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Investigating the neural mechanisms underlying auditory and audio-visual perception in younger and older adults

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Abstract

This thesis aimed to address questions in two distinct areas of research in ageing and cognitive neuroscience. Firstly, given that the pre-stimulus state of cortical oscillations had been shown to predict behavioural and neural responses, we addressed the question of whether pre-stimulus oscillatory mechanisms change or remain consistent in the ageing brain. Secondly, previous research had shown that Audio-visual (AV) speech influences the amplitude and latency of evoked activity. Our research addressed the questions of whether/how AV enhancement and visual predictability of AV speech is represented in evoked activity in noisy listening conditions, and whether such Electroencephalographic (EEG) signatures remain stable with age.

In Chapter 3 we investigated the consistency of how pre-stimulus activity influences auditory frequency discrimination performance in young and older participants. In both groups the power of pre-stimulus activity influenced the encoding of sensory evidence reflected by early evoked components, while the phase influenced choice formation in later-activated EEG components. Importantly, for the early EEG components we did not find evidence for a systematic difference in the time scales of the perceptually relevant pre-stimulus activity. In the later-activated EEG component we found a trend for perceptually relevant rhythmic activity to arise from slower frequencies in the ageing brain. At the same time our data replicate previous findings of a significant age-related slowing of Auditory Evoked Potential (AEP) latency, modulations of AEP amplitudes, and a flattening of the spectral profile of EEG activity.

In Chapter 4, we investigated the consistency of behaviour and evoked activity underlying AV speech integration in a speech-in-noise discrimination task in younger and older adults. Behaviourally, younger and older adults performed comparably. Performance was greater for Audio-visually informative (AV_{inf}) speech compared to Auditory-only informative (AO_{inf}) speech across groups and noise levels, and was poorer at low noise levels. AV enhancement was greater in high noise levels, across all participants, and older adults derived greater AV enhancement compared to younger adults (an effect that was consistent across noise levels). In terms of visual predictability, we found that word discrimination performance was greater for target words with non-labial initial phonemes (assumed least visually predictive), compared to labial initial phonemes (assumed most visually predictive). Furthermore, we found that AV enhancement was greater for labial initial phonemes, compared to non-labial initial phonemes, and this was consistent across age groups.Neurally, we found that AV enhancement is represented by a centro-parietal P3-like activity in older adults and an N4-like fronto-central activity in younger adults, but found that this activity did not correlate with behavioural AV enhancement. Our results point to distinct patterns of late evoked activity underlying AV enhancement between younger and older adults, possibly representing distinct cognitive (memory) strategies in predicting upcoming target stimuli. At the same time our data replicate previous findings of a significant age-related slowing of AEP latency, modulations of AEP amplitudes, and a flattening of the spectral profile of EEG activity.

In Chapter 5 we investigated the consistency of evoked activity underlying the visual predictability of AV speech. We found that visual predictability was reflected by late fronto-central negativity in older adults, but not in younger adults. However, we did not find evidence of an interaction between visual predictability and AV enhancement in terms of evoked activity, raising further questions about how visual predictability of speech is represented the brain’s electrophysiology. Our results point to distinct patterns of late evoked activity underlying visual predictability of visual speech, again possibly reflecting differential strategies in predictive coding.

In summary, the results of this thesis demonstrate that pre-stimulus mechanisms in auditory pitch perception remain consistent in the younger and older adult brain, while spectral dynamics change with age. Our results also replicate previous work demonstrating age-related delays in peak latency, and changes in peak amplitude, of early auditory evoked activity. And lastly, we demonstrate that differences in the EEG signatures of AV enhancement between younger and older adults emerge in late evoked activity, and that visual predictability of speech is represented in late evoked activity only in older adults.

Table of Contents

Chapter 5 Neurophysiological correlates of phonemic visual predictability in audio-visual speech-in-noise discrimination in younger and older adults 105

List of Tables

List of Figures

1

List of Publications

Kayser, S. J., McNair, S. W., & Kayser, C. (2016). Prestimulus influences on auditory perception from sensory representations and decision processes. *Proceedings of the National Academy of Sciences*, *113*(17), 4842–4847. https://doi.org/10.1073/pnas.1524087113

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Abbreviations/Definitions

A1	Primary Auditory Cortex
AEP	Auditory Evoked Potential
ANOVA	Analysis of Variance
AO	Auditory Only
AO_{inf}	Acoustically/Auditory only informative
AV	Audio-visual
AV_{inf}	Audio-visually informative
BHI QHQ	Better Hearing Institute Quick Hearing Questionnaire
BSA	British Society of Audiology
CRUNCH	Compensation-Related Utilization of Neural Circuits Hypothesis
Dspan	Digit Span
EEG	Electroencephalography(/gram)
EOG	Electrooculography(/gram)
ERP	Event Related Potential
fMRI	functional Magnetic Resonance Imaging
FDR	False Discovery Rate
GABA	Gamma Aminobutyric Acid
HAROLD	Hemispheric Asymmetry Reduction in Older Adults

HC	High Contrast
LC	Low Contrast
LDA	Linear Discriminant Analysis
MEG	Magnetoencephalography(/gram)
MoCA	Montreal Cognitive Assessment
ORN	Object Related Negativity
PASA	Posterior-Anterior Shift in Ageing
PFC	Pre-frontal Cortex
PSD	Power Spectral Density
PTA	Pure Tone Audiometry
ROC	Receiver Operator Characteristic
SNR	Signal to Noise Ratio
SST	Socioemotional Selectivity Theory
TFR	Time-Frequency Representation
THI	Tinnitus Handicap Inventory
V1	Primary Visual Cortex
VAS	Visual Acuity Score
VO	Visual only

Chapter 1 Ageing and behaviour

1.1 Contributions of the thesis

As we get older, we find that our hearing abilities decline. It takes us longer to make decisions about the sounds we have heard, and we can find it difficult to keep track of conversations in noisy environments. We also find that sounds become, perceptually, much clearer when we have a visual cue accompanying the sound. However, the computational mechanisms underlying auditory and audio-visual (AV) perceptual processes, their neural correlates, and whether these processes and neural correlates change with age, are not yet fully understood.

Of particular interest in the cognitive psychology and neuroimaging fields is, firstly, the state of the brain prior to stimulus presentation. One way of investigating such brain states is to look at rhythmic patterns of brain activity characterized by a specific time scale (so called cortical oscillatory activity). The pre-stimulus state of cortical oscillations can be predictive of behavioural and neural responses, however little research has addressed the way by which oscillations do this (e.g. by influencing bottom-up or top-down processing, or both). Additionally, it is unclear whether pre-stimulus oscillatory mechanisms change or remain consistent in the ageing brain. Secondly, neural representations of AV speech perception have received much attention, with particular focus on AV influences on specific components of evoked activity that systematically emerge at specific time points (in the literature known as N1, P2). Little is known about AV influences on evoked potentials in the AV processing of speech-in-noise, and again whether such electroencephalographic (EEG) signatures remain stable with age. Furthermore, few studies addressed the extent to which phonemic visual predictability of speech stimuli influences evoked potential dynamics.

This thesis will expand on the areas of research described above. The main contributions of this work are:

1. Demonstrating that pre-stimulus mechanisms in auditory pitch perception remain consistent in the younger and older adult brain

2. Demonstrating age-related delays in peak latency, and changes in peak amplitude, of early auditory evoked activity.

3. Demonstrating that older adults have flatter pre-stimulus power spectra compared to younger adults.

4. Demonstrating that differences in the EEG signatures of AV enhancement between younger and older adults emerge in late evoked activity.

5. Demonstrating that visual predictability of speech is represented in late evoked activity only in older adults.

1.2 Sensory acuity

Age-related hearing loss (presbycusis) is considered a marker of healthy ageing, however the profile of the hearing loss in terms of onset, severity and progression can be highly variable (Gates & Mills, 2005) and subject to such factors as genetics (DeStefano et al., 2003; Gates et al., 1999), underlying pathological heterogeneity (Schuknecht & Gacek, 1993) and previous noise exposure (Gates et al., 2000). Presbycusis is characterised structurally as a natural degeneration of the stria vascularis within the cochlea (Schuknecht & Gacek, 1993), malfunction of the auditory nerve (Gates & Mills, 2005), and structural changes within the auditory cortex (Peelle et al., 2011), thus leading to reduced sensory acuity.

Consequently, elderly adults often find particular listening situations increasingly difficult with advancing age. For example older adults are less sensitive to higher acoustic frequencies (Brant & Fozard, 1990; Gates & Mills, 2005; F. Lee et al., 2005; Pedersen et al., 1989), and tend to have higher frequency difference limens (Clinard et al., 2010), compared to younger adults. Furthermore, older adults generally show poorer frequency discrimination performance (Clinard et al., 2010; He et al., 1998) and reduced frequency-modulation detection (Grose & Mamo, 2012; He et al., 2007; Mahajan et al., 2017; Paraouty et al., 2016; Wallaert et al., 2016; Whiteford & Oxenham, 2017). Listening to acoustic targets that are played rapidly (Schneider et al., 2005; Wingfield et al., 2006), or that have been degraded by noise or distracting auditory streams (Pichora-Fuller & Souza, 2003; Wöstmann et al., 2015), also present themselves as particular challenges for older listeners.

The visual system also undergoes age-related changes. As we get older, the prevalence of eye diseases such as macular degeneration, cataracts, and glaucoma increases with age (Owsley, 2011). Thus, age-related changes in low-level visual functions, such as visual acuity (Gittings & Fozard, 1986) and contrast sensitivity (Owsley et al., 1983) could cause delays in processing speeds for visual information. However, there is evidence which suggests that low-level functions alone cannot account age-related differences in processing speed (Bieniek et al., 2013) or visual discrimination (Boutet et al., 2015). Within a multisensory context, declines in visual acuity can lead to poorer signal re-weighting in response to changes in signal reliability (Garcia et al., 2017), wider (i.e. less accurate) temporal binding windows (Richards et al., 2017), and poorer AV speech perception (Narinesingh et al., 2014).

In summary, both the peripheral auditory and visual systems are subject to changes with age. In this thesis we accept that some decline in hearing and visual abilities is to be expected, however we screen all participants (younger and older adults) for pathological changes (no more than mild loss) using objective and subjective measures where relevant.

1.3 Cognitive abilities

Beyond the sensory systems, healthy ageing typically results in changes within various aspects of cognition. Areas of cognition that are often the subject of investigation in the ageing literature are memory, processing speed, attention, and decision making. One particular issue that will be discussed within this research is whether the influence of age on cognition occurs within cognitive functions independently or interdependently. Another debate within the literature is the mechanism by which ageing influences cognition: can sensory and cognitive decline be attributed to a general ageing process, or does a decline in bottom-up processing drive the decline in top-down process, or vice versa? In this light, various models of age-related cognitive decline will be discussed.

1.3.1 Memory and processing speed

Research has shown that, as we get older, it becomes more difficult to monitor and control information in working memory (Hasher & Zacks, 1988) due to age-related reductions in storage capacity (Gilchrist et al., 2008; Naveh-Benjamin et al., 2007). There is also considerable evidence that long-term episodic memory declines with age (La Voie & Light, 1994; Prull et al., 2000; Spencer & Raz, 1995; Verhaeghen & Salthouse, 1997). Declines in episodic memory persist even in when task conditions are made more ecologically valid by replicating real-life environments (Kirasic et al., 1996; Molander & Bäckman, 1990), and have been demonstrated using both meaningless (e.g. pictures of novel objects; Schacter et al., 1992) and meaningful stimuli (e.g. information on medicine labels; Morrell et al., 1990). Semantic memory, on the other hand, is often found to be resilient to the effects of ageing (D. V. Howard et al., 1980; Nyberg et al., 1996); however, Bowles and Poon (1985) found age-related differences in semantic memory when task load was high.

Another cognitive function that is subject to ageing is the speed in which sensory information is processed in the brain. In the ageing brain information processing becomes slower (Birren & Fisher, 1995; Salthouse, 1996), which can be observed as an increase in reaction times in tasks requiring rapid responses (Salthouse, 2000a). Older adults typically take longer to perform simple cognitive and perceptual tasks (Salthouse & Ferrer-Caja, 2003; Verhaeghen & Salthouse, 1997), even when age-related differences in motor-dexterity are controlled for (Ebaid et al., 2017).

