapter 2.
Figure 3.5: Experiment 1B design, depicted here for the visual condition. In a two-interval forced choice task, a standard interval containing 10 Hz flicker and 10 Hz flutter was compared to a test interval that contained a fixed task-irrelevant flutter rate (8, 9, 10, 11, 12, 14 or 16 Hz; here 12 Hz) and a test flicker rate, which varied as a method of constant stimuli. The order of test and standard intervals was randomised across trials. Participants reported which interval flickered faster. The mean of the resultant psychometric function gave the point of subjective equality (grey dashed line), the temporal rate perceived to match the 10 Hz reference (black dashed line). The auditory condition was the reverse, with a fixed task-irrelevant flicker rate and a variable test flutter rate, and participants reported which interval fluttered faster.

Analysis

The temporal rates subjectively equivalent to 10 Hz for younger and older adults were analysed using two mixed ANOVAs, one for the auditory condition and one for the visual condition, with task-irrelevant rate (8, 9, 10, 11, 12, 14 and 16 Hz) as the within-subjects factor and age group the between-groups factor. Responses for 2 participants were excluded from analysis of the auditory task due to inability to adequately complete some task-irrelevant rates (8 & 9 Hz and 14 & 16 Hz for the respective participants). In these cases, the proportion faster did not span from approximately 0 to approximately 1 across the range of test rates for input parameters for the method of constant stimuli (centre, step size) typical of other participants. This resulted in undesirable psychometric function fits, as one participant evidenced unacceptably high guess rates (0.43, 0.45) and the other high lapse rates (0.38, 0.48).
Results

Effect of task-irrelevant rate
There was a main effect of task-irrelevant rate on the physical rate perceived as equivalent to 10 Hz whether participants were discriminating changes in flutter rate ($F(6,102)= 30.9$, $p<0.001$) or flicker rate ($F(3.5, 65.6)=39.8$, $p<0.001$). As Figure 3.6 shows, physical rates greater than 10 Hz were required in the presence of slow task-irrelevant rates (8 and 9 Hz) whereas physical rates slower than 10 Hz were required in the presence of fast task-irrelevant rates (11, 12, 14, 16 Hz). This pattern reflects partial integration of conflicting auditory and visual rates, which results in a bias of the apparent rate in the attended sensory modality towards the rate of modulation in the ignored modality. Consequently, the temporal rate perceived as equivalent to 10 Hz shifts in the opposite direction, resulting in a non-veridical point of subjective equality as previously demonstrated by Roach et al. (2006).

Effect of age
As Figure 3.6 shows, the mean test rate subjectively equivalent to the true rate of 10 Hz was comparable across age groups for all task-irrelevant rates on both the auditory (Figure 3.6A) and visual tasks (Figure 3.6B). Upon analysis, no main effect of age was found for either the auditory task ($F(1,17)= 0.26$, $p=0.62$) or the visual task ($F(1,19)=0.13$, $p=0.73$). Therefore, task-irrelevant rates induced similar shifts in rate perception in the younger and older participants when auditory and visual reliability was individually balanced. This suggests that aging does not affect the degree to which asynchronous auditory and visual rates are integrated under conditions controlling for age-related sensory decline.

Interaction between age and task-irrelevant rate
Since there was no interaction between age and task-irrelevant rate (audition: $F(6, 102)= 0.35, p=0.91$; vision: $F(3.5, 65.6)= 0.69$, $p=0.58$), task-irrelevant rate influenced temporal rate perception in the same systematic manner in young and old. As can be seen in Figure 3.6, this held true even for the more discrepant rates of 14 and 16 Hz where the influence of the task-irrelevant modality began to wane. This indicates that both age groups possess the same facility for resolving conflicting auditory and visual rates.
Figure 3.6: A) Mean temporal rate of auditory flutter that was subjectively equivalent to the 10 Hz reference for each of the task-irrelevant visual flicker rates. Younger adults are closed circles and older adults are open circles. Error bars are 95% confidence intervals of the mean. The dashed line indicates the physical temporal rate B) Mean temporal rate of visual flicker that was subjectively equivalent to the 10 Hz reference for each of the task-irrelevant auditory flutter rates.

Tendency to segregate asynchronous rates

Roach et al (2006) demonstrated that segregation of auditory and visual stimuli occurs for large differences in temporal rate, resulting in veridical temporal rate perception. In contrast, complete segregation of the auditory and visual stimuli was not observed over a similar range of task-irrelevant rates for group mean subjectively equivalent rates in my experiment. Consideration of single participant responses reveals individual variability in the range over which auditory and visual cues become too dissimilar to integrate. An example of this is shown in Figure 3.7. When judging visual rate in the presence of an auditory rate of 16 Hz, one
participant placed little weight on the auditory stimulus while the other was still greatly influenced by the task-irrelevant auditory stimulus.

Figure 3.7: Psychometric functions are shown for two separate participants, one in panel A) and the other in panel B), who represent the extremes in the flutter rate subjectively equivalent to the 10 Hz reference in the presence of task-irrelevant flicker at 16 Hz. In this condition, participants indicated which of two successive intervals contained the faster rate of flutter. The 10 Hz reference was contrasted with a test interval of variable flutter rate and 16 Hz flicker. The dashed line indicates the mean of the psychometric function, which was taken as the point of subjective equality. In A), the subjective equivalent was a flutter rate considerably slower than 10 Hz, reflecting the influence of the task-irrelevant flicker. In B), the subjective equivalent was approximately equal to the true physical rate of 10 Hz, indicating minimal influence of the task-irrelevant flicker.

**Maximum likelihood estimation**

For slight discrepancies, the brain is thought to implement reliability based weighting of the auditory and visual estimates of a stimulus property through maximum likelihood estimation (Ernst & Bulthoff 2004; Witten & Knudsen 2005). This entails summing the individual sensory
estimates weighted by their inverse variance (Equation 3.1). Results consistent with this model have been shown for audiovisual integration of temporal information, such as in the sound-induced flash-illusion (Andersen et al. 2005; Shams et al. 2005). Therefore, the data was further modelled for each participant individually over a restricted range of task-irrelevant rates where the relationship with perceived rate was acceptably linear (excluding 14 and 16 Hz, see Figure 3.6A) in order to further characterize the relationship between perceived rate and task-irrelevant rate in a manner consistent with the literature. I was therefore able to include data from the participants that were excluded from the mixed ANOVA due to inadmissible data for some task-irrelevant rates. Results of the linear regression were then compared with the maximum likelihood prediction. Since auditory and visual variances were equivalent by experimental design (see Experiment 1A), maximum likelihood estimation predicts a linear combination of auditory and visual rate information where the brain weights each source of rate information equally to arrive at a final integrated representation of audiovisual rate information. To illustrate, Figure 3.8A shows the linear fit for a sample participant in contrast to the maximum likelihood prediction. In keeping with my hypothesis of unchanged integration ability with older age, the parameter of interest in the linear fits is the slope, where participants integrating asynchronous rates to a greater degree will have a steeper slope.

$$\hat{AV} = \hat{A} \left( \frac{1}{\sigma_A^2} + \frac{1}{\sigma_V^2} \right) + \hat{V} \left( \frac{1}{\sigma_A^2} + \frac{1}{\sigma_V^2} \right)$$

Equation 3.1: Maximum likelihood estimation predicts that the audiovisual rates, $\hat{AV}$, results from the sum of the individual auditory, $\hat{A}$, and visual, $\hat{V}$, rates, with each weighted in proportion to their reciprocal variance $\sigma_A^2$ and $\sigma_V^2$, respectively, such that the weights sum to one (Ernst & Banks 2002).

No age-related differences were found in median slope for the auditory task (Mann Whitney test, $U=48$, $p=0.65$) or mean slope for the visual task ($t(19)= 1.2$, $p=0.25$). This agrees with the previous analysis that showed no interaction between age and the temporal rate subjectively equivalent to the 10 Hz reference. Furthermore, maximum likelihood estimation predicted a greater degree of integration than was found in either age group, as can be seen in Figure 3.8B & C. Considered in combination, these two asynchronous tasks show that older adults were no more susceptible than younger adults to integrating irrelevant rate information in the non-test sensory modality.
Figure 3.8: A) Linear regression (solid line) of the point of subjective equality and task-irrelevant rate (closed circles) for the auditory asynchronous task for a sample participant. B) Box plots of auditory slope derived from linear regression for younger and older adults. C) Box plots of visual slope derived from linear regression for younger and older adults. Median (central line), interquartile range (box) and 10th and 90th percentiles (whiskers) are shown in all box plots. The dashed line gives the maximum likelihood prediction for panels A through C.
Supplementary analyses

Effect of asynchrony on the precision of temporal rate discriminability

Visual temporal rate discrimination becomes less precise in the presence of crossmodal rate asynchrony (Roach et al. 2006). Consequently, the addition of an asynchronous rate of auditory flutter was expected to degrade discrimination of flicker rate, as reflected by a larger standard deviation on the psychometric function. Comparing this across age groups would provide a measure of whether older adults found the asynchronous auditory tasks perceptually more difficult to complete. Note that asynchronous flicker has the same effect on flutter rate discrimination, but this could not be usefully compared across participants as auditory modulation varied individually by experimental design (see Experiment 1A). I therefore compared flicker rate discrimination thresholds across all experimental conditions (vision-alone and vision combined with each of the seven task-irrelevant flutter rates) using a mixed ANOVA. Experimental condition was the within-subjects factor and age group the between-subjects factor.

There was a main effect of auditory task-irrelevant rate on temporal rate discrimination thresholds for visual flicker ($F(4.4,83)=3.7$, $p=0.006$). As Figure 3.9 shows, adding an asynchronous flutter rate made flicker discrimination more difficult as participants required a greater difference to distinguish between rates. However, rate asynchrony degraded flicker rate discrimination to the same extent in younger and older adults as there was no main effect of age ($F(1,19)=0.6$, $p=0.44$). Nor did older adults struggle at discriminating temporal rate in the presence of any particular task-irrelevant rates as there was no interaction between age group and task-irrelevant rate ($F(4.4,83)=0.880$, $p=0.49$). Since older age did not adversely affect rate discrimination, it seems unlikely that there were any age-related differences in task difficulty confounding my earlier analysis of perceived rate.
Figure 3.9: Mean temporal rate discrimination thresholds for 10 Hz flicker in the presence of each of the task-irrelevant flutter rates for younger adults (closed circles) and older adults (open circles). Flicker rate discrimination thresholds when the visual stimulus was presented in isolation are shown on the left for comparison (note that these were obtained in Experiment 1A, see Figure 3.2). Younger adults are the closed diamonds and older adults the open diamonds. Error bars are the 95% confidence interval of the mean.

Comparison between auditory and visual asynchronous tasks

The degree to which auditory and visual temporal rates were integrated was expected to be the same regardless of the sensory modality to which participants attended. Indeed, comparison of Figure 3.6A and Figure 3.6B suggests that the subjective equivalent to 10 Hz for each task-irrelevant rate was similar for the auditory and visual asynchronous tasks. To illustrate this further, Figure 3.10 contrasts the subjective equivalent for a task-irrelevant rate of 12 Hz on the auditory task with the subjective equivalent for the same task-irrelevant rate on the visual task for each participant. For both the younger and older age groups, the data points are clustered together. This suggests that the temporal rates perceived as the equivalent to 10 Hz were comparable across the two sensory modalities for both younger and older participants.
Figure 3.10: The temporal rate judged the subjective equivalent of the standard with a physical rate of 10 Hz for auditory (y axis) and visual (x axis) asynchronous tasks when task-irrelevant rate in the other sensory modality was 12 Hz. Younger adults are shown as filled circles and older adults as unfilled circles. The dashed line indicates where auditory and visual temporal rates are equal (y=x).

Preliminary discussion

Older adults retained the ability to flexibly resolve intersensory conflict through partial integration of asynchronous auditory and visual temporal rates. The change in subjective equivalent with task-irrelevant rate was not consistent with the integration model of maximum likelihood estimation even for small rate discrepancies as this predicted a greater influence of task-irrelevant rate. Rather, both younger and older adult responses reflected the waning influence of task-irrelevant rate as the degree of rate disparity increased at 14 and 16 Hz. This suggests that participants were sensitive to the likelihood that increasingly disparate rates did not correspond to the same object, as was previously modelled by Roach et al. (2006). However, complete segregation of asynchronous rates was not observed over the same range of task-irrelevant rates, likely reflecting differences in participant expertise with psychophysics between my experiment and prior work (Roach et al. 2006). The experienced psychophysical observers that took part in the original experiment by Roach et al. (2006) may have more readily distinguished any disparity between the visual and auditory rates, therefore segregating rates earlier than the naive observers that took part in my experiment. Differences in experimental stimuli may have also contributed as the base stimuli that were amplitude modulated in each experiment differed. My experiment used a green LED with maximum
luminance of 876 cd/m² and a 65 dB pure tone in comparison to the green LED with maximum luminance of 6400 cd/m² and 65 dB white noise used by Roach et al. (2006). Differences in the shape of the modulation waveform may also have contributed, as my experiment used a sinusoidal waveform and the experiment by Roach et al. (2006) employed a square waveform. For audition, steady state responses vary in amplitude with modulation waveform due to nonlinearities in the processing of auditory amplitude modulation (Prendergast et al. 2010). For vision, flicker sensitivity for a square waveform differs to that of a sinusoidal waveform, due to the presence of discernible edges at light onset and offset in square waveforms (Bowen et al. 1992).

In summary, younger and older adults experienced comparable shifts in perceived rate when integrating asynchronous auditory and visual rates. By presenting participants with a physical auditory cue tailored to their individual sensitivity, I circumvented the age-related decline in auditory temporal modulation sensitivity. In doing so, I demonstrated that the ability to integrate asynchronous auditory and visual temporal rate was preserved in older adults. This finding will be commented on further in the general discussion (see Chapter 5). However, unlike natural environmental conditions, older and younger adults were not presented with the same auditory stimulus by experimental design. The results of Experiment 1A indicated a decrease in the perceptibility of auditory rate information relative to visual. It remains to be seen whether this is sufficient to cause appreciably different integration when younger and older adults perceive the same physical stimuli. This question will be addressed in an upcoming supplementary experiment, which is described in Chapter 4. The remainder of this chapter will present the results for the remaining audiovisual task, which looked at the integration of synchronous auditory and visual rates.
Experiment 1C: Integration of synchronous (identical) flicker and flutter rates

Aim:

to investigate whether older age alters the integration of synchronous auditory and visual temporal rate under conditions of normalised auditory and visual rate discriminability

Hypotheses:

a) Discrimination of a change in temporal rate based on synchronous flicker and flutter will be equally precise in younger and older adults under conditions of normalised auditory and visual rate discriminability

b) The relative improvement in discrimination precision will be consistent with statistically optimal integration in both age groups

Task overview

This task measured how precisely participants could discriminate between temporal rates when basing their responses on both flicker and flutter, presented simultaneously at the same rate. This audiovisual rate discrimination threshold was given by the standard deviation of the psychometric function. Further description of the experimental task may be found in Chapter 2.

Analysis

Analysis of temporal rate discrimination thresholds for synchronous auditory flutter and visual flicker was two-fold. First, mean thresholds were directly compared between age groups using a t-test. However, it is the relative improvement in performance under the audiovisual condition compared to visual or auditory alone conditions for each participant that provides a measure of multisensory facilitation (Stein et al. 2009). Specifically, comparison to maximum likelihood predictions is more meaningful given that research indicates that combined rather than separate presentation of equally reliable auditory and visual rates improves temporal rate discrimination in a statistically optimal fashion in younger adults (Koene et al. 2007). Consequently, thresholds were compared, on an individual basis, to maximum likelihood
predictions derived from visual flicker rate discrimination thresholds obtained in Experiment 1A. This integration model predicts that auditory and visual rates are weighted according to their relative reliability to achieve a combined estimate with the smallest possible variance (Ernst & Banks 2002). Since auditory and visual variances were equivalent by experimental design (see Experiment 1A), maximum likelihood estimation predicts a $\sqrt{2}$ improvement (Equation 3.2). The maximum likelihood prediction was also compared between age groups using both parametric and Bayesian t-tests, the latter of which was run in JASP (Version 0.8.1.2, JASP Team (2017), Amsterdam, NL) using a default Cauchy prior of width 0.707.

$$\sigma_{AV} = \frac{\sigma_A^2 \sigma_V^2}{\sigma_A^2 + \sigma_V^2}$$

Equation 3.2: Temporal rate discrimination threshold, $\sigma_{AV}$, based on auditory and visual rates as predicted by maximum likelihood estimation (Ernst & Banks 2002).

Results

As Figure 3.11 shows, the mean temporal rate discrimination thresholds based on synchronous flicker and flutter are similar in younger and older adults ($t(19)=-0.924, p=0.367$). Paired t-tests indicated that younger but not older adult audiovisual discrimination thresholds were consistent with maximum likelihood predictions (younger: $t(10)=0.70, p=0.50$; older: $t(9)=2.7, p=0.02$). This suggests that older adults were less able to benefit from the addition of synchronous flutter to flicker when discriminating temporal rate changes despite similar overall performance. Note that the mean maximum likelihood prediction did not differ between age groups ($t(19)=1.2, p=0.25$), in line with the lack of an age-related difference in flicker rate discrimination thresholds upon which the predictions were based (see Experiment 1A). A follow up Bayesian t-test provided weak evidence in favour of the null hypothesis of no age-related difference in the maximum likelihood predictions ($BF_{10}=0.643$).