One issue concerning the influence of age on cognition is that it is unclear whether the influence ageing has on cognitive processing speed is independent from its influence on memory functions (as well as other executive functions). In modelling the relationship(s) between age and cognition, considering such influences as independent have resulted in poorly fitting models (Salthouse, 1998; Salthouse & Czaja, 2000). Furthermore, there is a body of evidence demonstrating that associations between age and memory (Salthouse et al., 2004, 2008; Siedlecki et al., 2005), and age and executive functioning can be explained by age-related differences in processing speed, among other factors (Salthouse, 2005; Salthouse et al., 2003; Salthouse & Davis, 2006; Salthouse & Meinz, 1995). Salthouse (1996) put forth a model suggesting that slower processing speeds influence other cognitive domains by way of two mechanisms: a time limited mechanism and a simultaneity mechanism. Firstly, by the time-limited mechanism, slow actioning of cognitive processes results in less time available within which cognitive operations can be completed. Secondly, by the simultaneity mechanism, information from earlier stages in the cognitive processing pipeline may not be available by the time later processes are complete, thus there is less information available for higher order processing.

In this thesis, we control for the influence of pathological changes in working memory and declarative memory by screening our older adults using a battery of cognitive tests. We do not investigate behavioural reaction time in any of our experiments, however we do investigate changes in the timing of evoked responses in Chapter 3, Chapter 4,and Chapter 5. We also consider differential predictive coding strategies involving differential memory processes between younger and older adults in the processing of AV speech-in-noise stimuli in Chapter 4

1.3.2 Auditory attention

Older listeners also tend to find difficulty in controlling attention (H. Meister et al., 2013; Passow et al., 2014) and ignoring irrelevant stimulus information, such as noise or distractors (Chao & Knight, 1997; Gazzaley et al., 2005; Tun et al., 2002). Cocktail Party scenarios therefore pose a particular challenge to older adults (Pichora-Fuller et al., 2017) as reduced capabilities in selective attention (H. Meister et al., 2013; Passow et al., 2012, 2014; Zanto & Gazzaley, 2014) often results in less effective top-down filtering of irrelevant information from the acoustic signal (Chao & Knight, 1997; de Villers-Sidani et al., 2010; Gazzaley et al., 2005; Rossi-Katz & Arehart, 2009; Tun et al., 2002). Attentional filtering deficits can stem from a failure to encode certain features of the input auditory signal that would otherwise enhance target signal saliency (Shinn-Cunningham & Best, 2008).

In this thesis, as part of our cognitive screening, we control for pathological changes in attention span. While we do not experimentally manipulate attentional demand, each of our paradigms involve discriminating an acoustic target from a noisy acoustic background. In Chapter 3 we asked participants to discriminate changes in acoustic pitch while listening to a background cacophony of naturalistic noises (e.g. city sounds, animals, tools). In Chapter 4 and Chapter 5, we asked participants to discriminate an auditory or AV target word from a background consisting of a multi-talker babble.

1.3.3 Decision making

According to Carstensen et al.'s (1999) Socioemotional Selectivity Theory (SST), the perception of available time can influence one's decision making process. Older adults are more likely to engage in behaviours that result in positive emotional outcomes, and less so in behavioural that would result in negative emotional outcomes (positivity bias, Mather & Carstensen, 2005). Under SST and the positivity bias, it could be hypothesised that older adults are therefore less likely to make decisions in which there is a risk of a negative outcome (Mather, 2006) . However, this hypothesis is complicated by evidence showing that people are generally more risk aversive when experiencing fear, and less risk aversive when experiencing anger (Lerner et al., 2003; Lerner & Keltner, 2001).

There is conflicting evidence of age-related differences in risk-taking behaviour and strategies. Recent research has shown evidence of a reduction in risk-taking tendencies of older adults on a range of decisions spanning ethical, financial, health, recreational, and social domains (Rolison et al., 2014). However, some studies have found that older and younger adults do not differ in risk-taking strategies, such as in the likelihood of selecting cards from a deck which yields high reward at a high risk in gambling tasks (MacPherson et al., 2002), or in changing behaviour as a function of risk by taking fewer cards as risk increases (Dror et al., 1998).

In perceptual decision-making tasks, age-differences in decision strategy are much clearer (Dully et al., 2018). Older adults require more evidence than younger adults in order to reach a decision (i.e. increased decision boundaries) (McKoon & Ratcliff, 2012, 2013; Ratcliff et al., 2001, 2004, 2006a, 2006b, 2007, 2010, 2011; Ratcliff & McKoon, 2015; Spaniol et al., 2008; Starns & Ratcliff, 2010; Thapar et al., 2003), and make smaller adjustments in re-evaluating decision boundaries compared to younger adults (Forstmann et al., 2011). While clear age-related differences are evident in terms of decision criteria, age-related differences in the time required to gather adequate task-relevant sensory evidence (a parameter in decision-making models known as drift rate) seems to be task dependent (McGovern et al., 2017). While younger and older adults were comparable in drift rate on a signal detection task (Ratcliff et al., 2001), younger adults had higher drift rates (faster evidence accumulation) on a letter discrimination task (Thapar et al., 2003), and lower (slower) drift rates on a motion discrimination task (Forstmann et al., 2011).

In summary, there is evidence that younger and older adults differ in the decision-making strategies they use, both in perceptual tasks and in naturalistic settings. The experiments discussed in this thesis involve perceptual decision-making tasks, however in Chapter 3 we explicitly investigate how pre-stimulus brain state influences behaviour along the sensory-decision cascade.

1.3.4 Models of cognitive ageing

Cognitive ageing has been explained under several theoretical standpoints. Firstly, the common cause hypothesis argues that age-related changes in sensory and cognitive processes occur simultaneously and are attributable to wide-spread changes in the ageing nervous system (Baltes & Lindenberger, 1997; Christensen et al., 2001; Lindenberger & Baltes, 1994). Evidence from this comes from Lindenberger and Baltes' (1994) study in which they found that auditory and visual acuity accounted for 93.1% of the age-related variance in cognitive function (measured by testing speed, memory, reasoning, knowledge and fluency). Furthermore, Christensen et al. (2001) used a multiple indicators, multiple causes model to investigate the nature of the common cause by modelling a common cause factor based on reaction time, visual acuity, grip strength, respiratory efficiency, blood pressure, cognitive function and a composite measure of memory and crystallized intelligence in a sample of older adults aged 77.4 to 98.7 years old. All indicators, with the exception of blood pressure, loaded significantly on the common cause factor. Age-related neurobiological changes are discussed in further depth in Chapter 2.

Secondly, there are models which argue that reduced quality and/or quantity of sensory input, through reduced sensory acuity, has a knock-on declining effect on cognition. The sensory deprivation hypothesis posits that sensory decline over a prolonged period of time results in the degradation of central neural functioning (Oster, 1976; Valentijn et al., 2005). Whereas, the information degradation hypothesis argues that degraded sensory input influences higher-order cognitive processes (Schneider & Pichora-Fuller, 2000). Under this hypothesis, age-related reductions in sensory acuity leads to the accumulation of degraded sensory evidence, which in turn results in perceptual processing errors. Avoiding these errors imposes a higher cognitive load, thus increasing the need to recruit additional cognitive sources to attain more accurate behavioural performance. There is, therefore, a trade-off between cognitive performance and cognitive resources (Zekveld et al., 2011). The key difference between the Sensory Deprivation and Information Degradation hypotheses is the time over which declines in sensory acuity influence cognition. Under the sensory deprivation hypothesis, the impact of sensory decline is observed following a prolonged period of time, whereas in the impact within the information degradation model sensory decline is immediate.

Lastly, it is possible that deterioration of cognitive abilities influences sensory processing via top-down control (cognitive load on perception hypothesis). For example, it is more difficult to discriminate auditory speech under high cognitive load conditions induced by divided attention tasks (Mattys et al., 2014; Mattys & Wiget, 2011). As discussed earlier, this effect is amplified given that older adults typically find attentional control more difficult (Pichora-Fuller et al., 2017).

1.4 Multisensory integration

1.4.1 Non-linear modelling of multisensory integration

Successful multisensory integration relies on three principles. Firstly, multisensory integration is more likely to occur if sensory cues are spatially congruent. Bolognini et al. (2005) found that perceptual sensitivity in detecting a visual target at a specific location is enhanced when an auditory cue was presented at the same location. Furthermore, the McGurk effect shows that when participants are presented with conflicting auditory and visual phonemes at the same location, they will often hear a third phoneme which is a fused percept of the input cues (McGurk & MacDonald, 1976). Thus, visual cues are more dominant during spatial ventriloquist tasks. Secondly, multisensory integration is more likely to occur when sensory cues are temporally congruent. For example, Bolognini et al. (2005) found that perceptual sensitivity in detecting a visual target is enhanced when an auditory cue is presented simultaneously, compared to when presented with a time lag between 100 and 500ms. Additionally, Shams et al. (2002, 2000) presented participants with a sound-induced flash illusion paradigm, in which each trial comprised of a visual flash paired with one or two auditory beeps. When the visual flash was paired with two beeps, participants incorrectly reported also perceiving two visual flashes, thus providing evidence that auditory cues are weighted more. Thus, auditory cues are more dominant during temporal ventriloquist tasks. Lastly, the principle of inverse effectiveness states that multisensory integration is stronger when responsiveness to unisensory cues is weak. Behaviourally, Van de Rijt et al. (2019) tested participants’ recognition of sentences in noise in auditory only (AO), visual only (VO), and AV conditions, whilst varying the auditory SNR. Audio-visual speech integration was determined by the difficulty in recognising unisensory stimuli, as there was greater AV enhancement at lower SNRs and in those with poorer lip-reading abilities. These principles of multisensory integration are also supported by electrophysiological evidence using single cell and EEG recordings, and will be discussed in Chapter 2; however, initial evidence stems from the observance of enhanced or depressed neuronal responses for multisensory stimuli compared to unisensory stimuli, or multisensory responses that were larger than the sum of individual unisensory responses (for review see Stein and Meredith, 1993).

Much of the work investigating AV speech integration draws comparisons between the multisensory percept and the unisensory percepts. Capitalizing on the superadditivity of multisensory responses researchers often model AV speech integration as the difference between the multisensory response and the summation of the unisensory responses (i.e. AV = AV – [A + V], where AV, A and V represent the audio-visual, auditory and visual responses respectively). Many studies exploit this representation of multisensory response as a measure of the benefit derived from AV stimuli in comparison to unisensory stimuli (e.g Besle et al., 2004; Stekelenburg & Vroomen, 2007).

Older adults often find it difficult to listen to a speaker in a noisy environment (Babiloni et al., 2006; de Villers-Sidani et al., 2010; Pichora-Fuller et al., 2017; Sommers et al., 2005), however being able to see a speaker clearly can help the listener recognise what is being said faster and more easily (Bernstein et al., 2004; Besle et al., 2004; Eskelund et al., 2011). The effect that visual speech has in enhancing comprehension is believed to be due to how predictive the visual cues provided by articulatory facial movements are of the acoustic content (Sumby & Pollack, 1954). These visual cues help to prime the listener, and thereby reduce the uncertainty about the acoustic signal (Peelle & Sommers, 2015; van Wassenhove et al., 2005). The perceptual and behavioural benefit (and their neural correlates) in discriminating acoustic stimuli afforded by the presence of visual cues is referred to as visual, or AV, enhancement. AV enhancement has been reported to be comparable between younger and older adults (Gordon & Allen, 2009; Maguinness et al., 2011; Sommers et al., 2005), suggesting that the extent of the benefit older adults derive from visual cues is similar to that of younger adults despite age-related changes in auditory processing. However, some studies suggest that older adults derive more benefit, and thus experience greater AV enhancement, than younger adults (Sekiyama et al., 2014; Sheldon et al., 2008). Furthermore, AV enhancement is strongest when the visual stimulus is reliable and becomes weaker when the visual stimulus becomes less reliable. AV enhancement varies as a function of hearing loss (Puschmann et al., 2019), and with signal-to-noise ratio (SNR; Ross et al., 2007), suggesting that visual cues benefit listening more when acoustic signals are degraded. However, it has been reported that this is only the case when visual cues are reliable; when visual cues are made unreliable through blurring (Gordon & Allen, 2009; Maguinness et al., 2011), or are used ineffectively used (Sommers et al., 2005), AV enhancement is reduced in older adults, but not in younger adults.

In Chapter 4 we investigate age-differences in behavioural and evoked neural correlates of AV enhancement in a speech-in-noise paradigm by using a similar model of audio-visual integration as discussed in this section. In Chapter 5, using a similar approach, we extend this work and examine age differences in the evoked neural correlates of phonemic visual predictability.