Supplementary analysis of psychometric functions across age groups found no difference in mean guess rate (Mann-Whitney $U=52.5, p=0.87$) or mean lapse rate (Mann-Whitney $U=50, p=0.71$). Nor was there any evidence of greater heterogeneity in older adult responses since the 95% confidence interval of the mean for each group are comparable in width (see Figure 3.11). Therefore, age-related differences in audiovisual facilitation of rate discrimination did not stem from any age-related differences in task difficulty.
Preliminary discussion

Temporal rate discrimination for synchronously presented, equally discriminable auditory and visual rates appeared unaffected by age when differences in group mean thresholds were considered in isolation. However, analysis of audiovisual performance is most meaningful when considered in relation to visual and auditory alone performance, as this indicates whether integration facilitated or hindered participant responses (Stein et al. 2009). Younger adults audiovisual temporal rate discrimination thresholds were indistinguishable from the maximum likelihood prediction based on their flicker rate discrimination thresholds. This extends the finding that integration of auditory and visual rates is statistically optimal when reliability is controlled by adding noise (Koene et al. 2007) to noise-free conditions.

Unlike younger adults, older adults did not combine synchronous rate information in a statistically optimal fashion. Suboptimal statistical inference in older but not younger adults has previously been demonstrated for the integration of visual and vestibular cues in a spatial navigation task (Bates & Wolbers 2014) as well as in individuals with central vision loss when performing an audiovisual localisation task (Garcia et al. 2017). This is the first study to demonstrate an age-related deviation from statistically optimal integration when older adults with intact sensory functioning integrate auditory and visual cues. Together, these three studies demonstrate that a gradual decline in sensory abilities, whether from advancing age or
progressive disease, is sufficient to reduce the behavioural advantage of integrating multisensory cues. The gradual development and recalibration of sensory modalities during childhood also results in suboptimal integration of visual and haptic cues in young children (Gori et al. 2008; Nardini et al. 2013), indicating that statistically optimal cue combination is not a fixed property of multisensory mechanisms. The implications of Experiment 1C will be discussed further in the upcoming general discussion (Chapter 5).

Statistically optimal combination of auditory and visual rates produced only a small improvement in temporal rate discrimination thresholds in younger adults. Consequently, the age-related impairment in integration may not cause significant age-related differences in audiovisual rate perception in an everyday setting. However, reduced facilitation of temporal rate discrimination by rate synchrony in older adults is also likely to be compounded by the age-related impairment in flutter rate discrimination. The combination of age-related deficits may be sufficient to significantly impair older adult perception of synchronous auditory and visual rates.

**Conclusion**

While older age did not impair discrimination of visual flicker rate changes, discrimination of auditory flutter rate changes was less precise in older adults due to impaired amplitude modulation sensitivity. Older adults retained the ability to partially integrate equally reliable but asynchronous temporal rates of flutter and flicker since distortions in perceived rate were similar to that of younger adults. In contrast, integration of synchronous auditory and visual rates did not facilitate temporal rate discrimination in older adults relative to visual alone performance in a statistically optimal fashion, though group audiovisual rate discrimination thresholds themselves were unaffected by aging.
Chapter 4: Experiment 2

Introduction

The preceding chapter outlined the effect of audiovisual rate asynchrony on perceived temporal rate in a group of younger and older adults, who were presented with the same physical visual stimulus (flicker of 100% amplitude modulation) but different auditory stimuli (flutter of variable amplitude modulation). Individually manipulating the depth of auditory modulation normalised individual differences in auditory and visual sensitivity. Under these controlled conditions, older age neither impaired nor enhanced the degree to which asynchronous auditory and visual temporal rates were integrated. Therefore, we can conclude that the perceptual ability to integrate auditory and visual rates is unchanged in aging.

Of course, under everyday conditions age-related sensory loss is not controlled for and older and younger adults must respond to the same physical rates. One of the factors governing whether the brain chooses to integrate or segregate asynchronous auditory and visual rates is the degree of rate disparity between the senses (Roach et al. 2006). In my first experiment, older adults required greater change in the amplitude of auditory flutter over time for fine discrimination of changes in flutter rate to be comparable to discrimination of differences in visual flicker rates. As the aged auditory system therefore specifies temporal rate less precisely, the ability of older adults to appropriately integrate or segregate auditory and visual stimuli according to rate similarity could be compromised. This raises the question of whether older and younger adults would perceive natural stimuli with the same audiovisual temporal rate content differently.

Accordingly, this chapter explores how asymmetries in sensitivity between audition and vision – as may accompany aging – affects the integration of asynchronous auditory and visual temporal rates. To do this, I conducted an experiment investigating how temporal rate perception changed in younger adults under the same stimulus conditions as the average older adult in the first experiment – that is, visual flicker and auditory flutter with fixed amplitude modulation depth of 100% and 20%, respectively. 20% auditory amplitude modulation is well above the modulation depth used for younger adults to match flicker and flutter rate discriminability in the previous experiment (see Chapter 3, Figure 3.3). Consequently, auditory temporal rate discrimination performance is expected to be significantly improved relative to visual.
Aim and hypothesis

Aim:
To determine whether more precise discrimination of changes in flutter rate in younger adults due to their heightened sensitivity to auditory amplitude modulation is sufficient, on its own, to alter sensory weighting of auditory and visual rate information

Hypothesis:
Audition will contribute more than vision to temporal rate perception due to its increased reliability

It is unclear whether the age-related differences in auditory sensitivity are sufficient to significantly affect audiovisual temporal rate perception. Multisensory theory predicts that a relative increase in auditory temporal rate discriminability induces a corresponding increase in the weighting of flutter relative to flicker upon their integration. Previous work does demonstrate that the contribution of audition and vision to the integrated percept of temporal rate is consistent with a weighting scheme affected by the relative reliability of auditory and visual rates, as well as the degree of rate disparity and the attended sensory modality (Roach et al. 2006). Therefore, as the modulation depth of auditory flutter increases, younger adults are expected to give more weight to what they hear and less weight to what they see. As a result, I hypothesise that the temporal rate subjectively equivalent to a 10 Hz reference will be closer to the true physical value when judging flutter rate, reflecting a decreased integration of asynchronous auditory and visual rates. Likewise, the temporal rate subjectively equivalent to a 10 Hz reference will be further from the true physical value when judging flicker rate, reflecting increased integration of asynchronous auditory and visual rates.

A priori, an estimate of the change in flutter rate discrimination thresholds could be derived from the linear regression of flutter rate discrimination thresholds against modulation depth performed for younger adults in Experiment 1A (Equation 4.1). Based on the median modulation depth of 8.3% that equated flicker and flutter rate discriminability for younger participants in Experiment 1A, the increase in modulation depth needed to reach a modulation of 20% can be estimated at 11.7%. This would correspond to a change in rate discrimination threshold of 0.98 Hz, based on Equation 4.1.
Equation 4.1: The change in rate discrimination threshold, $\Delta D$ (Hz), may be calculated as a function of the step change in the depth of auditory amplitude modulation, $\Delta M$ (%), multiplied by the decrease in rate discrimination per unit Hz, which may be approximated by the median slope of the linear regression of flutter rate discrimination thresholds against modulation depth, -0.0841, for younger adults in Experiment 1A (see Chapter 3, Figure 3.4).

Note that for most participants a modulation depth of 20% was outside the range of the four modulation depths tested, limiting the accuracy of the estimate as it is an extrapolation. Recall that the relationship between modulation depth and rate discriminability follows a power function when tested over a wide range of modulation depths (Roach et al. 2006; also see Chapter 2, Figure 2.9). Therefore, flutter rate discriminability plateaus once modulation depth is sufficiently high, indicating a limit on the precision of flutter rate discrimination. Since the relationship is only acceptably linear over a restricted range of modulation depths, 0.98 Hz is expected to be an overestimation of the true value. Indeed, the resulting predicted flutter rate discrimination threshold of 0.26 Hz, derived using a mean threshold of 1.24 Hz in younger adults in Experiment 1A as a reference, may be beyond the physical capacity to discriminate changes in flutter rate. As such, the likely change in auditory rate discriminability by increasing amplitude modulation cannot be confidently predicted from available information. A limit to the influence of auditory amplitude modulation sensitivity on the relative reliability of auditory and visual rates is expected.

In conclusion, current multisensory theory predicts that audition will contribute more than vision to temporal rate perception provided that increasing auditory amplitude modulation to 20% significantly improves the reliability of auditory relative to visual rate information. However, if the increase does not affect sensory weighting, this is not inconsistent with the literature as the degree to which the step change in modulation depth in question impacts rate discriminability is uncertain.
Experimental method

Participants

Recruitment
A group of 6 younger adults (age range: 23-28, mean 26) were recruited from the University of Melbourne and from the lab contact list of previous participants if they had expressed an interest in participating in other experiments. One of the participants also took part in the first experiment. Participants typically attended two sessions, each of no more than two hours in duration.

Screening procedure
As described in Chapter 2, participants were screened with a detailed history, eye examination and digital audiometry to determine their suitability for the study and ensure that they were free from any visual or hearing deficits.

Ethics
As for the previous experiment, this research had ethics approval from the University of Melbourne Human Research Ethics Council under the approval number HREC 1034933. All participants gave informed consent after receiving an explanation of the nature and purpose of the experiment. Please see the appendix for copies of the plain language statement and consent form, which were identical to those used in the first experiment.

Experimental tasks

This experiment contrasted the physical test rate that was subjectively equivalent to a 10 Hz reference under two different conditions, which differed in the depth of auditory amplitude modulation.

Experiment 2A: Equating auditory and visual temporal rate discriminability
For the matched condition, the fluttering stimulus was degraded by reducing its modulation percentage to equate the discriminability of a change in temporal rate across vision and audition. Consequently, the experiment began by determining the desired modulation depth for each participant (Figure 4.1, Experiment 2A). This followed the format of Experiment 1A, which is outlined in Chapter 2. The desired modulation depth was calculated on an individual basis by interpolation based on the linear regression of flutter rate discrimination thresholds at four different modulations depths, each a multiple of the individual’s threshold for detecting
amplitude modulation. For the unmatched condition, flutter modulation was set at 20% for all participants, as this was the average modulation percentage required to equate discriminability of flicker and flutter rate in older adults in Experiment 1.

Experiment 2A: Equating auditory and visual temporal rate discriminability

<table>
<thead>
<tr>
<th>Vision</th>
<th>Audition</th>
<th>Audition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flicker rate discrimination</td>
<td>Amplitude modulation detection</td>
<td>Flutter rate discrimination</td>
</tr>
<tr>
<td>Threshold: standard deviation (σ)</td>
<td>Threshold: mean (μ)</td>
<td>Threshold: standard deviation (σ)</td>
</tr>
</tbody>
</table>

Experiment 2B: Matched condition
modulation from 2A

<table>
<thead>
<tr>
<th>Audiovisual- attend audition</th>
<th>Audiovisual- attend vision</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flutter rate discrimination</td>
<td>Flicker rate discrimination</td>
</tr>
<tr>
<td>Threshold: point of subjective equality (μ)</td>
<td>threshold: point of subjective equality (μ)</td>
</tr>
</tbody>
</table>

Experiment 2B: Unmatched condition
modulation 20%

<table>
<thead>
<tr>
<th>Audiovisual- attend audition</th>
<th>Audiovisual- attend vision</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flutter rate discrimination</td>
<td>Flicker rate discrimination</td>
</tr>
<tr>
<td>Threshold: point of subjective equality (μ)</td>
<td>threshold: point of subjective equality (μ)</td>
</tr>
</tbody>
</table>

Figure 4.1: Flowchart of experiment tasks. Experiment 2A equated the participant’s flutter rate discrimination, measured at various multiples of the participant’s amplitude modulation detection threshold, to their flicker rate discrimination threshold for a visual standard of fixed modulation. In Experiment 2B, the subjective equivalent to a reference temporal rate for a task-irrelevant rate of 12 Hz is determined when judgments are based solely on vision or audition. Experiment 2B is performed at two different modulation depths. The matched condition used the modulation depth determined in Experiment 2A. The unmatched condition used a modulation of 20%.

Experiment 2B: Integration of asynchronous (non-identical) flicker and flutter rates

As described in Experiment 1B (see Chapter 2), temporal rate discrimination tasks followed a two-interval forced choice format with synchronous 10 Hz auditory flutter and visual flicker, presented in phase, as a reference. For the auditory task, the test interval contained an
auditory flutter rate, which varied as a method of constant stimuli, and a fixed task-irrelevant visual flicker rate of 12 Hz. For the visual task, the test interval contained a visual flicker rate, which varied as a method of constant stimuli, and a fixed task-irrelevant auditory flutter rate of 12 Hz. Participants selectively based their judgements regarding which interval contained the faster temporal rate on what they heard for the auditory condition and what they saw for the visual condition. A single task-irrelevant rate of 12 Hz was used as I previously found substantial integration at this frequency (see Experiment 1: Chapter 3, Figure 3.6).

Presentation of the seven stimulus levels from the method of constant stimuli were divided into four blocks of five. Blocks for auditory or visual judgements under matched or unmatched conditions were interleaved. Task order was counterbalanced across participants. This procedure generated four psychometric functions, corresponding to the number of experimental conditions (auditory matched, auditory unmatched, visual matched, visual unmatched). The point of subjective equality (the physical rate apparently equivalent to the 10 Hz reference) for each condition was given by the mean of the psychometric function.

The auditory amplitude modulation was expected to be greater in the unmatched than the matched condition (Figure 4.2), giving rise to more readily perceptible fluctuations in amplitude and more easily discriminated changes in flutter rate (as per Experiment 1: see Chapter 3, Figure 3.4). As the auditory cue would then be more reliable in the unmatched condition, participants were expected to give more weight to what they see when discriminating temporal rate in the unmatched condition compared to the matched condition. Under matched conditions, a fast task-irrelevant rate (such as 12 Hz) results in a point of subjective equality slower than the physical rate of a 10 Hz reference due to partial integration of asynchronous auditory and visual rates (Roach et al. 2006; also see Chapter 2, Figure 2.11B & Chapter 3, Figure 3.5). For the auditory task, where participants discriminate flutter rate, increased auditory weighting would result in a point of subjective equality closer to 10 Hz (Figure 4.3). For the visual task, where participants discriminate flicker rate, increased auditory weighting would result in a point of subjective equality further from 10 Hz.
Figure 4.2: The top panel shows a sample auditory stimulus for the matched condition, where the modulation depth was individually determined. Here the modulation depth is 6.3%. The bottom panel shows the auditory stimulus for the unmatched condition, where the modulation depth was 20% for each participant. The fluctuations in sound amplitude were more distinct in the unmatched condition.
Figure 4.3: Flutter rate discrimination in the presence of task-irrelevant flicker rate of 10 Hz, demonstrating a shift in the point of subjective equality between matched (grey) and unmatched (black) conditions. The data and psychometric function are shown for a single participant as an example. The point of subjective equality, which is the mean of the psychometric function, is indicated by a dashed line. The point of subjective equality is higher under unmatched conditions, indicative of increased auditory weighting since the perceived rate is closer to the true rate of the 10 Hz reference.

Analysis

Statistical testing was carried out using SPSS (Version 22, IBM Inc., New York, NY, USA) and plots generated using SigmaPlot (Version 11, Systat Software, Inc. San Jose, CA, USA).

Results

Experiment 2A: Equating auditory and visual temporal rate discriminability

Thresholds for the visual and auditory tasks are displayed in Table 4.1. As expected for a group of younger adults (see Chapter 3, Figure 3.3), modulation detection thresholds were low. Accordingly, thresholds for flicker and flutter temporal rate discrimination were equivalent when auditory amplitude modulation was significantly lower than the 20% employed in the unmatched condition, as hypothesised.
<table>
<thead>
<tr>
<th>Modality</th>
<th>Task</th>
<th>Mean</th>
<th>95% CI of the mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Visual</td>
<td>Flicker discrimination (Hz)</td>
<td>0.99</td>
<td>1.04 – 1.23</td>
</tr>
<tr>
<td>Auditory</td>
<td>Modulation detection (%)</td>
<td>2.02</td>
<td>1.29 - 2.45</td>
</tr>
<tr>
<td>Auditory (matched to visual)</td>
<td>Modulation match (%)</td>
<td>6.41</td>
<td>3.78 - 9.03</td>
</tr>
</tbody>
</table>

Table 4.1: Results for Experiment 2A, in order by row: the temporal rate discrimination threshold for the flickering visual standard of 10 Hz, the threshold for detecting sinusoidal amplitude modulation at 10 Hz in a 500 Hz pure tone, the modulation percentage that equates the temporal rate discrimination threshold for 10 Hz flutter with the threshold obtained for the visual standard.