1.4.2 Bayesian models of multisensory integration

Bayesian probability models estimate the posterior probability distribution of an event, given prior information and new evidence. Bayesian probability models have been applied to multisensory integration as a method of estimating the combination of sensory cues in multisensory environments. The aim of these models is to estimate the posterior probability distribution of a multisensory event or response, given various input sensory cues which vary in reliability, and given prior knowledge, expectation and assumptions regarding the multisensory scenario. However, one issue that a Bayesian multisensory integration model must consider is whether the sensory cues are assumed to be generated by the same source, as in a linear cue combination model, or not, as in a causal inference model.

1.4.2.1 Linear Cue Combination

The linear cue combination model assumes that there is a single source which generates noisy sensory cues (e.g. visual and auditory information). For example, consider the scenario of conversing with a friend in a café and that you are paying close attention to what they are saying. A cue combination model of audio-visual speech perception assumes that the visual representation of the speaker, and the language being heard come from the same source. However, these cues become unreliable if, for example, there is a lot of background chatter, hence making the auditory cue noisy, or if the viewer does not see the speaker clearly because they have forgotten their spectacles, hence making the visual cue noisy. In addition, there may also be internal sources of noise, such as noise introduced by neuronal activity, muscle activity, or cardiovascular function. The aim of a Bayesian probability model in this case is to estimate an optimal linear combination of the two cues, by way of maximum likelihood estimation, in forming a fused percept, as a weighted average of the cues in terms of their precision. The model predicts that multisensory cues provide a more precise estimate than unisensory cues, and that the weighting given to a cue varies as a function of its reliability. Thus, in the café scenario, if the visual and auditory cues of the speaker are equally reliable, audio-visual perception would be based on equal weighting of the visual and auditory cues. However, if there is a lot of background chatter making the auditory cue unreliable, audio-visual perception would be based on unequal weighting of the sensory cues; specifically the visual cue would be weighted higher.

Indeed, studies have shown that the brain integrates multisensory cues in a statistically optimal way. For example, Alais and Burr (2004) investigated cue combination in the ventriloquist illusion by asking participants to localise auditory clicks and visual gaussian 'blobs' presented unimodally and bimodally. They found that, in bimodal trials, when visual localisation was made difficult by increasing the amount of blur in the visual modality, visual localisation was driven by the auditory information (i.e. auditory information was weighted more than visual information); however, when viewing conditions were good, visual localisation was driven by the visual information (i.e. visual information was weighted more than auditory information). Additionally, they found that bimodal localisation performance was greater than unimodal localisation performance in either modality. In another study, Sheppard et al. (2013) investigated cue weighting in an audio-visual rate discrimination task. Human and rat subjects were tasked with judging which of two sequential streams, presented visually, aurally or audio-visually, had a higher flicker rate. Cue reliability was manipulated by adding noise, and in audio-visual trials the streams flickered at different rates. The authors found that performance was greater in the audio-visual condition, compared to the unimodal conditions, in both humans and rats. Additionally, in the audio-visual condition, the modality that contained the least noise, and hence more reliable modality, was weighted more than the noisier, and hence less reliable, modality.

In ageing studies, it has been found that younger and older adults weight cues similarly in audio-visual rate discrimination tasks, resulting in minor improvements in behavioural performance in younger adults (Brooks et al., 2015). Furthermore, Braem et al. (2014) reported optimal cue weighting in both younger and older adults in a visuo-haptic vertical alignment task. However, there is evidence of age-related differences in reliability-based cue weighting. Bates and Wolbers (2014) found that when completing a homing task requiring the integration of visual landmark and self-motion cues, older adults underweighted visual cues in comparison to what would have been optimal.

Age-related differences in reliability-based cue-weighting could be attributed to sensory decline, as age related changes in visual and/or auditory sensitivity could introduce greater noise to the sensory cues. Controlling for perceptual threshold has shown comparable reliability cue weighting between younger and older adults (Brooks et al., 2015). Additionally, less-than-optimal cue weighting in older adults could be due to an age-related increase in sensitivity to irrelevant sensory cues, for example due to changes in sensory control (Hugenschmidt et al., 2009).

1.4.2.2 Causal inference

In contrast with the linear cue combination model, the causal inference model makes no assumption regarding a unitary source of the sensory cues. Instead the optimal estimate of multisensory integration is the nonlinear weighted average of an estimate assuming that sensory cues are generated by the same source and an estimate assuming that sensory cues are generated by independent sources (Körding et al., 2007). In essence, this model aims to establish the probability distribution of the multisensory event given that, in the noisy café example, the speech being attended to either comes from the friend who is speaking, or from someone at a nearby table. This model therefore considers the case of sensory cues being fused but can also consider partial fusion and segregation of sensory inputs.

Age-related differences in causal inference are well-reported in the literature. Older adults tend to have wider multisensory temporal binding windows compared to younger adults (Bedard & Barnett-Cowan, 2016; Stevenson et al., 2018), thus making them more susceptible to multisensory illusions such as the ventriloquist illusion (De Boer-Schellekens & Vroomen, 2014) and stream-bounce effects (Bedard & Barnett-Cowan, 2016), and poorer at judgments of temporal order when stimuli is presented in quick succession (Bedard & Barnett-Cowan, 2016). Park et al. (2020) suggest that age-related changes in temporal binding is a result of sensory decline. In their study, participants were tasked with localising an auditory stimulus during AV and AO trials, or a visual stimulus during VO trials. Bayesian modelling revealed that the ventriloquism bias, the influence the visual information had in biasing perception away from the true sound location, was more linear in older adults than in younger adults in AV trials. Coupled with the fact that older adults performed more poorly in a spatial hearing test, compared to younger adults, the authors attribute their findings to an age-related loss in spatial hearing. Additionally, a recent study found no age-related differences in ventriloquism biases when younger and older adults had comparable spatial hearing abilities (Jones et al., 2019). However, age-related changes in causal inference have also been attributed to changes in cognitive function. Causal inference has been attributed to activity in parieto-frontal brain regions and has been modelled using Bayesian models of causal inference (Cao et al., 2019; Körding et al., 2007; Rohe & Noppeney, 2015; Wozny & Shams, 2011). Frontal regions are particularly vulnerable to age-related structural and functional changes, with particular impact on cognitive function (for review, see Chapter 2). Furthermore, the influence prior sensory information has on subsequent sensory events can be influenced by age-related changes in working memory (Allred et al., 2016; Dobreva et al., 2012), which might be integral to multisensory recalibration (Hame Park & Kayser, 2019). Thus, age-related changes in causal inference may be a result of low-level changes in peripheral hearing abilities, higher-level changes in cognitive function, or both.

In Chapter 4 and Chapter 5, we are interested in studying the benefit of visual information when auditory information is made unreliable in an audio-visual speech-discrimination-in-noise paradigm. Though we do not consider Bayesian models in our analyses in these chapters, or investigate multisensory binding itself, studies which have used Bayesian approaches in modelling multisensory integration may shed some insight on our results (see Chapter 6).

Chapter 2 Ageing and the brain

2.1 Neurobiological Changes

Post-mortem studies of the brain have documented a number of age-related changes in brain structure. For example, ageing is associated with widespread structural changes in both white and grey matter in the brain (Raz & Rodrigue, 2006). The prefrontal cortex (PFC) is one of the most susceptible brain structures to the effects of ageing. This has been explained by a retrogenesis, or a “last in first out” (Bender et al., 2016; Brickman et al., 2012), hypothesis wherein brain structures that mature earlier in development (e.g. primary sensory cortices) are more robust to the effects of ageing compared to structures that mature later (e.g. frontal cortex). Grey matter volume in the PFC is estimated to decline at a rate of around 5% per decade from the age of 20 years onwards (Raz et al., 2004), however how reductions in PFC grey matter volume relate to cognitive decline is less clear (Kaup et al., 2011). There is evidence of negative relationships between PFC grey matter volume and cognitive function in ageing (Raz et al., 1998; Salat, 2002; Van Petten, 2004), however the nature of such relationships have been reported inconsistently in the literature on memory, learning, and attention (Kaup et al., 2011). In healthy ageing, there is a decline of around 20 to 30% in white matter volume across the lifespan (Marner et al., 2003). Age-related decline of white matter integrity has been associated with changes in cognitive processing speed (Charlton et al., 2006; Penke et al., 2010) and working memory (Charlton et al., 2006, 2008, 2010).

Age-related decreases in hippocampal volume are associated with decline in multiple areas of cognition including working memory, episodic memory, processing speed, and executive function (O’Shea et al., 2016). However, the link between hippocampal volume and memory deficits may not be as strong as previously though, given that further evidence has shown that smaller hippocampal volume is associated with better memory performance in younger adults, and a weak positive relationship between hippocampal volume and memory performance in older adults (Van Petten, 2004).

White matter plays a key role in nerve conduction, ensuring that the speed and efficiency of neural signals are maintained (Nave, 2010; Salzer & Zalc, 2016), thus a loss of white matter are likely to contribute to age-related delays in neural processing speed. Indeed, there is evidence that, in the visual domain, age-related delays in evoked activity are mediated by white matter structure in the optic radiation connecting the lateral geniculate nucleus with the primary visual cortex (V1; Price et al., 2017). In auditory perception, age related hearing loss is associated with myelin degeneration in the cochlea in both animals (G. M. Cohen et al., 1990; Hoeffding & Feldman, 1988) and humans (Xing et al., 2012). However, slowing of auditory processing has been associated with degeneration of grey matter in auditory cortex (A1), rather than white matter (Price et al., 2017). Furthermore, Peelle et al. (2011) found that age-related hearing loss was associated with reduced grey matter volume in A1.

There is evidence that age-related decline in auditory processing may not be solely due to changes in neuroanatomical or neuro-molecular structure, but that age-related differences in functioning at the neuronal level may have some influence. It has been reported that healthy ageing results in poorer A1 frequency tuning (Caspary et al., 2008; de Villers-Sidani et al., 2010; Kamal et al., 2013; J. G. Turner, 2005) and desynchronized spiking (de Villers-Sidani et al., 2010; Kamal et al., 2013). This can be explained by age-related molecular changes within A1, such as a reduction in Gamma-Aminobutyric Acid (GABA; Burianova et al., 2009; Gao et al., 2015; Ling et al., 2005). However, it is also reported that neuronal activity becomes downregulated with exposure to degraded acoustic input, as is the case in age-related hearing loss (Kamal et al., 2013; Peelle et al., 2011; Peelle & Wingfield, 2016), and can be reversed, to some degree, by reducing the degradation (Kamal et al., 2013) or with training (de Villers-Sidani et al., 2010).

In summary, there are widespread neuroanatomical changes in the ageing brain. Changes in PFC grey matter volume is linked with age-related declines in cognition and cognitive processing speed. The neural processing of visual information slows due to degradation of white matter microstructure in the early visual pathway (before V1), while the neural processing of auditory information slows due to degradation of grey matter in A1. In Chapter 3, Chapter

4, and Chapter 5 we investigate differences in the timing of evoked potentials between younger and older adults. Therefore, any such differences observed may be attributed to changes in neuroanatomical structure.

2.2 Models of compensatory brain activity

Given that changes in sensory acuity, cognition, brain structure, and neuronal function have been observed in the ageing brain, one question that arises is how are these reflected in scalp-level neural activity? As discussed in Chapter 1, a general decline in behavioural and cognitive processing speed is typical in health ageing. Similarly, a steady decline in neural processing speed has been observed. In the visual domain, Rousselet et al. (2010) have shown that neural processing in a visual face discrimination task slowed at a rate of approximately 1 ms per year from age 20 years onwards. Furthermore, there is evidence that the peak amplitude of event related potentials (ERPs) become delayed in ageing (this will be discussed in more detail in relation to specific ERP components relevant to this thesis in sections 2.5 and 2.6).

Another question that arises is how does the ageing brain compensate for these changes in an attempt to ensure normal functioning? It may be that the slowing of neural processing speed, just discussed, may be a neural correlate of cognitive slowing, or it may be as a result of compensatory mechanisms that activate in an attempt to maintain good task performance in light of sensory, cognitive and/or neural decline. Models of compensatory mechanisms in the ageing brain have reported topographical shifts in brain activity in the recruitment of additional brain areas. One such model is the Hemispheric Reduction in Older Adults model (Cabeza, 2002). The HAROLD model suggests that an increase in bilateral recruitment of pre-frontal brain regions acts as a compensatory mechanism in neurocognitive decline. Evidence supporting this model comes from studies observing bilateral activation in pre-frontal cortices in older adults in working memory tasks (Reuter-Lorenz et al., 2000), and in perceptual tasks (Grady et al., 1994, 2000). However, the Compensation-related Utilization of Neural Circuitry Hypothesis (CRUNCH) suggests that compensatory activity is only useful when cognitive load is low; when cognitive load is high, compensatory recruitment of neural resources becomes less effective (Reuter-

Lorenz & Cappell, 2008). Therefore, compensatory neural recruitment may not always result in enhanced performance on perceptual or cognitive tasks.

Another model describing a shift in topographical shift in brain activity with ageing is the Posterior Anterior Shift in Ageing model (PASA; Davis et al., 2008). Whereas the HAROLD model described compensatory recruitment along the sagittal plane, the PASA model suggests a shift in neural recruitment along the coronal plane. Grady et al. (1994) observed an age-related recruitment of the pre-frontal cortex in response to reduced activity in the visual cortex due to the decline of sensory processing functions in the occipital and temporal cortices. However, these effects are not limited to basic perception and attentional function, but have also been observed in tasks involving working memory (Grossman et al., 2002; Rypma & D'Esposito, 2000) and episodic memory (N. D. Anderson et al., 2000; Cabeza et al., 1997, 2004; Daselaar et al., 2003; Dennis et al., 2007; Grady et al., 2002; Madden et al., 1999). It is important to note that PASA effects are not always observed in these domains (Grady et al., 1995; Iidaka et al., 2001; Milham et al., 2002; Stebbins et al., 2002), and in one case the reverse pattern of an anterior to posterior shift in activity has been observed (Nyberg et al., 2010).

Together, both the HAROLD and PASA models describe the recruitment of additional brain areas in compensation for age-related decline, however, neither model addresses over-recruitment of particular brain areas or changes in the selectivity of brain areas with age. Dedifferentiation describes a reduction in neural selectivity, and thus over-recruitment, of brain areas to certain stimuli (Grady, 2008). For example, an age-related reduction in specificity has been found in in the fusiform face area during face processing tasks (Burianová et al., 2013; Zebrowitz et al., 2016). In auditory speech perception, older adults do not show the same hemispheric specificity typical in younger adults in the processing of slowing changing speech cues (Keller et al., 2019).

Much of the work investigating these compensatory mechanisms in the ageing brain have used functional Magnetic Resonance Imaging (fMRI), which excels in locating the sources of changes of brain activity. In this thesis we use EEG to measure brain activity, which does not have good spatial resolution, however our focus is not on where in the brain changes in activity occur, but on when and how these changes occur in terms of timing and magnitude. We do, however, investigate topographical differences in EEG projections in Chapter 3 (see section 3.3.4) and in evoked activity in Chapter 4 and Chapter 5, between younger and older adults. Changes in scalp topography with age are likely to be due to compensatory mechanisms (described above), due to changes in underlying neuroanatomical structure (discussed in section 2.1).

2.3 Measuring brain function using EEG

2.3.1 What is EEG?

In this thesis we will use EEG to non-invasively record electrical signals from the brain. EEG allows us to record changes in electrical brain activity with millisecond precision. The signals recorded represent an a summation of dendritic postsynaptic potentials in populations of pyramidal neurons (M. X. Cohen, 2017; Lopes da Silva, 2013; Mitzdorf, 1985; P. L. Nunez & Srinivasan, 2009). From the signal, we can extract information such as the amplitude, latency, and oscillatory frequency in an attempt to understand the behaviour and function of the underlying neuronal populations. However, direct mapping of EEG characteristics and neural (micro-) circuitry (the inverse problem) is made difficult due to the low spatial resolution of EEG recordings. EEG can only measure broad activity from neuronal populations that are parallel and that activate in synchrony. In addressing the inverse problem, source localisation techniques can estimate sources to centimetre accuracy (Cottereau et al., 2015; Cuffin et al., 2001; Fuchs et al., 2002; Stenroos & Hauk, 2013), however a given EEG topography could be generated by dipoles in varying locations, and the number of dipoles that can be reliably identified is dependent upon the number of scalp channels used in recording. The work in this thesis focused primarily on the timing, amplitude and/or oscillatory frequency of neural events reflecting auditory or audio-visual perception, rather than on the neuroanatomical sources involved in these perceptual processes. In doing this we quantify EEG activity using event-related potentials, time-frequency representations, and using linear discriminant analysis.

2.3.2 ERPs

ERPs represents a positive or negative deflection in the voltage of EEG signals, relative to baseline, in response to an event or stimulus. Metrics quantifying the peak amplitude and latency of these deflections are used as indices of sensory encoding, as well as top-down computations such as attentional control, memory, and decision-making. While EEG provides an accurate measurement of peak amplitude and latency, the process of averaging over trials assumes that noise or other task-irrelevant signals are averaged out, leaving only the task-relevant deflections of interest. The process of averaging removes variation in the signal, which can be informative. Other analysis methods preserve dimensionality in the EEG data, which can be exploited as further indices into sensory and cognitive processing.

2.3.3 Time Frequency Representations (TFRs)

Ongoing EEG signals fluctuate over time in rhythmic cycles (neural oscillations). Neural oscillatory activity represents fluctuations in the excitatory and inhibitory states of the underlying neuronal population, and correlate with behaviour relating to information processing (Fries et al., 2007; Rajkai et al., 2008; Sirota et al., 2008). Thus, neural oscillations can serve as indices to cognitive and perceptual processes (Fries et al., 2007; VanRullen et al., 2011).

Neural oscillations can be quantified in several ways. Firstly, neuronal populations vary in the speed of their excitation-inhibition fluctuations, thus we can examine the speed (or frequency) of oscillations in the EEG signal. Oscillatory activity has been described in several frequency bands: delta (δ, 1 – 4 Hz), theta (θ, 4 – 8 Hz), alpha (α, 8 – 12 Hz) beta (ß, 13 – 30 Hz), and gamma (γ, > 30 Hz). Each frequency band has been implicated in various and differential sensory, cognitive, and pre-stimulus processes (Fries et al., 2007; Harmony, 2013; Klimesch, 1999; Klimesch et al., 2007; Spitzer & Haegens, 2017).

TFRs are representations of EEG data which carry information about time, space, frequency, power, and phase. Frequency, power and phase are dimensions of the EEG signal which are not afforded by ERP analyses. Oscillatory power is an estimate of the magnitude of excitatory post-synaptic potentials reaching a given neuronal group at a given time point (Varela et al., 2001), and is associated with neuronal spiking in brain areas generating the potentials (Coenen, 1995; Schroeder et al., 1991; Whittingstall & Logothetis, 2009). Oscillatory phase, on the other hand, indexes the location within an oscillatory cycle, thereby indexing temporally precise excitatory or inhibitory windows in which information is encoded (Jensen & Lisman, 2000; O'Keefe & Recce, 1993).

2.3.4 Linear Discriminant Analysis (LDA)

Using ERP and TFR analyses can be computed across the whole scalp, and thus considering spatio-temporal profiles of event-related and ongoing electrical activity, or at single (or a group average of) channels. Both methods have their limitations: whole scalp analyses require multiple comparison correction which can result in the diluting of weaker effects, while single (or averaged) channel analyses require a priori assumptions about the channel(s) which best represent task-relevant activity.

One approach which considers the whole scalp, but which eliminates the multiple comparison problem is to reduce the spatial dimension of the EEG data to a single dimension through a linear combination of EEG signals. By combining information across channels rather than across trials, we can derive a single trial representation of cognitive function, allowing us to model neural signals and behaviour on a single trial basis. Several studies have shown that information about sensory encoding and cognitive processing can be derived from such neural signals (Gherman & Philiastides, 2015; S. J. Kayser et al., 2016; McNair et al., 2019; Philiastides et al., 2014; Philiastides & Sajda, 2006).

LDA is not without its own limitations, however. Firstly, the method assumes that neural activity can be linearly modelled. There is evidence that linear models predict neural activity in monkeys in multisensory cue integration tasks (Fetsch et al., 2012), however there is also evidence showing that neural activity can be non-linear (Rombouts et al., 1995), particularly in the ageing brain (Babiloni et al., 2006; Zappasodi et al., 2015). Secondly, LDA assumes that the data is normally distributed, and that there is independence of feature (e.g. electrodes, time points), equality of covariances for each condition being classified. However, research has shown that despite these assumptions, LDA can be robust to violations of the assumptions of equal covariances and normality, while using regularising the covariance matrices can account for unequal covariance (Blankertz et al., 2011; Philiastides et al., 2014).

2.4 Cortical oscillatory activity

Cortical oscillatory activity measured via EEG or magnetoencephalography (MEG) is known to reflect neuronal excitation and inhibition (Buzsáki & Draguhn, 2004; Fries et al., 2007; Sirota et al., 2008). Cellular level oscillations facilitate mechanisms underlying cortical processes, such as biasing neural and network input selectivity, plasticity, and neural assembly binding (Buzsáki & Draguhn, 2004). Cortical oscillations can therefore be considered as indices into conscious cognitive computations, decision making processes and sensory representations in the brain (Donner & Siegel, 2011; VanRullen et al., 2011; Varela et al., 2001; Ward, 2003).

2.4.1 Pre-stimulus oscillatory activity

The pre-stimulus power of oscillatory activity has been consistently shown to predict conscious perception of psychophysical stimuli in a variety of detection tasks in multiple modalities, wherein increases in power often precede stimuli that have gone undetected (Babiloni et al., 2006; Ergenoglu et al., 2004; Hanslmayr et al., 2011; Linkenkaer-Hansen, 2004; Mathewson et al., 2009; Romei et al., 2008; van Dijk et al., 2008). Specifically, in the auditory domain, power dependency in the lower frequency bands is implicated in the detection of acoustic targets. In a paradigm where listeners detected clicks embedded in noise, theta (~2-6 Hz) power was greater for targets that were missed, than for detected targets (Ng et al., 2012). Thus, given the wealth of evidence demonstrating power dependencies of perception, pre-stimulus oscillatory power serves an inhibitory role in psychophysical perceptual processing. It is argued that this inhibitory mechanism is the result of a modulation of response gain (Chaumon & Busch, 2014).

Ongoing oscillatory activity can also be characterized by metrics quantifying oscillatory phase. At the same frequency, variations in network state excitability occur on shorter temporal scales than variations in oscillatory power (Buzsáki &

Draguhn, 2004; Klimesch et al., 2007; Lakatos et al., 2005; Montemurro et al., 2008; Rajkai et al., 2008; Sirota et al., 2008). Therefore, oscillatory phase effects could be more informative as to the precise encoding of sensory information than power (C. Kayser et al., 2009).

As shown with oscillatory power, pre-stimulus phase can predict several facets of neural processing (VanRullen et al., 2011). This has been demonstrated in relation to the magnitude and latencies of ERPs (Brandt, 1997; Jansen & Brandt, 1991; Kruglikov & Schiff, 2003), and reaction times (Callaway & Yeager, 1960; Dustman & Beck, 1965; Lakatos et al., 2008). Furthermore, there is evidence that conscious visual perception is gated by pre-stimulus alpha-band oscillatory activity (N. A. Busch et al., 2009; Mathewson et al., 2009), but only when the stimulus is attended to (versus unattended; Busch and VanRullen, 2010)). In the auditory domain, stimulus detection paradigms have shown that pre-stimulus phase of slower oscillations predicts the detection of low-level acoustic targets embedded within complex acoustic scenes in theta (Ng et al., 2012) and delta (Henry & Obleser, 2012) bands. Meanwhile, performance on discrimination tasks incorporating more complex (i.e. speech, laughter) stimuli is dependent on the phase of pre-stimulus alpha (Strauss et al., 2015) and beta (Pinheiro et al., 2017) band activity.

Until recently, neuroimaging studies failed to establish the stability of oscillatory gating mechanisms across tasks in the same participants, as well as within which cortical processes the mechanisms are generated. In a recent study we collected EEG data in participants performing two auditory discrimination-in-noise tasks relying on distinct acoustic features. We delineated two mechanisms by which pre-stimulus activity influences perception across tasks: one in which power scales the quality of acoustic sensory representations in auditory networks, and one in which phase directly influences decision-making processes within later-activated fronto-parietal networks (S. J. Kayser et al., 2016). In Chapter 3, we extend the findings of this body of literature by investigating the stability of these mechanisms with age.