Experiment 2B: Integration of asynchronous (non-identical) flicker and flutter rates

As can be seen in Figure 4.4A, the point of subjective equality for flutter rate was closer to the true physical value of 10 Hz in the unmatched, compared to the matched condition, for each participant. As hypothesised, this is consistent with greater weighting of auditory cues in the unmatched condition. Figure 4.4B displays the reciprocal relationship, where the point of subjective equality for flicker rate was further from its true physical rate of 10 Hz in the unmatched compared to the matched condition, for each participant. This is also in keeping with my hypothesis of greater auditory weighting in the unmatched condition. Analysis of the difference in the point of subjective equality to 10 Hz between matched and unmatched conditions confirmed greater auditory influence for 20% modulation whether participants responded to flicker or flutter rate changes (flutter: $t(5)=-4.7$, $p=0.005$; flicker: $t(5)=2.7$, $p=0.04$; Figure 4.4C).
Figure 4.4: Individual participant perceptual matches for 10 Hz under matched and unmatched, auditory dominated rate discriminability for A) flutter and B) flicker asynchronous rate discrimination tasks with a task-irrelevant rate of 12 Hz. C) Individual (open circles) and mean (closed circles) differences in perceptual matches for flicker and flutter asynchronous rate discrimination tasks. Error bars are the 95% confidence intervals of the mean difference.
Discussion

In this supplementary experiment, audition dominated rate perception in younger adults for a modulation depth that equalised auditory and visual influence in older adults. Specifically, rate perception became more veridical in the auditory modality (point of subjective equality closer to 10 Hz) and more distorted in the visual modality (point of subjective equality further from 10 Hz), reflecting greater weighting of auditory rate information. Therefore, the physical difference in auditory amplitude modulation across age groups in Experiment 1A was sufficient to alter sensory weighting.

Of course, under normal circumstances, age-related changes in the auditory reliability are not normalised since older and younger adults interact with the same physical stimuli. Under everyday conditions, the age-related impairment in sensitivity to auditory amplitude modulation is expected to degrade the reliability of auditory temporal rate relative to visual rate in older adults. Furthermore, Experiment 1B demonstrated that older adults retain the ability to integrate asynchronous auditory and visual rates when rate reliability is balanced across the senses. Since the superior amplitude modulation sensitivity of younger adults was sufficient to significantly bias integration in favour of audition, it follows that the inferior amplitude modulation sensitivity of older adults should bias integration away from audition for the same physical audiovisual rate stimulus. Consequently, it is anticipated that perceived auditory rate will be distorted by vision more than perceived visual rate is distorted by audition.

As previously discussed, audition typically dominates temporal rate perception (Berger & Pelli 2001; Knox 1945; Regan & Spekreijse 1977; Shipley 1964; Welch et al. 1986). Once, auditory dominance in temporal rate perception was once believed to be hard-wired, since audition was innately more appropriate than vision for temporal rate judgements due to its superior temporal resolution (Welch et al. 1986). In contrast, Experiment 2 provides further evidence that auditory and visual rates are in fact weighted by their relative reliability, as the experiment by Roach et al. (2006) demonstrated. In fact, the results predict a move away from auditory dominance in older age due to age-related sensory loss. This agrees with a growing body of research demonstrating that apparent modality dominance in multisensory perception arises out of a flexible integration process that weights cues according to their relative reliability (for review see Ernst & Bülthoff 2004; Witten & Knudsen 2005).
However, could there be an age-related difference in how relative reliability affects the degree of integration? Currently, we only know how varying the relative reliability of auditory and visual rates affects younger adults. When reliability of either auditory or visual cues is reduced, older adults are worse integrators of auditory and visual speech cues than younger adults (Gordon & Allen 2009; Huyse et al. 2014; Stevenson et al. 2015; Tye-Murray et al. 2010; Tye-Murray et al. 2008; Tye-Murray et al. 2011). This raises the question of whether older adults may similarly display deficits in the integration of auditory and visual rates given that older age is expected to degrade auditory rate information. If so, the relative increase in distortions of perceived auditory rate and decrease in distortions of perceived visual rate under conditions of rate asynchrony may be less than anticipated. Future experiments could address whether older adults retain the ability to integrate asynchronous rates when reliability is unbalanced by systematically manipulating the reliability of the auditory stimulus relative to the visual.

Conclusion

Heightened sensitivity to amplitude modulation provides an advantage when younger adults discriminate the rate of suprathreshold amplitude changes, since increasing auditory amplitude modulation to 20% is sufficient to alter reliability-based sensory weighting when younger adults integrate asynchronous auditory and visual rates. The implications of this finding will be discussed further in the next chapter.
Chapter 5: Discussion and conclusion

Introduction

This thesis provides an account of how healthy aging affects the integration of visual flicker (the temporal modulation of luminance) with auditory flutter (the temporal modulation of sound amplitude) to produce a coherent, audiovisual percept of temporal modulation rate. In younger adults, integrating identical auditory and visual rates is advantageous as it facilitates discrimination of changes in rate (Koene et al. 2007). However, partial integration of non-identical rates is disadvantageous, as it distorts perceived rate such that the auditory or visual rate subjectively equivalent to a reference is nonveridical (Roach et al., 2006). The degree of integration is influenced by how reliably audition derives an estimate of temporal rate relative to vision, which may be determined by comparing the precision of flicker and flutter temporal rate discrimination thresholds (Roach et al., 2006).

As hypothesised, healthy aging was accompanied by sensory loss that deleteriously affected the reliability of auditory temporal rate estimates relative to visual estimates due to an impairment in auditory amplitude modulation sensitivity (Chapter 3: Experiment 1A). This was in line with findings of asymmetric age-effects across these sensory modalities on other tasks (Čeponienė et al. 2008; Cliff et al. 2013; Diaconescu et al. 2013; Guerreiro et al. 2013; Guerreiro & Van Gerven 2011; Lustig & Meck 2011). Therefore, in my experiment, integration of synchronous (identical) and asynchronous (non-identical) auditory and visual rates was tested under conditions that normalised for the age-related sensory loss found. This was achieved by individually tailoring the amplitude modulation of the auditory cue. As predicted, there were no age-related differences in the distortion of either auditory or visual perceived rate induced by rate asynchrony (Chapter 3: Experiment 1B). This indicates that the capacity to integrate asynchronous rates across the senses is retained in older age. When presented with the same physical stimulus as the average older adult in Experiment 1B, younger adults’ heightened sensitivities to auditory amplitude modulation were sufficient to increase the influence of audition on perceived rate (Chapter 4: Experiment 2). Therefore, the age-related difference in the reliability of auditory temporal rate estimates is expected to result in age-differences in the integration of asynchronous auditory and visual rates. Synchrony of flutter and flicker rates improved temporal rate discrimination thresholds in line with maximum likelihood predictions only in the younger adult group (Chapter 3: Experiment 1C). This
indicates an unexpected age-related deficit in the integration of auditory and visual rates when they are identical.

**Integration of asynchronous auditory and visual rates in aging**

**Implications of age-invariant integration**

Since the perceptual ability to integrate asynchronous rates was preserved in physiological aging, this has implications for the supporting role of factors such as presumed audiovisual correspondence, modality-specific attention and the filtering of task-irrelevant crossmodal information in older adults. Firstly, integration of asynchronous auditory and visual rates has previously been modelled as a Bayesian inference, where the magnitude of integration is influenced by prior assumptions regarding whether disparate auditory and visual rate estimates are likely to originate from a common source (Roach et al. 2006). In Experiment 1B, older adults retained the ability to flexibly decrease the degree of audiovisual integration as rate asynchrony increased, suggesting they could infer the likelihood of audiovisual correspondence as well as their younger counterparts. Though performance on multisensory tasks may be modelled as that of an ideal Bayesian observer (Battaglia et al. 2003; Knill & Pouget 2004; Roach et al. 2006), direct evidence that the brain performs Bayesian inference is lacking (Bowers & Davis 2012). Furthermore, if the brain performs Bayesian inference, how the Bayesian prior could be implemented neurally is unclear. One model posits that the brain forms a probabilistic model of the environment, shaped by previous sensory input, that generates predictions about new sensory input (Friston 2005; Friston 2010). In the context of multisensory processing, these predictions could serve as a Bayesian prior through modulation of the processing of incoming sensory input in lower level areas via feedback connections from the higher order cortex where a probabilistic model of the environment is maintained (Klemen & Chambers 2012; Talsma 2015). Alternatively, modelling of fMRI data from an audiovisual spatial localisation tasks suggests that the likely causal relationship between auditory and visual stimuli influences neural activity at the top of the processing hierarchy in the intraparietal sulcus, but not in lower level sensory cortex (Rohe & Noppeney 2015). However the brain infers the likelihood that auditory and visual rates correspond, this mechanism appears to operate successfully in older age. As a result, in Experiment 1B, the degree to which
older adults integrate conflicting rates is less than the predictions of the maximum likelihood model, in which the correspondence of auditory and visual cues is mandatory.

Research suggests that knowledge of crossmodal correspondences could be acquired by learning from previous sensory experience (Berniker et al. 2010; Brunel et al. 2015; Ernst 2007; Gau & Noppeney 2016; Van Wanrooij et al. 2010). Exposure to the natural statistics of the environment accumulated over an individual’s lifetime may shape their beliefs about the likely correspondence of auditory and visual stimuli (Murray et al. 2016; Noppeney et al. 2010). Given the greater lived experience of older adults, it is reasonable to consider whether this alters their assumptions about audiovisual correspondence. Greater experience with audiovisual speech is believed to enable middle aged adults to more readily detect when auditory speech precedes visual speech (Alm & Behne 2013; Alm & Behne 2014). However, the greater lifetime experience of older adults in my experiment did not appear to refine their tolerance to audiovisual rate asynchrony. Rather, audiovisual rate conflict posed just as much of a disadvantage to older adults as it did to younger ones, skewing perceived rate comparably across age groups. As a more ecologically relevant task, speech may be subject to greater modulation of prior expectations over an individual’s lifetime than simple temporal rate stimuli. In line with this, experience with simple temporally offset auditory and visual stimuli can reduce susceptibility to the sound-induced flash illusion in older adults but the effect requires training with feedback, not just passive exposure (Setti et al. 2014). Age-related differences in the tolerance to disparity may also have emerged if the point of segregation could have been compared across age groups in Experiment 1B. The ability to successfully resolve large disparities when auditory and visual cues are unlikely to correspond is a mark of robust cue combination. Whether this changes for better or worse with physiological aging would be an interesting extension of the present study.

There is, however, a cost in integrating unrelated auditory and visual rate estimates. Consistent with the literature (see Roach et al. 2006), visual temporal rate discrimination was impaired in the presence of incongruent auditory rate information in Experiment 1B. Integrating conflicting auditory and visual rates resolves the discrepancy between the senses by generating a unified audiovisual estimate of temporal rate. Disadvantageously, this produces less reliable estimates of temporal rate, as reflected in poorer rate discrimination thresholds. Research on the temporal non-correspondence of patterns of flashes and beeps suggests a possible neural correlate, since neural activity in auditory and visual cortices and superior temporal sulcus (STS) is reduced when temporally non-corresponding patterns are
presented together, relative to the neural activity elicited by each pattern presented in isolation (Noesselt et al. 2007). A change in neural response elicited by temporal non-correspondence may underlie the poorer rate discrimination when auditory and visual rates are in conflict. Task-irrelevant auditory rates did not impair flicker rate discrimination to a greater extent in older adults in Experiment 1B. Therefore, my experiments show that older adults retain the ability to resolve conflicting auditory and visual rates by forming a unified estimate audiovisual rate with the same precision as younger adults.

Another factor to consider is the role of attention in my experimental results. Top-down attentional modulation often governs the extent of the interaction between the senses (De Meo et al. 2015; Macaluso et al. 2016; for reviews see Talsma et al. 2010). Limited evidence from response time tasks suggests the ability of selective attention to modulate integration in older adults is intact (Hugenschmidt et al. 2009a; Hugenschmidt et al. 2009c). How the integration process for temporal rate is driven by the physical stimulus characteristics (i.e. degree of rate asynchrony, relative reliability) has been well-described (Roach et al. 2006), but it is unclear how much this integration process is modulated by the goal-driven direction of attention to the task modality. Both in Experiment 1B and the literature, distortions in perceived rate consistently occurred when auditory and visual rates were asynchronous even though participants were selectively attending to a single sensory modality (Recanzone 2003; Roach et al. 2006; Welch et al. 1986). Therefore, selective attention does not cause complete suppression of the task-irrelevant sensory modality as robust intersensory interactions occur. In some cases, audiovisual integration occurs pre-attentively. For example, integration is not affected by directing attention to a specific sensory modality in tasks such as the sound-induced flash illusion (Odegaard et al. 2016), ventriloquist effect (Bertelson et al. 2000) and speeded responses to semantically incongruent stimuli (Mozolic et al. 2008). While the results of Experiment 1B suggests that older adults retain the capacity to engage modality-specific selective attention, such a conclusion would be premature since the role of voluntary directing attention in the integration of temporal rate has yet to be elucidated. An experimental paradigm comparing the perception of asynchronous auditory and visual rates under conditions of divided and modality-specific attention would provide more conclusive results.

Moreover, in crossmodal distraction, performance in the task-relevant sensory modality is often impaired by presenting information in a task-irrelevant sensory modality that is either incongruent or unrelated. It has been proposed that older adults are generally not more susceptible to crossmodal distraction than younger adults despite the fact that they are often
more susceptible to within-modality distraction (Guerreiro et al. 2010). Experiment 1B supports this proposal as older adults were not more susceptible to task-irrelevant rate information than younger adults, since there were no age-related differences in either rate discrimination thresholds or distortions in perceived rate. However, review of the recent literature provides mixed evidence for age-equivalent crossmodal distraction. Some studies find that performance on an auditory task with visual distraction is impaired to a greater extent in older adults (Guerreiro et al. 2013; Guerreiro & Van Gerven 2011; Kato et al. 2016). Other studies find age-equivalent impairments in performance (Campbell et al. 2010; Einstein et al. 2002; Guerreiro et al. 2014a; Puschmann et al. 2014; Townsend et al. 2006). For a visual task with auditory distraction, there are both reports of age-related impairments (Andrés et al. 2006; Leiva et al. 2015; Puschmann et al. 2014) and no effect of age on behavioural performance (Alain & Woods 1999; Guerreiro et al. 2014a; Townsend et al. 2006; Van Gerven et al. 2007). This suggests that age-related deficits in inhibiting distracting crossmodal information do not occur universally. However, in the case of temporal rate perception, my findings show that there is not an age-related deficit in filtering irrelevant information presented crossmodally, since task-irrelevant rates did not skew perceived rate to a greater extent in older adults.

Implications for neural processing of asynchronous rates in older adults

While older adults retain the perceptual ability to integrate asynchronous rates, it is unclear whether this indicates the preservation of the underlying neural substrate. The neural processing of my experimental stimuli (i.e. audiovisual sinusoidal amplitude modulation) has yet to be investigated, but similar dynamic audiovisual stimuli elicit activity in a network of cortical sites that includes primary auditory and visual cortices, STS and parietal and frontal cortices (Laing et al. 2015; Marchant & Driver 2012; Marchant et al. 2012; Noesselt et al. 2007; Nozaradan et al. 2012; Werner & Noppeney 2011; see Chapter 1 for a review). Physiological aging results in a decrease in grey matter volume, cortical thickness, white matter integrity and/or altered morphology in these cortical regions (Chang et al. 2015; Coffey et al. 1992; Harris et al. 2009; Kochunov et al. 2005; Lemaitre et al. 2012; Liu et al. 2010; Lutz et al. 2007; Peiffer et al. 2009; Pfefferbaum et al. 2005; Profant et al. 2014; Salat et al. 2005; Sowell et al. 2003). This raises the question of whether this neural substrate can support integration in older adults as it does in younger. Though Experiment 1B found that perceptual integration of auditory and visual rates was intact in older adults, performance may have been maintained through compensatory changes.
Furthermore, it has been proposed that age-related changes in resting state neural activity and functional connectivity between cortical regions may increase crossmodal interactions in older adults (Freiherr et al. 2013; Mozolic et al. 2012; Puschmann & Thiel 2017). These changes are expected to put older adults at a disadvantage when resolving the conflict induced by discrepant auditory and visual rates. Intrinsic functional connectivity between auditory and visual cortical networks increases with older age (Siman-Tov et al. 2017) and age-related high frequency hearing loss (Puschmann & Thiel 2017). This increased functional connectivity in older adults is associated with activation of the visual cortex in an auditory-only speech recognition task (Kuchinsky et al. 2012). Consequently, it has been proposed that these alterations in functional connectivity will increase audiovisual interaction in older adults across a variety of contexts (Puschmann & Thiel 2017). Relative to younger adults, older adults also exhibit greater neural activity in the auditory cortex during resting state conditions (i.e. when not performing a task) and consequently, during selective visual attention even though relative suppression of auditory cortex activity remains unchanged (Guerreiro et al. 2015; Hugenschmidt et al. 2009b). Therefore, this greater processing of task-irrelevant auditory information during a visual task is a mechanism for increased crossmodal distraction in older adults (Hugenschmidt et al. 2009b) and correlates with their behavioural performance (Guerreiro et al. 2015). When engaged in a task, older adults also show reduced deactivation of the default mode network relative to younger adults (Brown et al. 2015; Grady et al. 2006; Park et al. 2010; Persson et al. 2007). This network includes cortical regions associated with the passive monitoring of sensory information (Gusnard & Raichle 2001; Raichle et al. 2001). Therefore, greater processing of background sensory information due to increased activity in the default mode network has been put forward as a mechanism supporting enhanced multisensory integration in older adults (Freiherr et al. 2013; Mozolic et al. 2012). However, counter to these changes, the interaction of discrepant auditory and visual rates did not increase with age in Experiment 1B.

There may be compensatory mechanisms at work in the brain of the older adult that permits them to achieve equivalent integration to younger adults, despite the changes in structure and function detailed above. In younger adults, crossmodal distraction is minimised by decreasing activity in those areas of sensory cortex that are irrelevant to the task and increasing activity in task-relevant areas (Weissman et al. 2004). When selectively attending to a task-relevant sensory modality (e.g. vision) while distractors are presented in a task-irrelevant sensory modality (e.g. audition), multiple studies suggest that older adults retain the ability to supress
neural activity in task-irrelevant sensory cortex (Guerreiro et al. 2014b; Guerreiro et al. 2015; Hugenschmidt et al. 2009b). However, they deactivate different regions of the visual cortex than younger adults during an auditory task, which may reflect a change in the strategy employed to minimise crossmodal distraction (Peiffer et al. 2009). Older adults also show a greater increase in activity in task-relevant sensory cortex than younger adults when selectively attending to vision or audition during audiovisual stimulation (Townsend et al. 2006). Furthermore, they additionally recruit frontal and parietal cortices, which may reflect a compensatory mechanism (Townsend et al. 2006). In summary, while the aged brain may process more task-irrelevant sensory information, evidence suggests it can inhibit irrelevant crossmodal information, though in some cases it may use different strategies than a younger brain.

In addition to the study by Townsend et al. (2006), there are other indications that older adults recruit additional cortical regions to younger adults when performing audiovisual tasks. Older adult recruitment of parietal and prefrontal cortices is also seen in audiovisual facilitation of response times (Diaconescu et al. 2013). Furthermore, older adults show stronger neuronal oscillations in the theta frequency band in the frontal cortex during an audiovisual discrimination task (Yan et al. 2016). The coherence of oscillatory neural signals across different areas of the brain may be a mechanism subserving multisensory processing by permitting functional connectivity between auditory, visual and multisensory cortical regions (Senkowski et al. 2008). Modulation of neuronal oscillations coordinates neural tracking of the temporal structure of dynamic stimuli across auditory and visual cortices (Luo et al. 2010) and also occurs with attentional selection (Fu et al. 2001; Gomez-Ramirez et al. 2011; Senkowski et al. 2005) and illusory percepts induced by audiovisual incongruence (Bhattacharya et al. 2002; Kaiser et al. 2004). Therefore, there is an emerging trend for increased activity in the frontal cortex during audiovisual integration in older adults, which parallels findings in older adults performing cognitive (e.g. Cabeza et al. 2002; Cabeza et al. 2004; Davis et al. 2008; Langenecker et al. 2004), visual (Grady et al. 1994; Grady et al. 2000; Madden et al. 2007; Plomp et al. 2012) and auditory tasks (Wong et al. 2009). While this may be interpreted positively as an adaptive change, it could also be interpreted negatively as an inability to selectively activate the brain (known as dedifferentiation) or a sign of greater demand on neural resources (for review see Antonenko & Flöel 2014; Goh 2011; Grady 2012; Reuter-Lorenz & Lustig 2005). Further study is required to determine if the neural underpinnings of
audiovisual rate integration remain intact in aging and if not, how the aged brain manages to successfully compensate.

Comparison to older adult performance on other incongruent audiovisual tasks

As discussed in the literature review (Chapter 1), the effect of age on the integration of incongruent temporal auditory and visual information has been investigated for a range of tasks with different results. Equivalent integration across younger and older adult groups was reported for most investigations of the McGurk effect, where participants fuse incongruent auditory and visual syllables into a novel percept (Ballingham & Cienkowski 2004; Cienkowski & Carney 2002; Huyse et al. 2014; Stothart & Kazanina 2016). Though the physical signal contains auditory and visual temporal modulations (Chandrasekaran et al. 2009), the McGurk effect requires interpretation of this signal as speech (Eskelund et al. 2011; Stekelenburg & Vroomen 2012). As such, studies of the McGurk effect in older adults do not resolve the question of whether the integration of temporal modulation per se is affected by age. Since Experiment 1B used simple temporal rate stimuli without semantic meaning, the experiment demonstrated for the first time that the ability to integrate incongruent auditory and visual temporal modulations does not change in physiological aging. Only one other study has demonstrated age-invariant integration using simple temporal stimuli. In this study, older adults experienced the sound-induced flash fusion, where two flashes are perceived as one in the presence of a single beep, with the same frequency as younger adults (McGovern et al. 2014). Experiment 1B indicates that age-invariant integration of simple temporal cues is possible for longer, dynamic stimuli, not just brief transients.

However, age-invariant integration of asynchronous auditory and visual rates contrasts with the bulk of the literature on the integration of temporally incongruent auditory and visual cues in older adults. Older adults integrate auditory and visual cues into a combined percept over a larger window of time than younger adults. Compared to younger adults, older adults require greater temporal offsets between auditory and visual stimuli to perceive asynchrony (Chan et al. 2014a; Hay-Mccutcheon et al. 2009; Noel et al. 2016) or identify temporal order (De Boer-Schellekens & Vroomen 2014; Virsu et al. 2003). My results may be reconciled with this literature by considering whether the integration process changes with stimulus duration. For example, auditory transients enhance visual search but sustained, synchronous sinusoidal modulations do not (Kösem & Van Wassenhove 2012; Van der Burg et al. 2010). In line with
this, neural processing differs for transient and sustained audiovisual stimuli, since low level sensory cortex exhibits audiovisual enhancements in neural activity at stimulus onset while the STS shows enhancement for sinusoidal intensity modulation (Werner & Noppeney 2011). Furthermore, temporal coincidence of flashes and beeps does not influence discrimination of average temporal rate (Raposo et al. 2012) or judgements of whether auditory and visual patterns share the same temporal structure (Denison et al. 2013). In infant perceptual development, the ability to detect temporal offset of auditory and visual components of a learned temporal sequence develops after the ability to discriminate between different temporal sequences (Lewkowicz 2003), suggestive of different underlying mechanisms. Additionally, our ability to appreciate simultaneity or temporal order of auditory and visual cues ceases at repetition rates of approximately 4 Hz, which is theorized to result from a central limiting mechanism (Vroomen & Keetels 2010). Consequently, it may not be appropriate to compare integration of temporally offset, brief auditory and visual stimuli with integration of longer, coincident stimuli that evolve dynamically over time.

Moreover, this distinction may also be relevant for comparison of my results for the asynchronous temporal rate task to the sound-induced flash illusion. In this illusion, apparent doubling of a single flash is induced by two beeps (Shams et al. 2000). Older adults are known to be more susceptible to the sound-induced flash illusion (De Loss et al. 2013; McGovern et al. 2014; Setti et al. 2011). This is in concordance with the illusion occurring more frequently in those with larger temporal binding windows (Stevenson et al. 2012) and occurring at larger temporal offsets in older adults than in younger adults (McGovern et al. 2014; Setti et al. 2011). Furthermore, counting stimulus number is not a feasible strategy when the rate of repetition is 10 Hz or above as individual peaks cannot be individuated (Edwards & Chang 2013; Joris et al. 2004; Nourski & Brugge 2011; Van De Grind et al. 1973) and as such, estimates of number are duration based for large numbers of repetitive stimuli (Philippi et al. 2011). Even at slow rates where individuation is possible, the influence of audition on perceived flicker rate is inconsistent with a counting strategy since it is independent of stimulus duration (Berger & Pelli 2001). As such, the different effect of age on distortions in perceived number and distortions in perceived rate due to audiovisual incongruence can also be reconciled upon consideration of the underlying task differences.

In summary, age-related effects on audiovisual perception are likely to be task-specific, rather than reflecting a global effect of age, as speculated in the literature review. In line with this, preliminary evidence suggests that the tendency of an individual to bind auditory and visual
cues, and hence the strength of observed integration effects, may be task-specific rather than governed by a single, global mechanism within the brain (Odegaard & Shams 2016). On the other hand, flexibility in the use of common neural mechanisms of integration as an adaption to stimulus factors and context may underlie this non-uniformity in the integration process across tasks (van Atteveldt et al. 2014). As such, it is less a case of the results of Experiment 1B being inconsistent with the literature, and more a case of adding further diversity to existing investigations of audiovisual integration in older adults by providing another example of integration that is unaffected by age.

Integration of synchronous auditory and visual rates in aging

Implications for the neural processing of synchronous rates in older adults

In Experiment 1C, audiovisual rate discrimination thresholds observed in older adults were significantly worse than predictions based on unisensory discrimination thresholds (see Chapter 3). Perceptual inference regarding temporal rate is based on uncertain evidence, reflecting sensitivity limits, environmental noise and neural variability. This uncertainty may be reduced by integrating rate information from audition and vision in a statistically optimal fashion (Koene et al. 2007). This is achieved by weighting each cue by its reliability (the inverse of its variance) so the combined temporal rate estimate has the smallest possible variance associated with it in accordance with a model of maximum likelihood estimation (Ernst & Bülthoff 2004; Fetsch et al. 2013; Witten & Knudsen 2005). As a consequence, when auditory and visual rates are equally reliable, a $\sqrt{2}$ improvement in temporal rate discrimination is expected to result from integration (Koene et al. 2007). Since older adult audiovisual rate discrimination thresholds were worse than the maximum likelihood prediction, this may reflect a suboptimal integration process in older adults, as has been observed on other multisensory tasks in physiological aging (Bates & Wolbers 2014). Of course, systematic investigation of audiovisual rate discrimination across a range of differences in intersensory reliability would provide a clearer indication of whether older adults weight auditory and visual rates optimally.

It is unclear how healthy aging could result in a suboptimal integration process. Models seeking to explain individual variability in multisensory perception implicate suboptimal inference resulting from approximate combination rules that can lead to overweighting of the less reliable cue (Beck et al. 2012). However, when auditory and visual rates are equally
reliable, unequal weighting will still produce a $\sqrt{2}$ improvement. In this scenario, approximate combination rules would only be disadvantageous if momentary fluctuations in sensory or neural noise sufficiently altered the relative reliability of auditory and visual rates. Electrophysiological studies in animals show that older age is accompanied by increased variability in the neural responses to visual stimuli (Yang et al. 2009) and greater spontaneous neural activity in auditory and visual cortex (Overton & Recanzone 2016; Yang et al. 2008). Greater variability in the neural response to repeat presentations of identical stimuli in older adults may have caused fluctuations in reliability across trials. Suboptimal inference can also result from variability in the decision process that arises from noise added at the computational stage of combining sensory cues (Acerbi et al. 2014). Whether physiological aging increases the tendency for combination rules to be approximate rather than probabilistic, or makes the decision process noisier, is a question for further study.

Another possibility is that physiological aging impairs the neuronal computations that underlie statistically optimal integration, rendering the process suboptimal. The neuronal representation of sensory reliability is proposed to result from sensory information being encoded by a population of neurons and decoded as an estimate of the stimulus property with some associated uncertainty due to variability in the responses of individual neurons (Jazayeri & Movshon 2006; Pouget et al. 2000; Sanger 1996; Zemel et al. 1998). A feedforward model of multisensory integration proposes that linear combination of two population codes, each from a different sensory modality, is sufficient to produce statistically optimal multisensory estimates of the stimulus property (Ma et al. 2006). Normalisation (that is, dividing by the sum of responses from the wider population of multisensory neurons) permits the weights to vary with unimodal reliability (Ohshiro et al. 2011). Electrophysiological studies in animals have provided some support that multisensory neuronal computations occur in this manner (Fetsch et al. 2011; Morgan et al. 2008). How aging affects this computation process has yet to be investigated, but here neural noise is also a candidate for age-related deficits. Given that, within trials, variable neural activity permits encoding of sensory reliability (Jazayeri & Movshon 2006; Pouget et al. 2000; Sanger 1996; Zemel et al. 1998), greater neural variability in older adults might be expected to be beneficial. However, across trials, increased neural variability can impair fine discrimination (Butts & Goldman 2006). As a consequence, the aging process may limit fine discrimination but spare coarse discrimination, as suggested by Baum and Beauchamp (2014). Thus, while some neural variability may be advantageous, it has been proposed that excessive variability may degrade multisensory representations (Baum et al.

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2016). For example, older adults have been shown to exhibit greater within-subject variability in neural activity on an audiovisual speech task, which may explain poorer audiovisual speech perception in older adults (Baum & Beauchamp 2014). Further research is required to clarify this issue.

Alternatively, statistically optimal integration could be implemented neurally as a decentralised process, which would be more robust to localised dysfunction and thus any age-related degradation of the neural substrate (Zhang et al. 2016). This proposal is consistent with the fact that multisensory integration often involves a distributed network of reciprocally connected areas (Bizley et al. 2016a; Chandrasekaran 2017; Yau et al. 2015) rather than a single region receiving feedforward unimodal inputs as proposed in the model by Ma et al. (2006). Indeed, functional magnetic resonance imaging in humans indicates that multisensory regions dynamically reweight their connectivity to unimodal sensory cortices according to sensory reliability (Beauchamp et al. 2010; Noppeney et al. 2010). There is some preliminary evidence of age-related changes in the ability to dynamically alter functional connectivity between different brain regions (Yin et al. 2016), but whether functionally connectivity in multisensory processing is similarly affected has yet to be investigated.

Moreover, in a postural task involving the integration of visual, somatosensory and vestibular cues, degraded information in one modality resulted in more distributed neural activity in older adults (Lin et al. 2017). This suggests that sensory reweighting requires more neural resources in older adults (Lin et al. 2017). Older adults are also less adept at reweighting visual information for the control of posture while walking (Berard et al. 2012). If older adults need to recruit more regions to perform probabilistic inference as a general trait, this less efficient process may impair the advantage of dual auditory and visual rate presentation. Lastly, it has been proposed that multisensory enhancement requires balanced crossmodal inhibition and excitation of sensory-specific cortex (Hoshino 2014). Given that there is a suggested age-related decline in GABA levels within the brain (Gao et al. 2013), impaired enhancement could ensue from an age-related inhibitory deficit. In summary, there are many potential explanations for why the integration process in older adults might be suboptimal, but insufficient evidence in the literature to pick between them. Statistically optimal inference is a cornerstone of multisensory theory but evidence is emerging that inference can be suboptimal in older adults (see Bates & Wolbers 2014). Given this, when and why older adult inference is suboptimal may receive more attention in the literature in the future.
Conversely, it may be that audiovisual temporal rate discrimination thresholds were less than the maximum likelihood prediction in older adults for reasons other than an impaired integration process. Integration may be susceptible to any age-related decline in the sensory coding of rate information, such as decreased phase locking to amplitude modulation for a 500 Hz carrier (Leigh-Paffenroth & Fowler 2006). Therefore, despite physical synchrony, intersensory asynchrony in the neural representation of auditory and visual rates in older adults could constrain the benefit they obtain from integrating identical rates. However, audiovisual facilitation of temporal rate discrimination occurs whether auditory and visual cues are presented simultaneously or sequentially (Koene et al. 2007). In fact, evidence suggests that auditory and visual rates are compared independent of their relative timing at a central site, where phase information is not retained (Raposo et al. 2012; Stockman et al. 2004). Based on these studies, it seems unlikely that the increased precision of temporal rate discrimination under audiovisual conditions in younger adults relies on intersensory phase synchrony. Furthermore, these studies suggest that the time-varying phase difference introduced when visual luminance and auditory amplitude were modulated at different temporal rates in Experiment 1B was unlikely to influence their integration. In fact, while periodically modulated auditory and visual stimuli elicit time-locked oscillatory neural activity in the auditory and visual cortex, respectively, audiovisual interactions in oscillatory responses are not evident at this level of the cortical hierarchy (Giani et al. 2012). This further suggests that the integration of auditory and visual temporal modulations occurs at a central cortical site, rather than relying on precise timing information in lower level sensory cortex. However, a dissenting study reported that audiovisual facilitation of rate discrimination was statistically optimal when auditory and visual rates coincided both spatially and temporally but suboptimal when they did not (Locke & Landy 2016). Consequently, intersensory asynchrony in the relative timing of auditory and visual rate representations cannot be ruled out as a factor contributing to suboptimal integration in older adults.

Another consideration is whether older adults can effectively spread their attention across auditory and visual cues when discriminating changes in temporal rate based on both sensory modalities. When younger adults distribute their attention between audition and vision on an audiovisual response time task rather than selectively attending to vision, their event related potentials are reduced in amplitude (Mishra & Gazzaley 2013). However, older adults only demonstrate similar changes if they are high performers (Mishra & Gazzaley 2013). Furthermore, older adults show a reduced capacity to divide attention between sensory
modalities when estimating the duration of auditory and visual events concurrently (McAuley et al. 2010). An age-related deficit in divided attention could feasibly impair the ability to integrate auditory and visual rates. However, as discussed for Experiment 1B, the role of goal-directed attention in audiovisual integration of temporal rate is as yet unknown.