2.4.2 Cortical oscillatory entrainment to speech

Oscillatory phase can also reveal insights into the auditory system's response to dynamic stimuli (Giraud & Poeppel, 2012b). Complex stimuli such as speech are rich in slow temporal features and modulations in amplitude and frequency (Chandrasekaran et al., 2010; Drullman et al., 1994a, 1994b), which elicit strong responses in the auditory cortex (Ding & Simon, 2009; Henry et al., 2014). Cortical oscillations have been shown to entrain to the temporal profile of dynamic acoustic input (Gross et al., 2013; M. F. Howard & Poeppel, 2010; Luo & Poeppel, 2007), resulting in increased neural gain (C. Kayser et al., 2015; Lakatos et al., 2008).There is evidence that the strength of entrainment increases with speech intelligibility (Ding & Simon, 2014; S. J. Kayser et al., 2015; Hyojin Park et al., 2015) and attention (Ding & Simon, 2014; Mesgarani & Chang, 2012). Thus cortical entrainment serves as an oscillatory mechanism facilitating conscious perception by tracking stimulus temporal features. In the ageing brain cortical oscillatory entrainment to speech within delta band activity is weaker and is less flexible (Henry et al., 2017).

In this thesis we do not examine cortical oscillatory entrainment itself, however this body of literature gives us important insights into the rhythmic properties of the brain, and into how the brain parses speech stimuli. In Chapter 3 we investigate how the rhythmic state of the brain prior to conscious perception influences perceptual decision making. In Chapter 4 and Chapter 5 we investigate the behaviour and neural gains of AV speech, and how this gain modulates with the visual predictability of speech.

2.4.3 Age-related differences in oscillatory frequency

A general age-related flattening of oscillatory power spectra has been reported, possibly as a result of greater neural noise and neuronal de-synchronization in the elderly brain, and is believed to be associated with cognitive decline (S. L. Hong & Rebec, 2012; Tran et al., 2016; Voytek et al., 2015). Additionally, peak alpha frequency shows age-associated slowing (Chiang et al., 2011; Hashemi et al., 2016; Hubbard et al., 1976; Oken & Kaye, 1992; Richard Clark et al., 2004; Woodruff & Kramer, 1979). Older adults' alpha power is also more sensitive to stimulus degradation (Wostmann et al., 2015) and attention (Henry et al., 2017) compared to younger adults.

Ageing is associated with increased alpha power and decreased theta power at rest (Cummins & Finnigan, 2007; Hartikainen et al., 1992; Polich, 1997; Vlahou et al., 2014; Volf & Gluhih, 2011; Widagdo et al., 1998). In memory tasks, older adults show reduced theta power and poorer theta modulation than younger adults at both encoding and retrieval (Cummins & Finnigan, 2007; Kardos et al., 2014; Karrasch et al., 2004; McEvoy et al., 2001; Tóth et al., 2014).

In summary, as the brain ages both task-related and baseline theta and alpha frequency activity changes, such that alpha frequency is slower and there is a flatter overall power spectrum. In Chapter 3, we are interested in the frequency bands in which pre-stimulus oscillatory activity influences sensory encoding, decision making processes, and behavioural choice. It is likely that differences in the balance of theta and alpha activity will be observed.

2.5 Early ERPs

Early auditory evoked responses have been characterised by components at distinct timescales. Of note are positive and negative deflections occurring at around 100 ms (P1 and N1 respectively), and a positive deflection occurring at around 200 ms (P2). The auditory P1-N1-P2 complex is a pre-attentive auditory evoked potential (AEP), which is involved in inhibitory control in sensory gating (P1) and detecting acoustic change (N1; Pratt, 2012). However, the functional significance of the P2 deflection is relatively unclear, as the extent of the exogenous and endogenous properties of the P2 are debated (Crowley & Colrain, 2004). As the brain ages cognitive and neural processes become slower (Bieniek et al., 2013; Price et al., 2017; Salthouse, 1996). Indeed, N1 and P2 responses of the P1-N1-P2 AEP are typically delayed (Anderer et al., 1996; Bertoli et al., 2005; Harkrider et al., 2005; Harris et al., 2007; Henry et al., 2017; Pfefferbaum et al., 1980; B. Ross et al., 2007; Tremblay et al., 2002, 2003) and larger (Amenedo & Díaz, 1998, 1999; Anderer et al., 1996; Harkrider et al., 2005; Pfefferbaum et al., 1980; Tremblay et al., 2003) in the aged brain. However, age-related diminishing of P2 amplitude has also been reported (Czigler et al., 1992; Henry et al., 2017; Rufener et al., 2014). Some studies report amplification and delaying of P1 responses with age (Bertoli et al., 2005; B. Ross et al., 2007; Tremblay et al., 2002) while others found no such effects (Harris et al., 2008; Henry et al., 2017; Tremblay et al., 2003).

Multisensory research has investigated how AV stimuli influences the dynamics of early evoked responses, in an attempt to understand the neural correlates of AV integration or enhancement. Successful AV integration is associated with an AEP with N1 and P2 peaks that occur earlier and/or have a larger amplitude compared to unisensory or mismatching AV conditions (Alsius et al., 2014; Baart, 2016; Baart et al., 2014; Frtusova et al., 2013; Ganesh et al., 2014; Kaganovich & Schumaker, 2014; Klucharev et al., 2003; Stekelenburg & Vroomen, 2007; Treille et al., 2014; van Wassenhove et al., 2005). In the ageing brain, N1 peak amplitude is enhanced by AV stimuli (Frtusova et al., 2013; Winneke & Phillips, 2011) and occurs earlier (Frtusova et al., 2013). It is unclear whether N2 peak enhancement in ageing is a result of compensatory mechanisms which are engaged to support sensory processing, or whether there is less effective use, or sensory processing of, additional visual information.

In Chapter 3, Chapter 4, and Chapter 5 we investigated temporal and amplitude differences in the P1-N1-P2 component of auditory evoked activity between younger and older adults. In Chapter 3 and Chapter 4 we look at these ERPs in response to the onset of background noise. However, in Chapter 4 and Chapter 5 we also investigate whether these components were sensitive to AV enhancement and phonemic visual predictability of word stimuli, and whether such effects interacted with age.

2.6 Late ERPs

The P3 component is a positive deflection occurring in evoked activity at around 300ms, and has been used as a measure, firstly, of processes involved in mapping incoming sensory information onto internal representations in working memory (Polich, 2012), and secondly, has been suggested as a marker of decision-making (Dully et al., 2018). In AV paradigms, the P3 peak amplitude is suppressed in response to congruent AV stimuli in comparison to incongruent AV stimuli (Andres et al., 2011; Stekelenburg et al., 2018), and in comparison to AO stimuli (Hernández-Gutiérrez et al., 2018; Hessler et al., 2013; Irwin et al., 2018, 2017; Starke et al., 2017). The P3 amplitude is also sensitive to changes in memory load (Segalowitz et al., 2001), but its topography appears to be task-dependent (Polich, 2012) in the younger adult brain. In older adults, the P3 peak has a more frontal topography and is delayed in comparison to younger adults (Fjell et al., 2005; Fjell & Walhovd, 2001, 2004).

The N4 component is observed as a negative deflection between 250 and 550ms, and is believed to index the mapping of sensory input to contextual representations (for review see Duncan et al., 2009) in semantic processing. The N4 peak is sensitive to semantic congruence, which in AV paradigms is observed as peak amplitude enhancement when AV stimuli is incongruent in terms of phonetic (Lebib et al., 2004), lexical (Kaganovich et al., 2016), and semantic content (Van Petten et al., 1999). Thus, the N4 component is sensitive to semantic congruence, however there is also evidence that it is sensitive to semantic cloze probability (Kutas & Federmeier, 2011). In an ageing context, the N4 amplitude is typically later (Gunter et al., 1992, 1996) and supressed (Cameli & Phillips, 2000) in older adults, compared to younger adults.

In Chapter 4 and Chapter 5 we investigated the temporal and amplitude differences in late evoked activity between younger and older adults. We were interested in whether these components were sensitive to AV enhancement and phonemic visual predictability of word stimuli, and whether such effects interacted with age.

2.7 Treatment of age as a variable

An important decision that must be made when designing ageing research is whether to treat age as a continuous or categorical variable, and whether to take to a cross-sectional or longitudinal approach. Studies which consider age as a continuous variable can easily model the changes in cognitive abilities and neural metrics as a function of age. For example, Rousselet et al. (2010) investigated age-related changes in noise sensitivity in facial stimuli across the visual processing time-course. The authors modelled the relationship between EEG amplitude and noise features (local and global coherence) at each time point and EEG channel. Assessing the fit of the models across time and across ages revealed a progressive age-related delay in noise sensitivity of around 1 ms per year. This kind of design allows for the investigation of whether age-related changes are progressive or non-linear across the lifespan. However, a ‘middle-aged’ sample, anecdotally, is more difficult to recruit.

Cross sectional designs have the benefit of being able to observe and draw group comparisons using several different metrics relatively quickly. Assuming that homogenous, representative samples can be recruited, the results of cross-sectional studies should, in theory, be consistent with the results of longitudinal studies. However, this is not always the case. Nyberg et al. (2010) conducted an fMRI study wherein participants aged between 49 and 79 years of age completed a semantic categorisation task. The task was completed twice, with an interval of 6 years between completions, and both cross-sectional and longitudinal analyses were conducted on the structure and functional neuroimaging data between time points. Cross-sectional analyses revealed an age-related over-recruitment of frontal regions, whereas the longitudinal analyses revealed an age-related under-recruitment of frontal regions. In a behavioural study, Rönnlund et al. (2005) investigated the progression of episodic and semantic memory processes from age 35 to 80 years old, tested across an interval of 5 years. Both types of memory showed similar age-related decline from age 60 onwards, as observed in both cross-sectional and longitudinal analyses. Differential patterns of progression were found between cross-sectional and longitudinal analyses, however, at the younger end of the age-spectrum. Cross-sectional analyses suggested that episodic memory declines gradually with age from 35 years onwards, whereas longitudinal analyses suggested that episodic memory remains stable until age 60. Furthermore, cross-sectional analyses suggested that semantic memory remains stable up to age 60, whereas longitudinal analyses suggested that semantic memory increases with age up to age 60. Lastly, Pfefferbaum and Sullivan (2015) studied age-related changes in hippocampal volume in a sample of adults aged 20 to 70 years old, scanned over a period of up to 8 years. A cross-sectional analysis approach revealed no linear relationship between age and hippocampal volume; instead, a quadratic (curvilinear) model appeared to be a better fit for the data. On the other hand, a longitudinal approach, taking into account the trajectory of hippocampal volume for each participant, revealed a linear decline in volume with age. Longitudinal research might offer more control over unobserved heterogeneity in the recruited sample, which is important considering that a number of different demographic, lifestyle, genetic and environmental factors might influence cognitive ageing (Daffner, 2010). However, longitudinal studies have been criticised for lacking sufficient power in detecting age-related decline (Salthouse, 2000b).

In this thesis we take a cross-sectional, group-comparison approach in studying age-related differences in oscillatory and evoked activity underlying auditory and audio-visual perceptual decision-making. This approach was taken primarily due to the time constraints imposed by the Ph.D. program. Across all three experimental chapters, we define our younger adults as those aged between 18 and 30 years old, and we define older adults as those aged 60 years old and above. This is consistent with previous ageing studies investigating pre-stimulus cortical oscillations (Henry et al., 2017; Herrmann et al., 2016; Wostmann et al., 2015), as in Chapter 3, and behavioural and neural correlates of audio-visual speech perception (Frtusova et al., 2013; Sekiyama et al., 2014; Winneke & Phillips, 2011), as in Chapter 4 and Chapter 5.

2.8 Thesis rationale

In young participants, the state of rhythmic brain activity prior to a stimulus has been shown to modulate the neural encoding and perceptual impact of this stimulus – yet it remains unclear whether, and if so, how, the perceptual relevance of pre-stimulus activity changes with age. In Chapter 3, using the auditory system as a model, we recorded EEG activity during a frequency discrimination task from younger and older human listeners. By combining single-trial EEG decoding with linear modelling we demonstrate consistent statistical relations between pre-stimulus power and the encoding of sensory evidence in short-latency EEG components, and more variable relations between pre-stimulus phase and subjects’ decisions in longer-latency components. At the same time, we observed a significant slowing of auditory evoked responses and a flattening of the overall EEG frequency spectrum in the older listeners. Our results point to mechanistically consistent relations between rhythmic brain activity and sensory encoding that emerge despite changes in neural response latencies and the relative amplitude of rhythmic brain activity with age.