Comparison to older adult performance on other congruent audiovisual tasks

Age-related impairments in audiovisual integration are not commonly reported in the literature. In the temporal domain, older adults exhibit decreased integration in the audiovisual bounce effect, since they perceive bouncing less frequently than younger adults (Roudaia et al. 2013). Enhancement of auditory speech detection by the addition of visible speech cues is also reduced in older adults (Tye-Murray et al. 2011). Additionally, audiovisual integration on speech recognition tasks is impaired in older adults when auditory or visual speech cues are degraded (Gordon & Allen 2009; Huyse et al. 2014; Stevenson et al. 2015; Tye-Murray et al. 2010; Tye-Murray et al. 2008; Tye-Murray et al. 2011) or words are lexically difficult (Dey & Sommers 2015). Outside the temporal domain, there is an age-related decrease in the integration of visual landmark and vestibular self-motion cues when navigating through space (Bates & Wolbers 2014), as mentioned in the previous section. Typically, having congruent auditory and visual cues benefits older adults more than younger adults, leading to the supposition that audiovisual integration tends to be enhanced in older adults (for reviews see de Dieuleveult et al. 2017; Freiherr et al. 2013; Mozolic et al. 2012). Even when crossmodal interactions are not greater in older adults, integration is at least maintained, as is the case for the recognition of congruent auditory and visual speech (Ballingham & Cienkowski 2004; Gordon & Allen 2009; Huyse et al. 2014; Legault et al. 2010; Smayda et al. 2016; Sommers & Phelps 2016; Sommers et al. 2005; Spehar et al. 2008; Tye-Murray et al. 2010; Winneke & Phillips 2011). Deficits in audiovisual integration have otherwise only been reported in manifest sensory impairment [such as amblyopia (Burgmeier et al. 2015) or hearing loss (Musacchia et al. 2009)] and disease [for example Parkinson’s (Fearon et al. 2015) and Alzheimer’s disease (Delbeuck et al. 2007)].

The most researched instance of enhanced audiovisual integration in aging is the greater audiovisual facilitation of response times in older compared to younger adults (Diederich et al. 2008; Hugenschmidt et al. 2009a; Laurienti et al. 2006; Peiffer et al. 2007; Ren et al. 2017). However, some studies report that audiovisual facilitation of response times is greater in their
younger participants, not the older ones (Mahoney et al. 2011; Stephen et al. 2010), and the reasons for these exceptions are unclear. In one study, suppression of the neural response to audiovisual stimuli was associated with slower response times in older adults, which may reflect impaired cortical integration (Stephen et al. 2010). Conversely, in another study, modelling implicated enhanced neural integration in the greater multisensory gains exhibited by older adults (Diederich et al. 2008). Furthermore, when older adults integrate visual and somatosensory stimuli, multisensory gains in response times are greater in those with poorer visual and somatosensory abilities (Dumas et al. 2016; Mahoney et al. 2014). It is plausible that age-related changes in sensory function may likewise influence audiovisual facilitation of response times in older adults.

Indeed, it has been postulated that reduced saliency of experimental stimuli may lead to apparently enhanced integration in older adult participants due to an interaction of age-related sensory loss with the principle of inverse effectiveness (Freiherr et al. 2013; Mozolic et al. 2012). This principle holds that the less effective unisensory stimuli are at eliciting a response on their own, the greater the relative change in response when they are integrated (Meredith & Stein 1983). Unfortunately, studies on the effect of aging on audiovisual response times include insufficient screening to exclude age-related sensory loss as a confounding factor. Vision and hearing were simply reported as normal (Diederich et al. 2008; Ren et al. 2017) or participants were screened for moderate vision loss (worse than 20/40 visual acuity) and hearing loss (worse than 40 or 50 dB) only (Hugenschmidt et al. 2009a; Laurienti et al. 2006; Peiffer et al. 2007). Subtle changes due to aging or pathology are uncaptured by the basic measures of visual acuity (Haegerstrom-Portnoy et al. 1999; Haegerstrom-Portnoy et al. 2000; Owsley 2011) and audiometric thresholds (Füllgrabe et al. 2014; Plack et al. 2014). Consequently, though older and younger adults were presented with the same physical stimuli, they may have been less salient to the older participants. Therefore, in theory, these stimuli could have induced a greater proportionate change in response times in the older adult cohort.

Though enhanced integration is often reported for audiovisual response times in older adults, it is not necessarily reasonable to expect this to translate to audiovisual rate discrimination. Firstly, in Experiment 1C, the reliability of the auditory temporal rate was individually matched to visual reliability, which didn’t differ between age groups (see Experiment 1A: flicker discrimination). Consequently, greater audiovisual gains for temporal rate discrimination were not anticipated in older relative to younger adults, as auditory and visual rates were equally
effective across age groups. Secondly, the integration mechanisms for response times and temporal rate likely differ. Auditory (Arnott et al. 2004; Zündorf et al. 2016), visual (Goodale 2014) and audiovisual pathways (Sestieri et al. 2006) are segregated into ventral and dorsal streams, which is believed to lead to a dissociation between the neural underpinnings of perception and action (Goodale 2014; Leone & McCourt 2015). The integration mechanism for response times may also be more susceptible to multisensory enhancement than the mechanism for temporal rate judgements. Animal studies indicate that crossmodal stimulation shortens neural response latency and causes amplitude enhancement mostly at the beginning of the response (Rowland, Rowland, Quessy, Stanford, & Stein, 2007). Likewise, in humans, enhanced neural responses occur for brief but not sustained audiovisual stimuli (Werner & Noppeney 2011). This pattern of enhancement is expected to favour response time tasks, where speed is emphasized, more than slower perceptual judgements such as temporal rate.

However, the possibility of enhanced audiovisual integration for temporal rate cannot be ruled out based on a single aspect of performance. The advantage in integrating auditory and visual cues with congruent temporal structure has been shown for other perceptual measures, such as spatial localisation (Parise et al. 2013) and detection of changes in intensity (Marchant et al. 2012). Temporal correspondence can also enhance behaviour since it shortens response times (Marchant et al. 2012) and facilitates tapping in time to a rhythm (Wojtczak & Viemeister 2008). Consequently, other avenues for multisensory facilitation through integration of congruent auditory and visual rates could be intact in older adults, but they were not assessed in this experiment. Further investigation is required to determine whether older adults benefit from the provision of rate information across the senses in other ways, or whether there is a global deficit in perception and behaviour driven by audiovisual rate content.

Age-related differences in the integration of synchronous versus asynchronous rates

Older adults exhibited a deficit when integrating identical but not conflicting rates, suggesting a dissociation between their respective integration mechanisms and their susceptibility to age-related decline. Currently, it is not known whether there is subspecialisation according to temporal correspondence (i.e. rate synchrony versus asynchrony) within the network of cortical regions processing audiovisual temporal rate. However, neural processing pathways for auditory and visual stimuli are known to vary with stimulus onset asynchrony for temporally patterned stimuli, including speech and both regularly and irregular times streams.
of transients. Specifically, the neural processing of coincident vs. temporally offset stimuli occurs in distinct subregions within the STS (Noesselt et al. 2012) and recruits a network of different cortical regions (Dhamala et al. 2007). Auditory and visual stimuli also differentially affect the strength of functional connectivity between regions when they are coincident compared to temporally offset (Noesselt et al. 2012; Noesselt et al. 2007). If processing pathways for temporal rate are similarly separated based on temporal correspondence, then a selective effect of aging on audiovisual integration of synchronous rates could occur if that pathway was particularly vulnerable to the aging process. A similar argument was raised for the selective effect of aging on sound-induced flash fission (McGovern et al. 2014), since sound-induced flash fission and flash fusion are likely subserved by different neural mechanisms (Mishra et al. 2008). Age-related changes are known to occur in cortical regions with multisensory functions, such as decreased grey matter (Sowell et al. 2003) and altered morphology in the STS (Kochunov et al. 2005; Liu et al. 2010). However, it is not known whether some subregions are relatively spared by the aging process. Further work is needed to clarify the neural pathways involved in integrating synchronous and asynchronous rates, and whether there are any age-related differences.

The role of age-related cognitive decline

A wide range of cognitive abilities are detrimentally affected by aging, including processing speed (Salthouse 2000), and attentional control and working memory (Fabiani 2012). In my study, older adult participants were fit and active members of the community, many of whom were still engaged productively in volunteering or employment. However, given that participant screening did not include a formal cognitive assessment, it could be asked whether age-related cognitive decline may have detrimentally affected older adult performance. Since no age-related differences were found in the integration of asynchronous auditory and visual rates (Experiment 1B), there is no need to invoke cognitive aging as a potential explanation of age-related declines in performance. Though there were age-related differences in the integration of synchronous auditory and visual rates (Experiment 1C), it seems unlikely this finding results from impaired cognition in the older participants, as discussed in more detail below.

Firstly, the experiment did not require explicit judgements of the relative timing of when stimuli occurred or measure response times, for which it might be reasonable to consider any potential effect of reduced processing speed. Rather, participants were asked which of two
intervals contained a stimulus oscillating at a faster rate and their responses were self-paced. For combined presentation of auditory and visual rates, research indicates that precise temporal detail such as relative phase is not retained at the cortical locus of auditory and visual rate comparison, suggesting a slow centralised mechanism based on rate information alone (Nishida & Fujisaki 2010; Raposo et al. 2012; Stockman et al. 2004). If there was a longer delay before temporal rate information reached central processing cites in older adults, it seems unlikely that this would have affected results since participant responses were self-paced.

Secondly, comparable psychometric function slopes between younger and older adults was a consistent finding across tasks (Experiment 1A: flicker task, Experiment 1B: the two asynchronous tasks and Experiment 1C: the synchronous task). Therefore, the capacity of the older adult participants to compare successive intervals in a two-interval forced choice task was intact. Guess and lapse rates for the psychometric function on the audiovisual rate discrimination task were comparable across age groups, demonstrating that older participants performed the task as reliably as the younger adults. Furthermore, individual discrimination thresholds varied over a similar range of values in both age groups, indicating that the older adult failure to attain the maximum likelihood prediction did not stem from a few outlying older adults with atypically poor performance. Altogether, this argues against any significant influence of age-related impairments in attentional control or working memory on the ability of older adults to complete the task. Furthermore, there is no rationale for cognitive aging to interact with rate disparity and produce a deficit when auditory and visual rates were identical but not when they were conflicting.

Reliability-based integration and age-related sensory loss

Experiment 2 demonstrated that the increased amplitude modulation sensitivity of younger compared to older adults was sufficient to alter the relative influence of audition and vision on perceived rate. There is some preliminary evidence in the literature that changes in sensory weighting in multisensory integration may be a feature of healthy aging. For example, older adults perform worse than younger adults when fixating auditory targets during an orientation task (Dobreva et al. 2012). Consequently, vision dominates the fixation of audiovisual targets in older adults (Dobreva et al. 2012). Furthermore, greater facilitation of audiovisual response times occurs relative to auditory but not visual performance in older adults on an object recognition task (Diaconescu et al. 2013). In this instance, visual dominance may stem from the
fact that visual response times are faster than auditory ones (Diaconescu et al. 2013). In line with this, the degree of response time facilitation for combined somatosensory and visual stimuli is modulated by sensory sensitivity (Dumas et al. 2016), with facilitation absent in a subgroup of older adults with fast response times to somatosensory stimuli (Dumas et al. 2015; Mahoney et al. 2014). Together, these studies demonstrate that multisensory perception and behaviour in older adults is influenced by unimodal sensory processing.

The findings of Experiments 1 and 2 underscore the value in separating the effects of age on relative sensory reliability from its effects on the process of integration itself. Research already indicates that sensory reliability influences the perception of audiovisual speech. Age-related differences in audiovisual speech perception occur because auditory and visual speech recognition is poorer in older adults, not because integration is worse (Gordon & Allen 2009; Sommers et al. 2005; Tye-Murray et al. 2016). As discussed in the literature review (see Chapter 1), it is well known that healthy aging impairs many aspects of auditory and visual function, impacting both the perception of basic stimulus attributes and performance on complex tasks (for review see Faubert 2002; Fitzgibbons & Gordon-Salant 1996; Owsley 2011; Stach et al. 2009). Though further study is needed, there is a general trend for uneven age-related decline across sensory modalities (Čeponienė et al. 2008; Cliff et al. 2013; Diaconescu et al. 2013; Guerreiro et al. 2013; Guerreiro & Van Gerven 2011; Humes et al. 2007; Lustig & Meck 2011). Unfortunately, the definition of normal vision and hearing varies across studies of integration in aging, and it is not uncommon for studies to report screening measures for vision only (e.g. Fiacconi et al. 2013; Roudaia et al. 2013) or audition only (e.g. Diaconescu et al. 2013; Puschmann et al. 2014; Sekiyama et al. 2014) despite using audiovisual stimuli. Given the increased prevalence of hearing loss and eye disease with age (Cruickshanks et al. 2003; Wang et al. 2000), it is unclear whether individual older participants in these studies may have greater sensory decline in audition relative to vision, or vice versa. Consequently, the extent to which relative reliability modifies the interpretation of studies reporting greater crossmodal interactions in older adults remains to be seen.

Typically, in studies investigating the impact of aging on integration, older and younger adults are presented with the same physical auditory and visual stimuli and changes in audiovisual perception are taken as a measure of the degree of integration. However, some of the experimental tasks employed in aging studies are known to be affected by sensory reliability in younger adults. For example, older adults are more prone to the sound-induced flash illusion (De Loss et al. 2013; McGovern et al. 2014; Setti et al. 2011). Susceptibility to the sound-
induced flash illusion varies with the saliency of auditory and visual cues (Andersen et al. 2005; Kumpik et al. 2014; Wozny et al. 2008) such that a relative loss in flash discriminability with age could theoretically lead to a greater tendency to perceive the illusion. Further research is required to determine whether age-related sensory loss mediates the greater susceptibility of older adults to the illusion. By the same token, relative reliability may play a role in susceptibility to the McGurk effect, since the effect is increased for more intelligible visual speech (Strand et al. 2014) and less intelligible auditory speech (Sekiyama & Tohkura 1991). Some studies report that older adults are more susceptible to the McGurk effect (Sekiyama et al. 2014; Setti et al. 2013) although most do not (Ballingham & Cienkowski 2004; Cienkowski & Carney 2002; Huyse et al. 2014; Stothart & Kazanina 2016). However, no study to date has controlled for the relative intelligibility of auditory and visual speech, which may contribute to the variability in results across studies.

Note that a relationship between sensory reliability and integration on a particular task does not necessarily mean that age-related sensory loss will explain age-related differences. For instance, older adults perceive auditory and visual stimuli as simultaneous at wider stimulus onset asynchronies than their younger counterparts (Hay-Mccutcheon et al. 2009; Noel et al. 2016). In younger adults, larger stimulus onset asynchronies are required to correctly perceive that simple auditory and visual stimuli are asynchronous for low relative to high intensities (Krueger Fister et al. 2016). However, older adults still needed wider temporal offsets to perceive asynchrony when stimulus intensity was scaled to individual detection thresholds, indicating the effect was independent of age-related declines in sensory sensitivity (Chan et al. 2014a). In another example, older adults perform worse than younger adults when tapping in time to randomly jittered auditory beats, but show the same proportionate increase in performance when a tactile cue is added (Elliott et al. 2011). Studies presenting stimuli at individually determined suprathreshold levels are needed to elucidate, on a case by case basis, whether known age-related changes in audiovisual perception are solely attributable to integration, or whether age-related changes in relative sensory reliability play a role.

**Future directions**

In discussing the results of Experiments 1 and 2, some outstanding questions on the effect of aging on audiovisual temporal rate integration have emerged. Firstly, older adults can flexibly integrate auditory and visual rates according to rate asynchrony across the range of rate disparities investigated in Experiment 1B. However, since complete segregation of auditory
and visual rate information was not observed in either age group, the question remains whether older adults can successfully resolve audiovisual conflict at large disparities. Given that differences were not observed across a wide range of rates (8 to 16 Hz), this seems unlikely. Hypothetically, an argument could be made that segregation will occur at smaller disparities in older relative to younger adults due to the mediating influence of prior knowledge about likely correspondence accumulated over a longer lifespan. However, the benefits obtained from increasing audiovisual experience may reach a saturation point, such that an individual learns auditory and visual correspondences during their development but, by adulthood, has acquired full knowledge of the world’s audiovisual relationships. Equally, older adults may be more tolerant of audiovisual asynchrony as suggested by greater thresholds for perceiving non-simultaneity (Chan et al. 2014a; Noel et al. 2016) and temporal order (De Boer-Schellekens & Vroomen 2014; Virsu et al. 2003). A follow up experiment could employ the same paradigm as Experiment 1 but test at faster task-irrelevant rates (for example 18 and 20 Hz) to determine the point at which complete segregation of auditory and visual rates occurs for older compared to younger adults. However, in testing at larger discrepancies, the percept of task-irrelevant and standard rates may differ significantly due to changes in the perceptual quality of auditory rate (Fastl 1997) and the perceived modulation depth of flicker and flutter (Mandler 1984; Marks 1970).

Secondly, older adults retained their ability to integrate asynchronous auditory and visual rates when reliability was balanced across the senses. However, in audiovisual speech perception, older adults exhibit selective deficits in audiovisual integration when either the auditory or visual cue is significantly degraded (Gordon & Allen 2009; Huyse et al. 2014; Stevenson et al. 2015; Tye-Murray et al. 2010; Tye-Murray et al. 2008; Tye-Murray et al. 2011). Other studies also indicate age-related impairments in dynamically adjusting the weights of cues across different sensory modalities (Berard et al. 2012; Lin et al. 2017). Further experiments could address whether older adults still retain the ability to integrate when the reliability of auditory rate is selectively degraded and if they can appropriately reweight auditory and visual information when relative reliability undergoes dynamic shifts. As in the original study by Roach et al. (2006), the auditory rate stimulus can be degraded by determining on an individual basis the auditory modulation depth that corresponds to a flutter rate discrimination threshold double that of the flicker rate discrimination threshold. However, flutter rate discrimination thresholds only vary linearly with auditory modulation depth over a restricted range (see Figure 2.9). Therefore, it may be necessary to test flutter rate discrimination at
additional modulation depths to describe the relationship as a power function in order to more accurately calculate the desired modulation depth.

How a broad range of differences in auditory and visual reliability affects integration in older adults is of relevance because relative reliability in older adults may be affected by physical stimulus characteristics other than auditory modulation depth. For example, age-related losses in sensitivity to auditory amplitude modulation or visual luminance modulation are typically reported as greater at higher temporal rates (Ajith Kumar & Sangamanatha 2011; He et al. 2008; Kim & Mayer 1994; Mayer et al. 1988). The level of impairment in audition relative to vision at higher rates is unknown. Further investigation, using the same paradigm as Experiment 1A, is required to determine the feasibility of matching rate discriminability at faster temporal rates, where thresholds will be elevated (Lee 1994; Mandler 1984; Waugh & Hess 1994). However, rate discrimination thresholds appear broadly comparable across the senses at faster rates upon inspection of previous research (Lee 1994; Mandler 1984; Waugh & Hess 1994), which suggests this approach may be feasible. The limiting factor on the temporal rate selected is the critical flicker frequency, above which flicker is no longer visible (Landis 1954), or the auditory transition frequency, where spectral cues contribute to amplitude modulation sensitivity (Fassel & Kohlrausch 1996; Sek & Moore 1994), whichever is lower for the stimulus parameters.

Given that older adults are less sensitive to luminance modulation (Wright 1985; Mayer et al. 1988; Kim and Mayer 1994), age-related deficits in flicker rate discrimination may emerge at modulation depths closer to threshold. A follow up experiment could address this by assessing flicker rate discrimination at a range of temporal contrasts to see if age-related deficits emerge for less modulated flicker. In some older adults, relative reliability will also vary due to impairments in flicker sensitivity due to ocular disease, such as glaucoma (Breton et al. 1991; Tyler 1981) or age-related macular degeneration (Mayer 1992c; Mayer et al. 1992a; Mayer et al. 1992b; Mayer et al. 1994), and impairments in auditory temporal rate discrimination due to sensorineural hearing loss (Grant et al. 1998). Consequently, the experience of audiovisual temporal rate in an older adult could involve a range of relative reliabilities. Future experiments could assess how age-related ocular disease and hearing loss affect the relative reliability of flicker and flutter rate, the integration of asynchronous auditory and visual rates and the integration of synchronous auditory and visual rates by employing the experimental design described for Experiments 1A, 1B and 1C, respectively.
Thirdly, research is needed in younger adults to definitively identify the neural substrate underlying the integration of auditory and visual temporal rate. In keeping with other studies employing audiovisual temporal stimuli (e.g. Marchant et al. 2012; Noesselt et al. 2007; Werner & Noppeney 2011), functional magnetic resonance imaging could be employed to determine changes in neural activity and functional connectivity elicited by dual compared to separate presentation of auditory and visual rates. Event related potentials could also be informative, providing additional information on the latency of audiovisual interactions. Both modalities would provide a means of investigating differences between synchronous and asynchronous conditions. Building on this, any age-related differences in the neural process of audiovisual temporal rate integration could be investigated. Based on older adult perceptions of audiovisual temporal rates, there are two main questions. Do older adults retain the perceptual ability to integrate asynchronous auditory and visual rates due to an intact neural mechanism or through compensatory activity? Given that older adults benefited less from integrating synchronous auditory and visual rates, is the neural process of synchronous rate integration affected by age?

Conclusion

For a slow temporal modulation rate, older age adversely affected the precision of estimated rate in audition relative to vision due to an age-related impairment in sensitivity to auditory amplitude modulation. This selective auditory impairment validated the experimental approach of balancing auditory and visual rate reliability to uncover whether audiovisual integration was affected by aging without the confound of asymmetric age-related sensory losses between audition and vision. This raises the question of how relative sensory reliability may mediate reports of greater audiovisual interactions in the literature, which are typically taken as evidence of enhanced integration.

When age-related sensory loss was normalised, the perceptual ability to integrate asynchronous auditory and visual rates was preserved in aging, since both perceived rate and rate discrimination were unaffected by older age. However, the final coherent percept of audiovisual rate is still expected to differ between younger and older adults. The age-related difference in amplitude modulation sensitivity was sufficient to alter sensory weighting, since audition dominated rate perception in younger adults for a modulation depth that equalised auditory and visual influence in older adults. Note that integration cannot simply compensate for age-related sensory decline, since greater reliance on vision will put older adults at more of
a disadvantage when making auditory rate judgements but less of one when making visual rate judgements, compared to younger adults.

In contrast, the integration of synchronous auditory and visual rates was impaired in healthy aging. Older adults did not combine synchronous rate information in a statistically optimal fashion, exhibiting less audiovisual facilitation of temporal rate discrimination than expected. Since this deficit was apparent when age-related sensory loss was normalised, it will be compounded by the age-related impairment in auditory reliability. Since younger adults exhibit only small improvements in temporal rate discrimination under audiovisual conditions, significant age-related differences in an everyday setting may be driven more by the deficit in auditory sensitivity than the deficit in integration.

In summary, the older adult experience of audiovisual temporal rate context is a complex product of the age-related interaction between rate synchrony and integration ability, and the age-related decline in auditory temporal rate reliability.
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*Canadian Journal of Experimental Psychology, 56*(3), 139.


Appendix A: Plain language statement

Participant information

Principal Investigator: Dr Allison M McKendrick
Student Investigator: Ms Cassandra Brooks (MPhil candidate)
Contact details: Laboratory phone 9349 7479, email: allisonmx@unimelb.edu.au
Location of testing: Clinical Psychophysics Unit, Department of Optometry and Vision Sciences, University of Melbourne.

Project title: Audio-visual integration and the role of aging and sensory decline.
Approval: University of Melbourne HREC 1034933
Funding: Australian Research Council Future Fellowship FT0990930

Introduction
You are invited to participate in a research study studying how the brain combines information from sight and sound. This project is specifically interested in how healthy normal ageing changes the way such information is processed. People between the ages of 20-35 and 60-75 years are invited to participate in this study.

It is well known that many aspects of both hearing and vision deteriorate with age. Typically, hearing performance and vision is studied independently. In this project, we will study performance for tasks where sight and sound are presented together. This project will enhance our knowledge of how ageing impacts on the interpretation of visual and auditory information regarding the timing and location of objects, essential precursors to many real-world tasks (for example: driving, particularly in the presence of modern distractions such as mobile phones; interpreting speech and hazard avoidance).

This study has been approved by The University of Melbourne Human Research Ethics Committee.

What will I be asked to do?
If you choose to participate in the study you will be invited to attend a series of up to four visits. Prior to scheduling your first visit, we will conduct a brief telephone interview to make sure you meet the main eligibility criteria (age range, self-reported normal hearing and vision, and no known systemic conditions known to affect vision or hearing). As some of the experiments involve small flickering light stimuli (see item 3 below), people with a known history of epilepsy will not be eligible to participate in this study.

1) Screening tests of hearing and vision
We will conduct a series of tests to determine whether you are eligible to participate in the study. A series of routine vision tests will be performed by a qualified optometrist. This includes measurement of intraocular pressure, which involves the use of local anesthetic eye drops. These eye drops may cause a temporary stinging on instillation. Rarely, they can cause a local allergic reaction and therefore it is important that you advise us of any previous reactions to eye drops. No research has been conducted regarding the safety of these eye drops in pregnant or breastfeeding women. It is important that you tell us if you are currently breastfeeding, pregnant or think you may be pregnant as, if so, an alternative technique for measuring intraocular pressure will be used, which does not require the use of drops.
The results of the eye examination may result in your exclusion from the study. Exclusion criteria include high refractive error, decreased vision, and any ocular health abnormality that is not considered normal for age. We will also conduct an abbreviated hearing test that will measure the sound levels required for you to hear tones of different frequencies. In the event of an abnormality being detected on these screening tests, you will be given advice by the Principal Investigator, who will correspond with your regular health-care practitioner at your request, to ensure appropriate follow-up.

2) Cognitive status examination (first visit only)
The Mini-Mental State Examination (MMSE) is a widely used, brief, quantitative measure of cognitive status in adults. This test will involve basic comprehension, reading, writing, and drawing tasks and will not be used to assess your suitability for the study, but simply to further quantify your results for the tests described below. You will not receive feedback in regards to this test.

2) Computerised tests of vision and hearing
The experiments will require observers to sit in a dimly lit room and observe a computer screen. We will test your ability to perceive information about the location and timing of briefly presented lights (short pulses and briefly flickering stimuli) and sounds (short tone bursts and briefly oscillating tones). The lights and sounds will either be presented at the same time, or independently. You will be required to respond by pressing a button on a computer mouse or keyboard. All of these tests are well accepted techniques and do not involve any invasive or painful procedure. Each individual test will take no longer than 10 minutes and you can break at any time.

How long will it take?
As this type of research requires a detailed assessment of visual function, participants will be asked to attend up to 4 sessions of testing, each of no more than 2 hour duration. The tasks are self-paced, which means that rest periods can be taken during the testing session. In most experiments this number of sessions is required but you are free to withdraw from the research at any time you choose.

Will I be reimbursed for my time?
Each participant will be reimbursed $20 for each session attended in order to cover any travel expenses.

How will my confidentiality be protected?
We intend to protect your anonymity and the confidentiality of your responses to the fullest possible extent, within the limits of the law. All records taken as a part of this study will remain confidential. Any information supplied and data collected will be kept in a password protected computer or in a locked drawer. Your name will not appear in any publications or reports arising from this study, and if needed you will be referred to by a pseudonym. We will remove any references to personal information that might allow someone to guess your identity. The data will be kept securely in the Department of Optometry and Vision Sciences for a minimum of ten years from the date of publication, before being destroyed.

How will I receive feedback?
This study will be of no direct benefit to you. However, a written summary of the findings will be available after the study has been completed. Please advise the investigators if you would like this to be available to you.

Project HREC #1034933.2  PLS Version 3: May 24, 2011
What if I do not want to be involved?
Participation in this study is voluntary. There is no penalty if you choose not to participate.
You may withdraw from the study at any time and/or withdraw any unprocessed data you have supplied without prejudice.

What if you are a student of the University of Melbourne?
As with all research projects within the Department, your participation will not affect you as a student, the way you are treated by the Department of Optometry and Vision Sciences or your academic results.

Where can I get further information?
Should you require any further information, or have any concerns, please do not hesitate to contact:
Dr Allison McKendrick on Phone: (03) 9347 7479 or email: allisonm@unimelb.edu.au

How do I agree to participate?
If you would like to participate, please indicate that you have read and understood this information by reading and signing the accompanying consent form, and returning it to the investigators.

If you have any concerns about the conduct of this research project you can contact:
Executive Officer, Human Research Ethics
The University of Melbourne - ph: 8344 2073; fax: 9347 6739
Appendix B: Consent form

THE UNIVERSITY OF MELBOURNE
DEPARTMENT OF OPTOMETRY & VISION SCIENCES

Consent form for persons participating in research projects

PROJECT TITLE: AUDIO-VISUAL INTEGRATION AND THE ROLE OF AGING AND SENSORY DECLINE

Name of participant:
Name of Investigator(s): Dr Allison McKendrick (Principal Investigator); Ms Cassandra Brooks (Student Investigator, MPhil candidate)

1. I consent to participate in the project named above, the particulars of which — including details of the screening tests and computerised visual and auditory testing — have been explained to me. A written copy of the information has been given to me to keep.

2. I authorise the researcher or assistant to conduct with me the tests referred to under (1) above.

3. I acknowledge that:

(a) The possible effects of the screening tests and computerised visual testing have been explained to me to my satisfaction, including
  1) The possibility of a local allergic reaction to the anaesthetic eye drops
  2) The fact that no research has been conducted on the safety of using anaesthetic eye drops in pregnant or breastfeeding women

(b) I have been informed that I am free to withdraw from the project at any time without explanation or prejudice and to withdraw any unprocessed data previously supplied.

(c) The project is for the purpose of research and not for treatment;

(d) I have been informed that the confidentiality of the information I provide will be safeguarded subject to any legal requirements, and that the research results will not identify any participants in the study.

(e) I also understand that I may receive a summary of the research results if I request it;

(f) I may at any time during the project express any concerns to the Human Research Ethics Committee whose address appears at the foot of this page.

Signature
Date

(Participant)

* Executive Officer, Human Research Ethics
The University of Melbourne  p: 8344 2071; f: 9347 6139

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Appendix C: Published work

The following journal article has been published from the work arising from Experiments 1 and 2:


Permission was granted from the publishers to reprint this journal article, included as an appendix below.

I acknowledge ARVO as the copyright holder.
Age-related changes in auditory and visual interactions in temporal rate perception

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Andrew J. Anderson, Department of Optometry and Vision Sciences, University of Melbourne, Parkville, Victoria, Australia

Neil W. Roach, School of Psychology, University of Nottingham, Nottingham, United Kingdom

Paul V. McGraw, School of Psychology, University of Nottingham, Nottingham, United Kingdom

Allison M. McKendrick, Department of Optometry and Vision Sciences, University of Melbourne, Parkville, Victoria, Australia

We investigated how aging affects the integration of temporal rate for auditory flutter (amplitude modulation) presented with visual flicker. Since older adults were poorer at detecting auditory amplitude modulation, modulation depth was individually adjusted so that temporal rate was equally discriminable for 10 Hz flutter and flicker, thereby balancing the reliability of rate information available to each sensory modality. With age-related sensory differences normalized in this way, rate asynchrony skewed both auditory and visual rate judgments to the same extent in younger and older adults. Therefore, reliability-based weighting of temporal rate is preserved in older adults. Concurrent presentation of synchronous 10 Hz flicker and flutter improved temporal rate discrimination consistent with statistically optimal integration in younger but not older adults. In a control experiment, younger adults were presented with the same physical auditory stimulus as older adults. This time, rate asynchrony skewed perceived rate with greater auditory weighting than balanced integration. Taken together, our results indicate that integration of discrepant auditory and visual rates is not altered due to the healthy aging process once sensory deficits are accounted for, but that aging does abolish the minor improvement in discrimination performance seen in younger observers when concordant rates are integrated.

Introduction

Slow periodic modulations in amplitude over time are a feature of both our auditory (Attias & Schreiner, 1997) and visual experience (Dong & Atick, 1995). Light and sound from the same object are likely to oscillate at similar rates, as do vocalizations and lip movements in speech (Chandrasekaran, Truhanova, Stilittano, Caplier, & Ghazanfar, 2009). Integrating redundant rate information across the senses permits more precise discrimination of temporal rate changes (Koene, Arnold, & Johnston, 2007; Recanzone, 2003). While greatly disparate auditory and visual rates are segregated, partial integration of smaller differences can distort the perceived rate (Recanzone, 2003; Rosch, Heron, & McGraw, 2006; Skigley, 1964). Initially, perceived rate was viewed as intrinsically dominated by audition (Welch, Dutton Hurt, & Warren, 1986). However, vision and audition contribute equally to rate perception when the auditory cue is sufficiently degraded by reducing the depth of amplitude modulation (Roach et al., 2006). It has been previously documented that healthy older adults require greater modulation depth than younger adults.
in order to perceive the fluctuation inherent in a fluttering pure tone or flickering light (He, Mills, Alderstrom, & Dubno, 2005; Kim & Mayer, 1994). It is also known that temporal rate discrimination is poorer for less perceptible modulations in amplitude (Roach et al., 2006; Vaughan & Han, 1994). Therefore, if older adults’ reduced modulation sensitivity is sufficient to impair sensitivity to the rate of supra-threshold amplitude changes, then their ability to appropriately integrate or segregate auditory and visual stimuli according to rate similarity could be compromised.

Integration itself can also be altered by aging for some aspects of temporal perception. Older adults can tolerate wider temporal gaps between auditory and visual stimuli yet still see them as simultaneous (Chan, Pianta, & McKendrick, 2014a) and they more frequently report illusory doubling of a single flash accompanied by two beads (De Lasa, Pierce, & Andersen, 2013; McGovern, Roudaia, Stapleton, McGannity, & Newell, 2014; Sciti, Burke, Kenny, & Newell, 2011). From this, an increased tendency to integrate conflicting auditory and visual rates might be expected. However, older adults fuse multiple flashes accompanied by a beep in the same way as younger adults (McGovern et al., 2014). Furthermore, flashes and beads need not be simultaneous to be perceived as corresponding when part of a matching sequence of repeats over time (Denison, Driver, & Ruff, 2013). Over longer time frames, older adults are more susceptible to integrating incongruent speech in the McGurk effect (Sekiya, Soshi, & Sakamoto, 2014; Setti, Burke, Kenny, & Newell, 2013) but they retain the ability to integrate congruent speech provided that the visual component is clear (Sommer, 2005; Tyrer-Murray, Spehar, Myerson, Sommer, & Hale, 2011). Though speech contains corresponding auditory and visual amplitude modulations (Chandrasekaran et al., 2009), semantic content also influences how older adults integrate speech (Maguin, Setti, Burke, Kenny, & Newell, 2011; Stevenson et al., 2014) thereby making it difficult to infer from speech studies what the influence of aging on basic mechanisms of audio-visual integration might be.