As we age, listening to a speaker in noisy environments becomes increasingly difficult due to changes in sensory acuity and attentional control. Most listeners benefit from the presence of reliable visual cues in speech-in-noise scenarios, and many studies have investigated the neural signatures of behavioural AV enhancement. Yet, it remains unclear how age, acoustic reliability and the presence of visual information interact to shape behaviour. Chapter 4, to address this and the underlying physiological processes, we recorded EEG activity during an audio-visual speech-in-noise paradigm in younger and older listeners. Speech was presented in two audio-visual conditions (AV informative, AV_{inf}; auditory-only informative, AO_{inf}) and at two acoustic noise levels. Behaviourally, younger and older adults performed comparably. Performance was greater for AV_{inf} speech compared to AO_{inf} speech across groups and noise levels, and was poorer at low noise levels. AV enhancement was greater in high noise levels, across all participants, and older adults derived greater AV enhancement compared to younger adults (an effect that was consistent across noise levels). Neurally, we found that AV enhancement is represented by a centro-parietal P3-like activity in older adults and an N4-like fronto-central activity in younger adults, but found that this activity did not correlate with behavioural AV enhancement. Our results point to distinct patterns of late evoked activity underlying AV enhancement between younger and older adults, possibly representing distinct cognitive (memory) strategies in predicting upcoming target stimuli.

Although it has been observed that visual speech enhances the perception of auditory speech, and that this has distinct influences on the amplitude and timing of evoked activity, little is known about how the predictability of visual speech about the upcoming auditory speech influences ERP dynamics. Studies have shown that evoked activity at multiple timescales is sensitive to different phonemic features of auditory speech, however it remains unclear whether and how behavioural AV enhancement might vary as a function of the visual predictability of speech targets, and how this is represented neurophysiologically. In Chapter 5, we address this by carrying out a secondary analysis of the data reported in Chapter 5. As well as considering behaviour and EEG data relating to age group, information condition, and noise, we also considered the articulation type (i.e. visual predictability; labial, non-labial).

Behaviourally, we found that word discrimination performance was greater for target words with non-labial initial phonemes, compared to labial initial phonemes. Furthermore, we found that AV enhancement was greater for labial initial phonemes, compared to non-labial initial phonemes, and this was consistent across age groups. Neurally, we found that visual predictability was reflected by late fronto-central negativity in older adults, but not in younger adults. However, we did not find evidence of an interaction between visual predictability and AV enhancement in terms of evoked activity, raising further questions about how visual predictability of speech is represented the brain's electrophysiology. Our results point to distinct patterns of late evoked activity underlying visual predictability of visual speech, again possibly reflecting differential strategies in predictive coding.

Chapter 3 Consistent pre-stimulus influences on auditory perception in younger and older adults

3.1 Introduction

In everyday life our acoustic environments are often teeming with incoming information. Yet, the auditory brain manages to filter target information from noise seamlessly, at least in the young and healthy brain (Bregman, 1994). With advancing age listening becomes more challenging, particularly in “cocktail party” scenarios (de Villers-Sidani et al., 2010; Pichora-Fuller et al., 2017; Rossi-Katz & Arehart, 2009). This difficulty could arise from age-related changes in peripheral and central auditory processes (S. Anderson et al., 2013; Clinard et al., 2010; Clinard & Cotter, 2015; Harris & Dubno, 2017), such as the poorer encoding in early sensory regions (Grose & Mamo, 2012; He et al., 2007; Mahajan et al., 2017; Paraouty et al., 2016; Wallaert et al., 2016). Changes in higher cognitive processes may also influence older adults’ performance via top-down feedback (Henry et al., 2017), through reduced attentional flexibility (M. D. Nunez et al., 2015; Zanto & Gazzaley, 2014), or changes in decision criteria when reporting perceptual performance (Dully et al., 2018).

As shown by recent work, perception depends not only on the qualities of the sensory signal but also on the state of the brain prior to stimulus occurrence (Henry et al., 2014, 2017; Henry & Obleser, 2012; S. J. Kayser et al., 2016; Ng et al., 2012; Pinheiro et al., 2017; Steinmetzger & Rosen, 2017). In many studies, the state (power or phase) of pre-stimulus rhythmic brain activity has been predictive of perceptual performance in a variety of tasks, in line with the view that perception in general is controlled by a cascade of rhythmic neural processes (Schroeder et al., 2010; VanRullen, 2016). Furthermore, changes in top-down influences by attentional and cognitive strategies are also reflected in rhythmic brain activity, especially in the alpha and beta bands (Henry et al., 2017; Petersen et al., 2015; Strauss et al., 2015; Wöstmann et al., 2017). In this context of relating rhythmic brain activity to perception we recently described two putative mechanisms by which pre-stimulus activity shapes auditory perceptual decisions in younger adults (S. J. Kayser et al., 2016); in that study the power of low-frequency and beta activity affected the encoding of sensory information in early auditory regions, while the phase of the alpha band influenced decision processes in high-level regions.

This importance of rhythmic activity for perception raises the question as to whether the underlying mechanisms and relevant time scales are conserved across the age span. For example, it is known that cognitive and neural processes become slower with age (Bieniek et al., 2013; Price et al., 2017; Salthouse, 1996), which is reflected in changes in the amplitude and latency of auditory evoked responses (Harris et al., 2008; Henry et al., 2017; Tremblay et al., 2003), an increase in response stereotypy (Garrett et al., 2011, 2013; Herrmann et al., 2016), and changes in the slope of the overall frequency spectrum of brain activity (S. L. Hong & Rebec, 2012; Tran et al., 2016; Voytek et al., 2015).This makes it possible that the patterns of rhythmic brain activity that shape perception systematically change with age.

We here capitalized on our previous study in a group of younger subjects to directly probe whether the mechanisms linking pre-stimulus brain activity, sensory encoding and decision-making are conserved with age. Specifically, we compared behavioural and EEG data from younger (<30 years) and older (>65 years) listeners with no, or only mild hearing loss, obtained during an auditory frequency discrimination-in-noise task. For each group we linked pre-stimulus oscillatory activity to neural signatures of stimulus encoding and decision making using single trial modelling. We expected to observe the same patterns of statistical relations between neural activity, sensory encoding and behavioural responses in both groups (i.e. significant relations between the same variables), but with the possibility that the precise time scales (i.e. frequency bands of brain activity) differed. For comparison with previous studies, we also quantified age-related changes in the amplitude and timing of evoked responses and the spectral slope of the overall EEG signal.

3.2 Materials and Methods

3.2.1 Participants

We collected data from 16 younger (6 male; mean ± SD age, 23.9 ± 1.1 years) and 17 older adults (8 male; mean ± SD age, 68.4 ± 3.6 years). We have reported data from the younger group, with the exclusion of power spectral density (PSD) and AEP analyses, in our previous study (S. J. Kayser et al., 2016) (the frequency task there). For this reason, we had set the target sample size for the group of older subjects to match the size of the younger group. Younger participants had normal self-reported hearing, as measured by the Better Hearing Institute Quick Hearing Questionnaire (Kochkin & Bentler, 2010). Older participants had no more than mild hearing loss as measured by the Better Hearing Institute Quick Hearing Questionnaire, Tinnitus Handicap Inventory (THI where applicable ; McCombe et al., 2001) and pure-tone audiometric (PTA) procedures. The PTA procedure was presented via MATLAB (2015b; The MathWorks Inc., Natick, MA) and was designed in accordance with guidelines from the British Society of Audiology (BSA; British Society of Audiology, 2012)). We tested participants' hearing thresholds at frequencies of 250Hz, 500Hz, 1000Hz, 2000Hz, 4000Hz and 8000Hz individually for each ear. Sound levels were calibrated using a Bruel&Kjaer sound-level meter. Older participants were also screened for cognitive impairment using the Montreal Cognitive Assessment (MoCA,Nasreddine et al., 2005), D2 test of attention (Brickenkamp & Zillmer, 1998), and the digit span working memory test (M. Turner & Ridsdale, 2004). Due to possible variability in participants' frequency discrimination abilities (Foxton et al., 2009; Liang et al., 2016; Semal & Demany, 2006), frequency difference limens (see below) were tested both at screening and immediately prior to the main experiment for each group. Group-level auditory and cognitive test scores are shown in **Table 1**. Four older participants were excluded at screening based on pre-defined criteria: two participants had moderate to severe hearing loss, as indicated by PTA testing, and in two participants frequency difference limens could not be measured reliably. Participants indicated no history of mental/neuropsychological disorders, stroke, or brain or ear injuries. Participants gave written informed consent and received £6/hour payment plus travel expenses for participating. This study is in accordance with the Declaration of Helsinki and was approved by the local ethics committee (College of Science and Engineering, University of Glasgow).

	PTA (dB)	BHI QHQ	THI	MoCA	D2		DSpan
					CP	TN-E	
Older	28.96 [18.93, 39.72]	7 [0, 33]	6 [2, 12] (n=3)	29 [26, 30]	199 [163, 251]	121 [113, 130]	105.5 [79, 121]
Younger	N/A	2.5 [0, 11]	N/A	N/A	N/A	N/A	N/A

Table 1. Auditory and cognitive test scores. Screening scores for younger (where applicable) and older participants who passed screening. Hearing scores are derived from pure tone audiometry (PTA), Better Hearing Institute Quick Hearing Questionnaire (BHI QHQ), and Tinnitus Handicap Inventory (THI). PTA scores reported are measured in decibels (dB) and represent the average threshold across ears and frequencies. THI was administered only as applicable, thus n is reported. Cognitive test scores are derived from Montreal Cognitive Assessment (MoCA), D2 test of Attention (D2) and digit span (DSpan) tests. Scores correspond to median across all participants in each age group. Square brackets indicate minimum and maximum scores. N/A indicates where data was not available.

3.2.2 Auditory stimuli

Participants completed a 2-alternative forced-choice auditory frequency discrimination task, as described in Kayser et al. (2016). Participants were presented with two sequential target tones embedded within a noisy background and had to discriminate which tone was higher in frequency (see **Figure 1**A). Targets were pure-tones of 50ms duration (including a 5ms cosine on/off ramp) and spaced 50ms apart. The noise was 4s in duration and comprised a naturalistic cacophony of sounds, consisting of environmental (forest and city) sounds, animal sounds, and sounds originating from tools (also used in Kayser et al. (2016) and Ng et al. (2012). The same noise clip was used in each trial. Noise intensity level was calibrated using a Bruel&Kjaer (model 2250) sound-level meter to an average of 65 decibels (dB) root-mean-square (rms) level. Target tones were equated in intensity at a SNR of +2dB relative to background intensity, based on the rms level. The second tone was kept at a constant 1024Hz while the first varied pseudo-randomly over 7 (younger participants) or 5 (older participants) equally-spaced (on an octave scale) levels of a frequency difference above or below the second (pseudorandomized and balanced across all trials), ranging from 0Hz difference to 2Δ in younger and 2.5ΔHz in older participants (where Δ is the participants' own 70% correct frequency difference limen). The reason we reduced the number of stimulus levels for the older adults was to keep the experimental duration to a minimum to avoid fatigue.

3.2.3 Experimental procedure

Auditory stimuli were controlled using MATLAB using the Psychophysics Toolbox Version 3 (Brainard, 1997) and presented using Sennheiser headphones. Prior to the main experiment, participants completed training trials to familiarize themselves with the task and their frequency difference (in noise) limens were obtained using three interleaved 2-down-1-up staircase procedures. In the actual experiment target tones were presented at one of six possible pseudorandom delays (2400 + n*33ms, where n = 0 … 5) relative to background onset. Trials were separated by an inter-trial period uniformly distributed between 1700 and 2200ms. Participants were instructed to respond as accurately as possible, and the background noise terminated once the response was provided, or after 4 s. Trials were presented in a block design of 120 trials per block, with each participant completing 360 trials in total.

3.2.4 EEG recording and pre-processing

EEG signals were recorded in a dark and electrically-attenuated room using an active 64-channel BioSemi system (BioSemi B.V., Netherlands). Electrooculogram (EOG) was derived from four electrodes placed at the outer canthi and below each eye. Electrode offsets were kept below 25mV, and data were recorded at a 500Hz sampling rate using a 208Hz low-pass filter.

Pre-processing and data cleaning were carried out as described previously in (S. J. Kayser et al., 2016). In brief, the data were filtered between 1-70Hz and Independent Components Analysis was used to identify eye movement and blink artefacts (Debener et al., 2010) and muscle artefacts (Beirne & Patuzzi, 1999; Hipp & Siegel, 2013). Trials were rejected if the peak signal on any electrode exceeded ± 100 µV. Further trials were rejected if participants responded faster than 400ms following the first target tone; to ensure that participants had allowed sufficient time for full attention to, and full availability of, sensory evidence. Based on these criteria we rejected an average of 5% of trials. EEG signals were re-referenced to the common average for further analysis.

3.2.5 Analysis methods

3.2.5.1 Evoked responses

We compute AEPs in response to the onset of the acoustic background based on trial-averaged data over a 3x3 grid of central channels (FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, CP2). Individual participants' P1, N1 and P2 component median peak latencies and amplitudes were taken at the maximum negative or positive deflection within component-specific time windows, and were then compared between groups.

3.2.5.2 Pre-target power spectra

Estimates of the frequency spectra of the ongoing EEG activity prior to the target stimuli were derived for each subject using Welch's method, using a sliding Hanning windows of 120ms length, with 0% overlap, in a time window of -0.6 s to 0 s relative to target onset. PSD estimates were initially calculated for each channel and subsequently averaged. PSD estimates were normalized by removing individual participants' mean and PSD slopes were then fit in semi-log space using linear regression at frequencies between 1Hz and 25Hz whilst excluding alpha power between 7 and 14 Hz (Tran et al., 2016; Voytek et al., 2015).

3.2.5.3 Single trial decoding of EEG signals

To link pre-stimulus activity with perception we used the same statistical modelling approach as in our previous study (S. J. Kayser et al., 2016). We computed pre-stimulus activity in task-relevant EEG components extracted using multivariate linear discriminant analysis (Boyle, 2018; S. J. Kayser et al., 2016; Parra et al., 2005; Philiastides & Sajda, 2006; Ratcliff et al., 2009). We searched for discriminant components within the EEG data that best discriminated between the frequency conditions (i.e. 1st or 2nd tone higher in frequency; see Kayser et al., 2016). Each projection $Y(t)$, of the EEG data, $x(t)$, is defined by spatial weights, $w(t)$, and a constant, c, as follows:

$$Y(t) = \sum_i w_i x_i(t) + c$$

with *i* summing across channels. Classification was based on regularized linear discriminant analysis (Philiastides et al., 2014), which was applied to the EEG data in 80ms sliding windows. We assessed classifier performance using the area under the receiver operator characteristic (ROC) curve (referred to herein as Az), based on 10-fold cross validation. The statistical significance of the performance was assessed by shuffling condition labels 1000 times, computing the group-average Az value for each randomization, and taking the maximal Az value along time to correct for multiple comparisons (Nichols & Holmes, 2003). We estimated the corresponding forward model for each component by computing the normalized correlation between the discriminating projection and the original EEG data (Parra et al., 2005).

To select scalp projections that reflect EEG activity that was temporally consistent across subjects, we selected three systematically different components which corresponded to three continuous time windows using K-means clustering based on component topographies (see Kayser et al.(2016) for details). For each participant, we then extracted the weight (*w*) from the time point associated with the maximal Az value within each component for further analysis, which allowed us to incorporate between-subject variability in response timing in the analysis.

Since *Y(t)* is indicative of the extent of separability between frequency levels, we exploit this as a measure representing the amount of encoded sensory evidence about the task relevant tones (Grootswagers et al., 2017; Guggenmos et al., 2017). We computed each components’ time course by applying the respective weight to all trials and time points, resulting in a one-dimensional projection of single-trial task-related activity which we then analysed further.

3.2.5.4 Pre-target time-frequency analysis

Time-frequency representations (TFRs) of the rhythmic brain activity prior to target were calculated using Morlet wavelets in FieldTrip (Oostenveld et al., 2011). Frequencies ranged from 2Hz to 40Hz in linear steps of 1Hz below 16Hz and 2Hz above. To achieve greater frequency smoothing at the higher frequencies the width of individual wavelets scaled with frequency (min = 4 cycles, max = 9 cycles). TFRs were calculated between -0.6s and -0.1s relative to target onset in 50ms bins. To avoid post-target contamination, we set the post-target period to zero for TFR analysis by applying a 40ms Hanning window to the last 40ms of the pre-stimulus period (Henry et al., 2014). For subsequent regression analyses, the power was z-scored within participants and frequency bands across time and trials (S. J. Kayser et al., 2016).

3.2.5.5 Statistical analyses

Group-level psychometric curves were computed for the percentage of correct responses as a function of stimulus level (averaging over temporal positions), and as a function of temporal position (averaging over frequency difference). The median performance, averaging across stimulus levels and temporal positions, between age groups was compared using a Wilcoxon rank sum test, with effect size (r) calculated by dividing the Z-value by the square root of N, where N represents the number of observations (Field, 2013). To test whether performance differed as a function of temporal position we used a non-parametric, one-way repeated-measures analysis of variance by ranks (Friedman Test).

AEP peak amplitudes/latencies and PSD slopes were compared between age groups using a non-parametric Wilcoxon rank-sum tests, with effect sizes (r) calculated following (Field, 2013).

To investigate the relationship between single-trial pre-stimulus activity (power/phase in particular frequency bands and time bins), sensory evidence, *Y(t)*, extracted from each component), and perceptual choice we used linear regression modelling (Figure 4). Model 1 tested whether pre-stimulus power/phase influences choice using regularized logistic regression. Model 2 tested whether pre-stimulus power/phase influences sensory evidence *Y(t)* using linear regression. Model 3 tested for a direct influence of sensory evidence on choice. Finally, we tested for possible mediation effects, where pre-stimulus activity state influence choice through mediation of sensory evidence (i.e. an indirect influence of pre-stimulus state on choice; see Kayser et al., 2016) using an additional model: regression of choice on both *Y* and power/phase. Mediation effects were tested by comparing this with model 3. We calculated each model separately for power and phase, and for each pre-target time-frequency point.

For regressions involving sensory evidence, we coded *Y(t)* as an unsigned variable and Z-scored it within each stimulus level, to reflect the amount of evidence about the respective stimulus. For phase, both sine- and cosine-transformed phase angles were submitted to the regression model. Mediation effects were defined by adjusting for dichotomous outcomes (MacKinnon et al., 2007).

Group-level statistical testing was performed using cluster-based permutation procedures (Maris & Oostenveld, 2007) and correcting for multiple comparisons across relevant dimensions, as described previously (S. J. Kayser et al., 2016). Specifically, we used 1000 randomization realizations, a 5th percentile cut-off to define significant clusters, defining clusters by at least four significant neighbours, and using the cluster mass index. A two-sided test at $p < 0.05$ was performed on the clustered data and we corrected for multiple comparisons across regression models and components using the false discovery rate (FDR) at $p < 0.05$. We report effect sizes for clustering statistics as the cluster mass across all bins within a cluster (T_{sum}).

The peak effect frequencies were compared across groups using a percentile bootstrap test (using 2000 samples). We randomly assigned participants to either group and compared the actual difference in group-level peak frequencies extracted from the respective statistical contrast for each regression factor to the distribution of differences in the randomized data. For this analysis effects were averaged over time for the duration of the respective clusters. Given that there were two significant clusters linking power to sensory evidence, we constrained the range of potential peak frequencies for each effect to distinct but overlapping ranges: for the alpha/beta cluster to 8-26Hz, and for the low-frequency cluster to 2-13Hz. We note that the results did not depend on the precise values of the respective cut-off frequencies.

To link changes in AEP amplitudes and latencies to the peak frequencies of pre-stimulus effects we first computed leave-one-out estimates of the respective peak-frequencies of the pre-stimulus effects and of AEP amplitudes and latencies. We relied on a leave-out-one (jacknife) approach as peak frequencies for pre-stimulus effects were more robust at the group-level than for individual subjects. We then used the six AEP characteristics (c.f. Figure 2) as predictors for the peak frequency of the pre-stimulus effect across the full sample of younger and older participants in a linear regression model, for which we obtained the overall model performance and significance.

3.3 Results

3.3.1 Behavioural Performance

As expected given the experimental design, the overall performance was comparable across group (averaged over stimulus level and temporal position younger median = 78.9% correct, older median = 74.4%, Z= 1.251, p = 0.211, r = 0.25; **Figure 1**B). To avoid expectancy effects, target tone pairs were presented at six temporal positions relative to background onset. Friedman's tests revealed no effect of target position on performance in either group (younger adults: $x^2(5)=5.28$, p = 0.382; older adults: $x^2(5) = 8.3$, p = 0.141; **Figure 1**C). This suggests that any influence of pre-target activity on performance would occur without explicit entrainment of auditory cortical activity to the acoustic noise in either group (Henry & Obleser, 2012; Ng et al., 2012). Furthermore, this also rules out the possibility that the duration of the background sound prior to the target acted as a priming signal, the duration of which could have influenced performance.

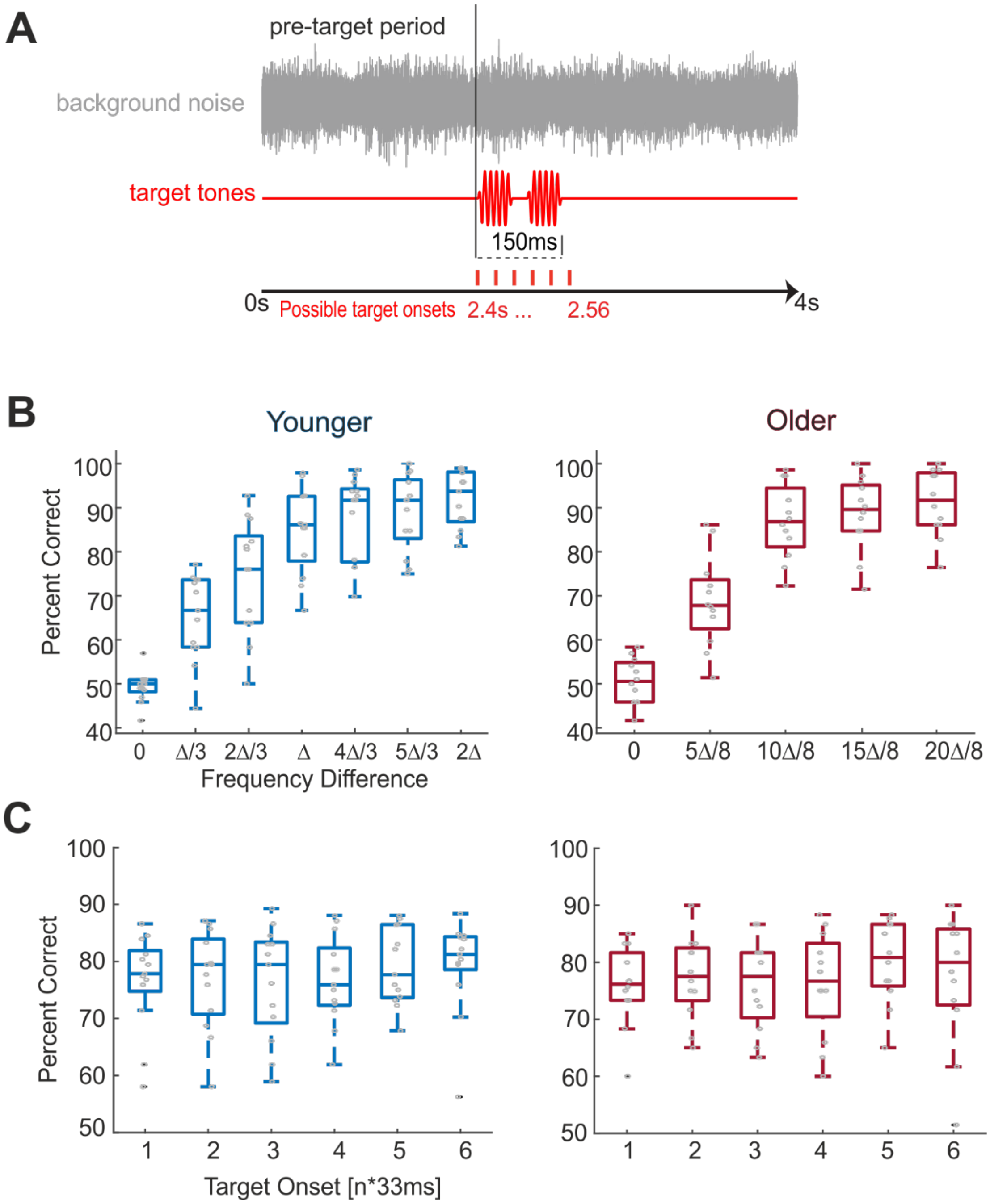

Figure 1.Auditory paradigm and task performance. (A) Auditory paradigm. Pure tone targets (50ms duration, spaced 50ms apart), were presented at one of six possible onsets against a continuous background noise cacophony. The second tone was kept at 1024Hz while the first varied over 7 (younger adults) or 5 (older adults) levels of frequency difference, titrated around participants' own frequency difference limens, Δ. (B) Group level task performance as a function of stimulus level, averaged across target positions. Younger and older adults show comparable task performance. (C) Group level task performance as a function of target position, averaged across stimulus levels. There were no significant effects of target position on performance in either group and overall there was no significant difference between groups (across stimulus levels and target positions). Grey circles indicate individual subject data.