Additionally, age-related changes in perception are often unequal when performance on complimentary auditory and visual tasks is directly compared in the same group of older adults. For example, duration judgments show greater age-related visual than auditory impairment (Luartig & Meck, 2011) but older adults are also more vulnerable to distracting visual information during an auditory task than vice versa (Guerrero-Murphy, & Van Gerven, 2013; Guerrero & Van Gerven, 2011). Event-related potentials diminish earlier latencies for visual than for auditory stimuli (Ceponiene, Westerfield, Torki, & Townsend, 2008), and fMRI blood oxygen level dependent signals decline with increasing presentation rates of visual but not auditory stimuli (Coffin et al., 2013). Current theory holds that the brain weights a pair of sensory cues according to their relative reliability (Ernst & Banks, 2002). Therefore, if aging differentially affects the precision of temporal rate estimates in vision and audition, changes in audiovisual perceived rate are possible even if the underlying ability to integrate is unaffected by aging.

In this study, we compared the effect of rate asynchrony on perceived rate, as well as the effect of rate synchrony on rate discrimination, in a group of younger and older adults. We accounted for potential age-related differences in the precision of temporal rate estimates across the senses by first equating auditory and visual temporal rate discriminability (Roach et al., 2006). This approach allowed us to separate the effect of aging on auditory, visual, and integration abilities.

**Experiment 1**

**Methods**

**Participants**

We recruited 11 young adults (age range: 22-32, mean 26) and 10 older adults (age range: 60-74, mean 68) from the university and the general population. Our recruitment strategy for older adults was similar to that used in previous experiments on aging from our laboratory (Kama & McKendrick, 2011; McKendrick & Battista, 2012; McKendrick et al., 2013; Chan et al., 2014a, 2014b), and typically attracts fit and active members of the community. Our participants had no history of excessive noise exposure, hearing aid use, or disorders or medications known to affect vision or hearing. Consistent with epidemiological research, normal hearing was defined as a pure tone average for 500, 1000, 2000, and 4000 Hz less than or equal to 25 dB (Crueckshanks et al., 2003). Best corrected visual acuity was 6/7.5 or better in both eyes, achieved with a spectacle prescription with spherical error less than five diopters and astigmatism less than two diopters. A clinical examination of anterior and posterior eye excluded the presence of ocular disease, as well as corneal or nuclear changes in the intracorneal lens greater than Grade 2 (Chylack et al., 1993). Participants with intracorneal pressure greater than 21 mmHg were excluded due to reduced flicker sensitivity (Tyler, 1981). All protocols were approved by the University of Melbourne Human Research Ethics Council, and the participants provided written informed consent ac-
cording to a protocol consistent with the Declaration of Helsinki.

**Experimental stimuli and setup**

We produced our auditory temporal rate stimulus (a fluctuating sound) by sinusoidally amplitude modulating a 65 dB 500 Hz pure tone presented via a speaker (AcousticMax Cube, BOSE, Framingham, MA). Our visual temporal rate stimulus, a flickering light, was a 0.7" diameter LED that sinusoidally varied in luminance over time about a mean of 438 cd/m². The LED sat on top of the speaker, surrounded by a black panel, so spatial cues facilitated the percept of a unified audiovisual object. A computer soundcard (SoundBlaster Live; Version 5.12) drove both the LED and speaker, enabling synchronous presentation of the visual and auditory stimuli. Luminance was controlled by inputting an amplitude modulated 2000 Hz carrier into the soundcard and subsequently demodulating it (Puts, Pokorny, Quinnan, & Glemme, 2003). The system was calibrated by measuring LED luminance across a range of input voltages using a PR-650 SpectraScan photometer (PhotoResearch, Chatsworth, CA). Stimulus generation and calibration software were custom written in Matlab (Version R 2008a, Mathworks, Natick, MA). The experiment was conducted in a quiet room with dim illumination. Spectacle correction was appropriate for the testing distance of 80 cm, including a near addition for older participants. Participants fixated on the LED during all tasks. A chin rest stabilized head position, and a computer keyboard was used to collect responses.

**Procedure**

Our procedure was based on the study by Roach et al. (2006). Participants completed the experiment tasks over three to four sessions, each approximately two hours in duration. Task order was counterbalanced. All tasks were two interval forced choice, with a 500 ms stimulus duration and interstimulus interval each 500 ms. A method of constant stimulus was employed with seven stimulus levels, each presented 20 times, with presentations divided into four blocks of five. Participants responded to each trial at their own pace and were provided with rest breaks between blocks as needed. Participants typically attended three sessions, each of no more than two hours duration. If experimental tasks were not completed within this time frame, participants attended a fourth session to complete the remaining trials. Practice trials were provided to ensure that subjects understood the task and to aid in the determination of the appropriate stimulus range. Data were fit with a cumulative Gaussian (Equation 1) using maximum likelihood estimation.

\[
\Psi(x; \mu, \sigma) = \gamma + (1 - \gamma - \lambda) \frac{1}{\sigma \sqrt{2\pi}} \int_{-\infty}^{x} e^{-\frac{(z-\mu)^2}{2\sigma^2}} dz
\]

Equation 1: The psychometric function (Ψ) with guessing rate (γ), lapsing rate (1 - γ) and cumulative Gaussian distribution of mean (μ) and standard deviation (σ) (Treutwein, 1995).

**Experiment 1A: Equating flicker and flutter discriminability**

We equated thresholds for discriminating a change in the temporal rate of 10 Hz flicker and flutter for each participant. For the visual task, the two interval forced choice format contrasted the standard 10 Hz flicker with one of seven possible test flicker rates, which varied according to a method of constant stimuli. Participants indicated which interval contained the faster flicker rate by key press. Flicker discrimination thresholds were derived from the standard deviation of the psychometric function (Equation 1). Equivalent discriminability for flicker and flutter required a low auditory modulation depth, so we first determined the smallest modulation in amplitude that gave rise to the percept of flutter (Figure 1A). The standard interval contained an unmodulated tone and the test interval 10 Hz flutter of variable modulation depth. Participants judged which interval contained the fluctuating sound. The mean of the psychometric function specified the modulation detection threshold. Flutter discrimination thresholds were then measured using the same format as the visual task (Figure 1B). Thresholds were obtained for four different modulation depths, each a multiple of the individual participant’s modulation detection threshold. As flutter rate discriminability varies approximately linearly with auditory modulation depth over this restricted range, we used a linear regression fit to the auditory data to approximate the unique modulation on each participant that equated temporal rate discriminability for 10 Hz flicker and flutter (Figure 1C). This modulation was used in all subsequent audiovisual tasks to allow investigation of integrative ability without the confound of individual differences in auditory and visual sensitivity.

**Experiment 1B: Integration of asynchronous flicker and flutter rates**

Perceived auditory temporal rate shifts when a concurrent visual stimulus oscillates at a different rate. Shifts in perceived visual rate can likewise be induced by asynchronous auditory rates (Roach et al., 2006). We measured this shift in perceived rate using a two
Figure 1. (A) Detection of modulation in a tone. (B) Discrimination of a change in temporal rate in either auditory flutter or visual flicker.

(C) Flutter discrimination performed at four different depths of modulation, each a multiple of the participant’s detection threshold. The intersection of the linear regression of these data with the flicker temporal rate discrimination threshold (green line) gives the modulation depth for matched discriminability. (D) Auditory asynchronous task: flutter discrimination in presence of task-relevant
interval forced choice task with synchronous 10 Hz auditory flutter and visual flicker, presented in phase, as a reference. For the auditory condition, the test interval contained an auditory flutter rate, which varied with a method of constant stimuli, and a fixed task-irrelevant visual flicker rate. Participants indicated which interval fluttered faster, basing their judgments solely on what they heard. This procedure was repeated for seven task-irrelevant rates (8, 9, 10, 11, 12, 14, and 16 Hz), generating a total of seven psychometric functions (Figure 1D, shown with a solid task-irrelevant rate). The mean of each psychometric function corresponded to the point of subjective equality, the physical test rate of flutter that was perceptually equivalent to the 10 Hz reference (Roach et al., 2005). The visual condition was the reverse with a test interval of variable visual flicker rate and a fixed task-irrelevant auditory flutter rate. Participants indicated which interval flickered faster, basing their judgments solely on what they saw (Figure 1E, shown with a solid task-irrelevant rate). This was repeated for the same range of task-irrelevant rates as the auditory condition (8, 9, 10, 11, 12, 14, and 16 Hz flutter). We restricted the range of rates tested to minimize differences in the perceived depth of amplitude modulation with changing temporal rate, and to avoid the fused perception of roughness (rather than flutter) that occurs at higher temporal rates for auditory stimuli (Fastl, 1997; Marks, 1970).

Experiment 1C: Integration of synchronous flicker and flutter rates

We measured how precisely participants could discriminate between temporal rates when flicker and flutter were presented simultaneously at the same rate and in phase with each other. In a two-interval forced choice task, the 10 Hz reference rate was compared to one of seven possible test rates using a method of constant stimuli. Participants indicated which interval contained the faster rate of fluctuation. The standard deviation of the psychometric function gave the visual rate discrimination threshold. This was compared, on an individual basis, to visual flicker rate discrimination threshold obtained in Experiment 1A (Figure 1F). Combined presentation of synchronous auditory and visual temporal rates is expected to improve discrimination between rates in line with statistically optimal integration (Kocon et al., 2007).

Results

Experiment 1A: Equating flicker and flutter discriminability

Younger and older adults showed no significant difference in their ability to discriminate between visual flicker rates, $t(19) = 1.2, p = 0.25$ (Figure 2A). However, median amplitude modulation detection thresholds were elevated in the older adults (Mann-Whitney, $U = 17, p = 0.008$; Figure 2B), indicating reduced sensitivity to auditory modulation in older age (note that auditory parameters were not normally distributed). Older adults required greater modulation depth than younger adults to match the discriminability of flicker and flutter temporal rate changes (Mann-Whitney, $U = 18, p = 0.01$; Figure 2C). This age-dependent difference was not statistically significant when the median modulation for a match was expressed as a multiple of each individual's threshold for detecting modulation (Mann-Whitney, $U = 29, p = 0.07$). Altogether, these results suggest that an age-related decrease in auditory temporal rate discriminability occurs secondary to reduced sensitivity to auditory amplitude modulation.

Experiment 1B: Integration of asynchronous flicker and flutter rates

To address the question of whether or not age altered the mechanisms of audiovisual integration for temporal rate, we performed two mixed ANOVAs, one for the auditory asynchronous task and one for the visual asynchronous task. Task-irrelevant rate (8, 9, 10, 11, 12, 14, and 16 Hz) was the within-subjects factor, and age group was the between groups factor. Responses for two participants were excluded from analysis of the auditory task due to inability to adequately fit psychometric functions to all their data (8 and 9 Hz condition for one participant, 14 Hz condition for another). There was a main effect of task-irrelevant rate on the physical rate perceived as equivalent to 10 Hz whether participants were discriminating changes in flutter rate, $F(6, 102) = 30.9, p < 0.001$, or flicker rate,
(C) Box plot for the flutter modulation (m) required to match the flutter temporal rate discriminability to the flicker temporal rate discriminability. Median (central line), interquartile range (box) and 10th and 90th percentiles (whiskers) are shown in all box plots.

$F(3.5, 65.6) = 39.8, p < 0.001$. As Figure 3 shows, physical rates faster than 10 Hz were required in the presence of slow task-irrelevant rates (8 and 9 Hz) whereas physical rates slower than 10 Hz were required in the presence of fast task-irrelevant rates (11, 12, 14, 16 Hz). This pattern reflects partial integration of conflicting auditory and visual rates, consistent with previous research (Roach et al., 2006). Complete segregation of asynchronous rates was not observed over the same range of task-irrelevant rates, likely reflecting differences in the modulation waveform and participant expertise with psychophysics between this experiment and prior work (Roach et al., 2006). However, a decline in influence is evident for the faster task-irrelevant rates tested, 14 and 16 Hz, where subjective equivalents level off (Figure 3).

With auditory and visual reliability individually balanced, there was no main effect of age on the subjective equivalent to 10 Hz; auditory: $F(1, 17) = 0.26, p = 0.62$; visual: $F(1, 19) = 0.13, p = 0.73$. This suggests that aging does not affect the degree to which asynchronous auditory and visual rates are integrated under conditions controlling for age-related sensory decline. There was no interaction between age and task-irrelevant rate: auditory: $F(6, 102) = 0.35, p = 0.91$; vision: $F(3.5, 65.6) = 0.69, p = 0.58$, indicating that rate asynchrony after perceived rate in the same systematic manner in young and old, even for large rate disparities.

It has previously been shown that visual temporal rate discrimination is less precise in the presence of cross-modal rate asynchrony (Roach et al., 2006). In a supplementary analysis, we performed a mixed ANOVA to compare flicker rate discrimination thresholds between younger and older adults across all experimental conditions (vision-alone and vision combined with each of the seven task-irrelevant flutter rates). There was no main effect of age, $F(1, 19) = 0.6, p = 0.44$, or interaction between age group and task-irrelevant rate, $F(4.4, 83) = 0.88, p = 0.49$, on the elevation of flicker rate discrimination thresholds due to concurrent but asynchronous flutter rates; main effect, $F(4.4, 83) = 3.7, p = 0.006$. This indicates that older adults did not find the asynchronous tasks perceptually more difficult to complete than younger participants, and is consistent with fact that psycho-

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Figure 2. (A) Box plot of thresholds for discriminating a change in the temporal rate of 10 Hz flicker. (B) Box plot of modulation detection thresholds (%) obtained by discriminating 10 Hz.
Figure 3. (A) Mean temporal modulation rate of auditory flutter that was subjectively equivalent to the 10 Hz reference for each of the task-irrelevant visual flicker rates. (B) Mean temporal modulation of visual flicker that was subjectively equivalent to the 10 Hz reference for each of the task-irrelevant auditory flutter rates. Younger adults are closed circles, and older adults open circles. Error bars are 95% confidence intervals of the mean. The dashed line indicates the physical temporal rate.

Figure 4. Individual and mean temporal rate discrimination thresholds for younger (closed circles) and older adults (open circles). Thresholds for synchronous flutter and flutter (black symbols) are compared with predicted thresholds for maximum likelihood integration (blue symbols). Error bars are 95% confidence intervals of the mean.

Neatness in older adult responses as 95% confidence interval of the mean for each group are of comparable in width. Supplementary analysis of psychometric functions across age groups found no difference in mean guess rate (Mann-Whitney U = 52.5, p = 0.87) or mean lapse rate (Mann-Whitney U = 50, p = 0.71) for each age group. However, it is the relative improvement in performance under audiovisual compared to visual or auditory alone conditions for each participant that provides a measure of multisensory facilitation (Stein, Stanford, Ramachandran, Perrett, & Rowland, 2009). In fact, combined rather than separate presentation of equally reliable auditory and visual rates is known to improve temporal rate discrimination in a statistically optimal fashion (Koele et al., 2007). This entails reliability-based weighting of the individual sensory estimates of a multisensory object through maximum likelihood estimation to achieve a combined estimate with the smallest possible variance (Ernst & Banks, 2002, Equation 2). Since auditory and visual variances were equivalent by experimental design (see Experiment 1A), maximum likelihood estimation predicts a √2 improvement (Equation 3). Predicted temporal rate discrimination thresholds were calculated for each participant based on their previously measured visual temporal rate discrimination thresholds (Experiment 1A). Paired t tests indicated that younger but not older adult audiovisual discrimination thresholds were consistent with maximum likelihood predictions; younger: t(19) = 0.70, p = 0.50; older: t(9) = 2.7, p = 0.02. This suggests that older adults were less able to benefit from
the addition of synchronous flutter to flicker when discriminating temporal rate changes despite similar overall performance.

\[
AV = \sqrt{\frac{1}{\sigma_A^2} \left( \frac{1}{\bar{x}_A} \right) + \frac{1}{\sigma_V^2} \left( \frac{1}{\bar{x}_V} \right)}
\]

Equation 2: Maximum likelihood estimation predicts that the audiovisual rate, \(AV\), results from the sum of the individual auditory, \(A\), and visual, \(V\), rates, with each weighted in proportion to their reciprocal variances, \(\frac{1}{\sigma_A^2}\) and \(\frac{1}{\sigma_V^2}\), respectively, such that the weights sum to one (Ernst & Banks, 2002).

\[
\sigma_{AV} = \frac{\sigma_A \sigma_V}{\sigma_A^2 + \sigma_V^2}
\]

Equation 3: Temporal rate discrimination threshold, \(\sigma_{AV}\), based on auditory and visual rates as predicted by maximum likelihood estimation (Ernst & Banks, 2002).

**Experiment 2**

As age unequally compromises auditory and visual temporal rate discriminability, we conducted a supplementary experiment (see below) to determine whether this resulted in any age-differences in the weight the brain applies when integrating flicker and flutter temporal rate estimates. A group of younger adults performed the asynchronous task with the same physical auditory stimulus that resulted in balanced integration in the average older adult. Since this modulation depth exceeded the average modulation for matched discriminability in younger adults in our first experiment, we hypothesized an increase in auditory influence on perceived rate relative to performance under matched discriminability.

**Methods**

Six younger adults (age range: 23–28, mean 26) discriminated changes in the temporal rate of 10 Hz flutter presented simultaneously with asynchronous flicker, and changes in the temporal rate of 10 Hz flicker presented simultaneously with asynchronous flutter as described in Experiment 1B. A single task-irrelevant rate of 1.2 Hz was used as this corresponded to substantial integration for participants in Experiment 1 (Figure 3). Temporal rate discrimination was performed under two conditions which differed in the depth of auditory modulation. For the matched condition, the flashing stimulus was degraded by reducing its modulation depth to equate temporal rate discriminability across vision and audition on an individual basis (see Experiment 1A). For the unmatched condition, flutter modulation was set at 29%, the average modulation for equated discriminability in older adults for Experiment 1. Four psychometric functions were generated for each participant to determine whether the physical rate subjectively equivalent to 10 Hz for each sensory modality changed with degree of auditory modulation. The point of subjective equality to the 10 Hz reference was given by the mean of the psychometric function.

**Results**

Equivalent flicker and flutter temporal rate discriminability was achieved with a modulation of 6.4% (95% CI [3.8, 9.0]), which was much lower than the average older adult modulation of 20%. As Figure 5A shows, the point of subjective equality was closer to true physical value of 10 Hz in the unmatched, compared to the matched condition for flutter. Figure 5B displays the reciprocal relationship, where the subjective equivalent for flicker is further from its true physical rate of 10 Hz in the unmatched condition. Analysis of the difference in the point of subjective equality to 10 Hz between matched and unmatched conditions confirmed greater auditory influence for 20% modulation whether participants responded to flicker or flutter rate changes; flicker: \(t(5) = -4.7, p = 0.005\); flutter: \(t(5) = 2.7, p = 0.04\) (Figure 5C).

**Discussion**

Whereas older age did not impair discrimination of visual flicker rate changes, discrimination of auditory flutter rate changes was less precise in older adults due to impaired amplitude modulation sensitivity. Older adults retained the ability to partially integrate equally reliable but asynchronous temporal rates of flutter and flicker since distortions in perceived rate were similar to those of younger adults. In contrast, integration of synchronous auditory and visual rates did not facilitate temporal rate discrimination in older adults relative to visual alone performance, though group auditory rate discrimination thresholds themselves were unaffected by aging.

Impaired auditory modulation sensitivity is characteristic of physiological aging (He et al., 2009), which causes a wide range of temporal processing deficits even in older adults with normal audiometric thresholds.
discrimination tasks with a task-irrelevant rate of 12 Hz. (C) Individual (open circles) and mean (closed circles) differences in perceptual match for flicker and flutter asynchronous rate discrimination tasks. Error bars are the 95% confidence intervals of the mean difference.

(Fitzgibbons & Gordon-Salant, 1996). Conversely, though temporal processing likewise declines in the aged visual system (Owsley, 2011), older adults retained the ability to discriminate changes in flicker rate. However, this may reflect saturation of temporal contrast responses given the highly modulated flicker used. Deficits in flicker rate discrimination may emerge at lower modulation depths since decreased sensitivity to flicker modulation also occurs in aging (Kim & Mayer, 1994). Though both audition and vision show impaired coding of temporal information in animal studies (Palombi, Buckoll, & Caspary, 2001; Schutterman, Hughes, & Caspary, 2006; Zhang et al., 2008), the vulnerability of temporal rate processing to aging may differ across the senses.

This age-related auditory deficit renders both amplitude modulation and changes in modulation rate less perceptible to older adults. Whereas our experiment demonstrates that the ability to integrate asynchronous auditory and visual rates is not affected by older age, the age-related decline in auditory rate perceptibility is not normalized in the natural world. The supplementary experiment in younger adults showed that the physical difference in auditory amplitude modulation across age groups was sufficient to alter sensory weighting since auditory dominated rate perception in younger adults for a modulation depth that equaled auditory and visual influences in older adults. Changes in sensory weighting with age have been shown to affect audiovisual orienting tasks, where impaired fixation of auditory targets with age leads to vision dominating fixation of audiovisual targets (Dobreva, O’Neill, & Paige, 2012). Since the mechanism of temporal rate integration is reliability based, our results suggest that auditory contribution to temporal rate perception may be reduced in older adults. This contrasts with previous supposition that audition was innately more appropriate for temporal rate judgments (Welch et al., 1986). Reduced facilitation of temporal rate discrimination by rate synchrony in older adults is also likely to be compounded by the age-related impairment in flutter rate discrimination. However, in this case, significant age-related differences in rate perception may not occur in an everyday setting, given that only a small improvement in temporal rate discrimination thresholds was found in younger adults.
Maintenance of asynchronous rate integration in aging contrasts with previous work showing altered integration of temporally offset cues. Older adults integrate auditory and visual cues into a combined percept over a larger window of time than younger adults (Alim & Dehaene, 2013; Chin et al., 2014a) and the sound-induced flash illusion persists for greater temporal lags between the flash and the sound (McGowan et al., 2014; Setti et al., 2011).

Our results may be reconciled with this literature by considering whether the integration process changes with stimulus duration. For example, auditory transients enhance visual search but sustained, synchronous sinusoidal modulations do not (Kosm & van Wassenhove, 2012; Van der Burg, Cass, O’Leary, Theeuwen, & Alais, 2010). Consequently, multimodal interactions have been speculated to operate differently depending on whether magno- or parvocellular visual pathways are stimulated (Jaeck, Pérès-Bellido, & Soto-Faraco, 2014). Consequently, comparison of the integration of temporally offset, brief auditory and visual stimuli and the integration of longer, coincident stimuli may not be appropriate.

Few age-related impairments in integration have been reported in the literature. For temporal perception, decreased audiovisual integration has previously been demonstrated for apparent motion in older adults (Roddian, Schacter, Bennett, & Schauer, 2013) and speech syllables in older adults with hearing impairment (Musch, 2009). Typically, provision of redundant cues across sensory modalities benefits older adults more than younger adults, such as greater facilitation of response times (Diederich, Colonius, & Schomburg, 2008; Hugheschmidt, Pfeifer, McCoy, Hayakawa, & Laurenti, 2009; Laurenti, Burdette, Malpass, & Wallace, 2006; Pfeifer, 2007). However, measures of temporal rate perception and response times may not be expected to align given the differences between tasks. Indeed, crossmodal stimulation shortens neural response latency and causes amplitude enhancement most at the beginning of the response (Rowland, Quassy, Stanford, & Stein, 2007) which is likely not an advantage for temporal rate judgments made over a longer period of time. That an age-related deficit was found for the integration of synchronous but not asynchronous auditory and visual rates suggests a possible dissociation between the mechanisms and their susceptibility to age-related decline. However, integration may be susceptible to any age-related decline in the sensory coding of rate information, such as decreased phase locking to amplitude modulation for a 50 Hz carrier (Leigh-Paffenroth & Fowler, 2006). The reducing inter-sensory asynchrony in the neural representation of auditory and visual rates resulting from such a loss in phase locking could limit the benefit derived from rate integration despite physical synchrony of the stimuli.

The role of generalized cognitive decline

As noted in our Methods, we did not use any cognitive assessments in the present study, and so it could be asked whether a generalized cognitive decline in our older participants may have influenced our results. We believe this is extremely unlikely for several reasons. Firstly, we find no influence of aging in our Experiment 1B (integration of asynchronous rates), and so there is no effect to be explained by cognitive decline. Secondly, where an ageing effect was present in Experiment 1C (integration of synchronous rates), our analysis of psychometric function gains and latency rates showed our older participants could perform our experiments as reliably as younger participants. Specifically, the capacity of older adults to compare successive intervals in the two alternate forced choice tasks was unimpaired, which argues against any significant influence of age-related decline in attentional resources or working memory on the ability of older adults to complete the experimental tasks. The range of performances in our older participants matched that of our younger group (Figure 4), indicating our older group was as homogenous as our younger group and that any difference between groups is not driven by a small number of outliers with poor performance. That we find no evidence for attentional or working memory decline is consistent with our observation that our recruitment strategy tends to attract older participants who are fit and active members of the community (see Methods).

Conclusions

Older adults retain the ability to flexibly resolve inter-sensory conflict in perceived rate through partial integration of asynchronous auditory and visual temporal rates. However, they are not able to benefit from audiovisual rate synchrony like younger adults when discriminating changes in temporal rate. Age-related decline in auditory modulation sensitivity, which affects perceptibility of both amplitude modulation and changes in flutter rate, is expected to further compound the age-related impairment in synchronous rate integration. However, this does not necessarily imply that age-related differences in discrimination performance will be practically significant since audiovisual facilitation produces only small improvements in precision. In contrast, under everyday conditions where age-related losses in audition are not controlled for, we...
predict that older adults will rely more on vision to achieve a coherent percept of asynchronous notes through their preserved ability to weight sensory information according to relative reliability.

Keywords: audiovisual, auditory, visual, aging, integration, reliability, temporal rate, flutter, flicker

Acknowledgments

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Commercial relationships: none.

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References


Guerreiro, M. J. S., Murphy, D. R., & Van Gerven, P.
175
Appendix D: Index of changes

The table below details amendments made to the thesis in response to the examiners’ reports.

<table>
<thead>
<tr>
<th>Examiner 1</th>
<th>Suggested changes</th>
<th>Response/change</th>
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<tbody>
<tr>
<td></td>
<td>Interpretation of the data in figure 3.10.</td>
<td>The following text was added: Pg 78, first paragraph: “The maximum likelihood prediction was also compared between age groups using both parametric and Bayesian t-tests, the latter of which was run in JASP (Version 0.8.1.2, JASP Team (2017), Amsterdam, NL) using a default cauchy prior of width 0.707.” Pg 78, second paragraph: “Note that the mean maximum likelihood prediction did not differ between age groups (t(19)=1.2, p=0.25), in line with the lack of an age-related difference in flicker rate discrimination thresholds upon which the predictions were based (see Experiment 1A). A follow up Bayesian t-test provided weak evidence in favour of the null hypothesis of no age-related difference in the maximum likelihood predictions (BF$_{10}$=0.643).”</td>
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<td></td>
<td>• Inquired whether prediction for older age group lower than that for the younger age group upon statistical testing.</td>
<td>Pg 78, second paragraph: “Note that the mean maximum likelihood prediction did not differ between age groups (t(19)=1.2, p=0.25), in line with the lack of an age-related difference in flicker rate discrimination thresholds upon which the predictions were based (see Experiment 1A). A follow up Bayesian t-test provided weak evidence in favour of the null hypothesis of no age-related difference in the maximum likelihood predictions (BF$_{10}$=0.643).”</td>
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<td>• Suggested use of Bayesian t-test.</td>
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<tr>
<td>Examiner 2</td>
<td>Fig 3.1:</td>
<td>Figure updated as suggested.</td>
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<tr>
<td></td>
<td>• X-axis label is “modulation”. Perhaps “Modulation depth” or “Modulation Index” would be more informative.</td>
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<td>• Y-axis label: perhaps “flutter discrimination threshold”</td>
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<td></td>
<td>• Perhaps a text label in the box indicating “10 Hz reference”?</td>
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<td>• “modulation for AV match”?</td>
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<tr>
<td>Examiner 2</td>
<td>Fig 3.2:</td>
<td>Label now included.</td>
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<td></td>
<td>• Perhaps a text label in the box indicating “Flicker: 10 Hz reference”?</td>
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<tr>
<td>Examiner 2</td>
<td>Chapter 3</td>
<td>On pg 67, for clarification purposes, an additional diagram was added for Experiment 1B. On pg 66, the final was paragraph amended to refer to figure as follows “The experimental task is depicted in Figure 3.5 and further details may be found</td>
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<td></td>
<td>• some diagrams of the design would help the reader be clear about what you did (more for Exp 1B than 1A).</td>
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</table>
in Chapter 2.”. As a consequence, subsequent figures in Chapter 3 were renumbered (pgs 68 – 78, 86) and the list of figures updated accordingly (pgs xii-xiii).

**Examiner 2**

**Fig 3.5:**
- Label the top plot “Flutter: 10 Hz reference” and the bottom one “Flicker: 10 Hz reference”. Also, please help your reader by including a legend showing what the symbols mean.

Labels and legend now added to Figure 3.6 (previously Figure 3.5).

**Examiner 2**

**Figure 3.6**
- Perhaps text box indicating subject number “S1”? Also, maybe a title indicating “flutter”?

Labels S1: flutter and S2: Flutter added to panels A and B, respectively, of Figure 3.7 (previously Figure 3.6).

**Examiner 2**

**Table on pg 88**
- put a column before the “task” column headed “modality” and rows labelled such as “visual”, “Auditory, and “AVmatched”.

Table amended to include a column headed “Modality” with rows headed ‘Visual’, ‘Auditory’, ‘Auditory (matched to visual)’. Auditory (matched to visual) was substituted for AVmatched, so as not to imply the task was audiovisual.

**Examiner 2**

**Fig 4.4:**
- Add a title “flutter” in A and “Flicker” in B.

Labels ‘Flutter: 10 Hz reference’ and ‘Flicker: 10 Hz reference’ added to panels A and B, respectively.

**Examiner 2**

**Chapter 5**
- bottom of p94 (second last line): “sensory cortex” Which: visual; auditory; multisensory?

Amended to read ‘auditory and visual cortices’ on pg 95.

**Examiner 2**

**Chapter 5**
- no discussion of the role of a time-varying phase difference between unmatched temporal frequency. This would have implications in terms of neural responses, entrainment of neural oscillations etc. There was a discussion of neural oscillations, but no mention of the difference sync vs async frequencies and how this entails a difference of both frequency and phase.

The following text “Furthermore, these studies suggest that the time-varying phase difference introduced when visual luminance and auditory amplitude were modulated at different temporal rates in Experiment 1B was unlikely to influence their integration. In fact, while periodically modulated auditory and visual stimuli elicit time-locked oscillatory neural activity in the auditory and visual cortex, respectively, audiovisual interactions in oscillatory responses are not evident at this level of the cortical hierarchy (Giani et al. 2012). This further suggests that the integration of auditory and visual temporal modulations occurs at a central cortical site, rather than
relying on precise timing information in lower level sensory cortex.” was added to the discussion of the role of phase and neural responses in synchronous audiovisual rate judgements on pg 105.

<table>
<thead>
<tr>
<th>Examiner 2</th>
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<tr>
<td><strong>Chapter 5</strong></td>
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<tr>
<td>• the “future directions” section could have given more thought to the specifics of future experiments</td>
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</table>

**Pg 113, first paragraph:**
“A follow up experiment could employ the same paradigm as Experiment 1 but test at faster task-irrelevant rates (for example 18 and 20 Hz) to determine the point at which complete segregation of auditory and visual rates occurs for older compared to younger adults.”

**Pg 113, last paragraph:**
“As in the original study by Roach et al. (2006), the auditory rate stimulus can be degraded by determining on an individual basis the auditory modulation depth that corresponds to a flutter rate discrimination threshold double that of the flicker rate discrimination threshold. However, flutter rate discrimination thresholds only vary linearly with auditory modulation depth over a restricted range (see Figure 2.9). Therefore, it may be necessary to test flutter rate discrimination at additional modulation depths to describe the relationship as a power function in order to more accurately calculate the desired modulation depth.”

**Pg 114, second paragraph:**
“Further investigation, using the same paradigm as Experiment 1A, is required to determine the feasibility of matching rate discriminability at faster temporal rates, where thresholds will be elevated (Lee 1994; Mandler 1984; Waugh & Hess 1994). However, rate discrimination thresholds appear broadly comparable across the senses at faster rates upon inspection of previous research (Lee 1994; Mandler 1984; Waugh & Hess 1994), which suggests this approach may be feasible. The limiting factor on the temporal rate selected is the critical flicker frequency, above which flicker is no longer visible (Landis 1954), or the auditory transition frequency, where spectral cues contribute to amplitude
modulation sensitivity (Fassel & Kohlrausch 1996; Sek & Moore 1994), whichever is lower for the stimulus parameters.

Pg 114, third paragraph: “A follow up experiment could address this by assessing flicker rate discrimination at a range of temporal contrasts to see if age-related deficits emerge for less modulated flicker.” and “Future experiments could assess how age-related ocular disease and hearing loss affect the relative reliability of flicker and flutter rate, the integration of asynchronous auditory and visual rates and the integration of synchronous auditory and visual rates by employing the experimental design described for Experiments 1A, 1B and 1C, respectively.’

Pg 115, first paragraph: “In keeping with other studies employing audiovisual temporal stimuli (e.g. Marchant et al. 2012; Noesselt et al. 2007; Werner & Noppeney 2011), functional magnetic resonance imaging could be employed to determine changes in neural activity and functional connectivity elicited by dual compared to separate presentation of auditory and visual rates. Event related potentials could also be informative, providing additional information on the latency of audiovisual interactions. Both modalities would provide a means of investigating differences between synchronous and asynchronous conditions.”