3.3.2 Age-related changes in auditory evoked responses

To confirm previous reports of an age-related slowing of sensory-evoked activity we compared the latency and amplitude of evoked components (P1, N1 and P2;

Figure 2A). Peak amplitudes were significantly stronger for P1 and N1 in the older group, while P2 amplitudes were reduced (P1: younger median = -0.077µV, older median = 0.517µV, Z =-3.291, p = 9.991x10^{-4}, r = -0.658; N1: younger median = -0.95µV, older median = -1.519µV, Z=2.094, p = 0.0362, r = 0.419; P2: younger median = 2.418µV, older median = 1.736µ, Z= 2.366, p = 0.018, r = 0.473; Figure 2B). The latencies of N1 and P2 in the older adults were significantly delayed (N1: younger median = 0.1s, older median = 0.115s, Z=-2.99, p = 0.003, r = -0.598; P2: younger median = 0.175s, older median = 0.22s, Z= -4.124, p = 3.721x10^{-5}, r = -0.825; Figure 2C). There was no significant difference in P1 latency (younger median = 0.07s, older median = 0.07s, Z = -1.013, p = 0.311, r = -0.203).

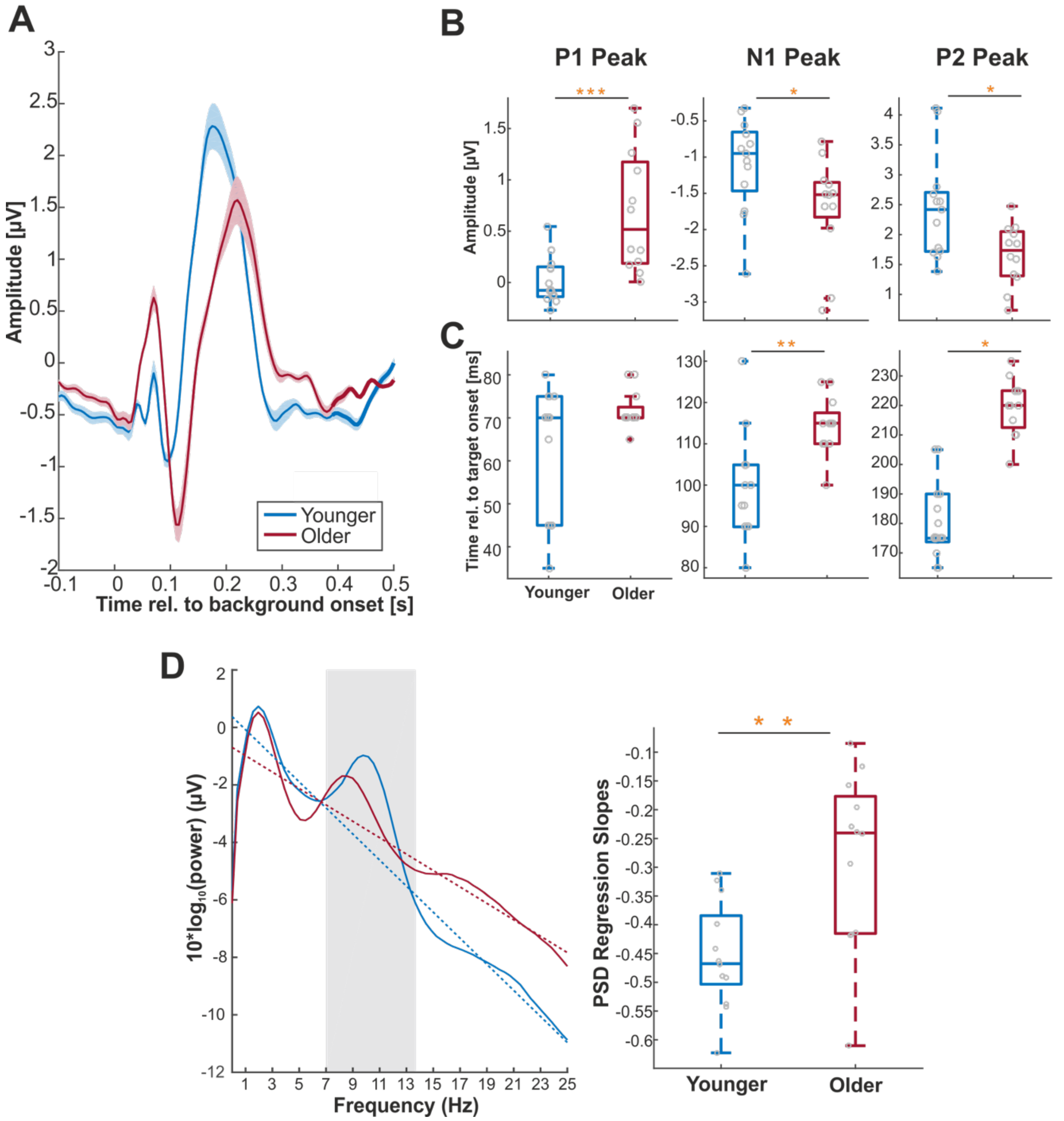

Figure 2. Auditory evoked responses to background onset and pre-stimulus power spectral density. (A) Grand-average AEPs with standard error (SEM) over central channels (FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, CP2). Both younger and older subject display a clear P1-N1-P2 potential. (B) A comparison of AEP peak amplitudes between groups revealed an age-related enhancement of P1 and N1 peaks, and a reduction in the P2 peak. (C) Component peaks were also compared in terms of latencies, revealing an age-related delay in N1 and P2 peaks. (D left panel) Group-averaged PSD estimates (smooth curves) and fitted regression slopes (dashed lines) for frequencies up to 25Hz, averaged over all channels. Slopes were computed whilst ignoring alpha power between 7-14Hz (indicated by shaded area). (D right panel) PSD slopes were flatter for the older adults. Grey circles indicate individual subject data. Yellow asterisks indicate significance as follows: * p<0.05, ** p<0.01, *** p<0.001.

3.3.3 Pre-target PSD flattens with age

Given previous reports of changes in the power spectra of ongoing brain activity with age (Klimesch, 1999; Tran et al., 2016; Voytek et al., 2015), we analysed the spectral slope of the EEG signal (Figure 2D). The PSD slopes of the older group were significantly flatter than those of the younger participants (younger median = -0.478dB, older median -0.24dB, Z = -2.91, p = 0.005, r = -0.582).

We also tested whether, across subjects, the observed changes in AEP latency and amplitude correlated with changes in spectral slope. Differences in PSD slope correlated significantly with differences in AEP latency for the P2 component (spearman rank-correlation: r=0.42, p=0.033, reduced slope corresponding to longer latency) but not the other AEP components (N1: r = 0.016, p = 0.93, P1: r = 0.165, p = 0.43). Differences in PSD slope also correlated with the amplitudes of the P1 (r = 0.43, p = 0.03) and N1 (r = -0.45, p = 0.025) peaks, with a flatter PSD spectrum correlating with stronger evoked responses. There was no correlation with the P2 amplitude (r = -0.25, p = 0.22).

3.3.4 Single trial decoding of EEG signals

Using single-trial modelling we extracted EEG components that maximally differentiated between the stimulus conditions on which the participants task relied (1st or 2nd tone higher). For both groups, classification performance became significant around 0.2s following target onset (randomization test, p < 0.01, corrected for multiple comparisons along time, Figure 3A).

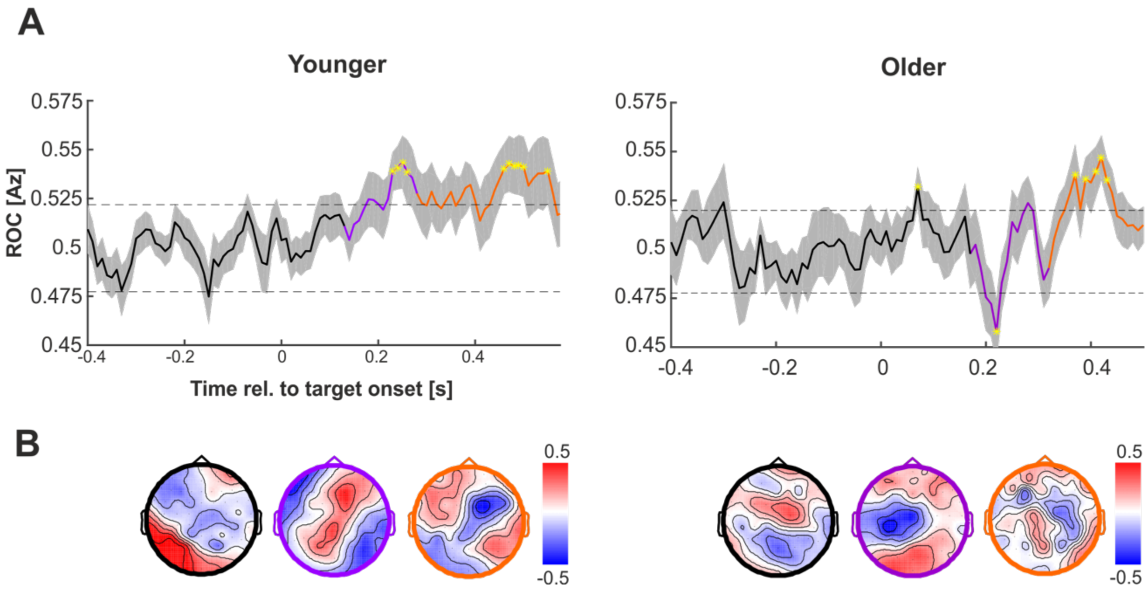

Figure 3. Task-relevant EEG components. (A) A linear classifier based on EEG data in 80ms windows was used to discriminate between the two frequency conditions of interest. The smooth curve reflects group-averaged ROC values (Az) with SEM represented by shaded boundaries. Yellow asterisks highlight projections in which Az reached significance, and the dashed lines represents significance, based on randomisation tests (at p < 0.001). Coloured curve segments indicate the k-means clustering of scalp projections derived from the classifier topographies. Clustering revealed three distinct components, each systematically different temporally and topographically. The first cluster (black curve) spanned the epoch in which the stimulus was being presented; the second (purple) cluster comprises shorter-latency activity possibly originating from sensory-specific regions; and the third (orange) cluster reflects later-activated processes originating from fronto-parietal regions likely reflecting decision-making processes. (B) Topographies represent the group-averaged scalp projections of peak Az performance within each cluster.

Using data-driven clustering based on individual subject’s component topographies we extracted three temporally and topographically distinct component-clusters for each group (S. J. Kayser et al., 2016). For each of these clusters we derived the respective group-level topographies and classifier performance (Figure 3B). Importantly, this analysis allowed us to incorporate inter-individual differences in the precise timing of relevant EEG activations, as within each of the three clusters, we selected for each subject the time point at which the respective discriminant component carried maximal information about the stimulus conditions.

The first EEG component spanned a time window encapsulating the majority of the stimulus presentation period (0s to 0.15s) in both younger (0s to 0.12s) and older (0s to 0.16s) participants. Given the overlap with ongoing stimulation, this component was not considered further. The second component (hereinafter termed the “auditory component”) spanned an early epoch (0.13s to 0.28s in younger, and 0.17s to 0.31s in older adults) and had a central topography in both groups. The third component (hereinafter termed the “decision-making component”) spanned a later epoch (0.28s to 0.5s in younger, and 0.32s to 0.5s in older adults). This late component likely reflects the transition between sensory encoding and perceptual decisions and was characterized by parieto-frontal topographies (J. A. Diaz et al., 2017; Giani et al., 2015; Marti et al., 2015). Both components significantly discriminated between frequency conditions in both age groups (ROC >0.5; randomization test, p<0.01).

Noteworthy, while the overall topographic sequence of EEG components was the same across groups, the timing of each component was delayed by about 40ms in the older group, matching the latency shift observed in the AEP P2 component.

3.3.5 Influence of pre-target activity within the auditory component

Having derived projections of single-trial task-related activity within meaningful EEG components we computed pre-target oscillatory activity for each of these (Figure 4A). We then used statistical modelling to understand the tri-partite relation between pre-stimulus activity, the encoding of task-relevant information (as reflected by the EEG component) and behavioural choice (Figure 4B). Specifically, we statistically tested the relations between power/phase (individually) and choice (model 1); power/phase and sensory evidence (model 2); and sensory evidence and choice (model 3).

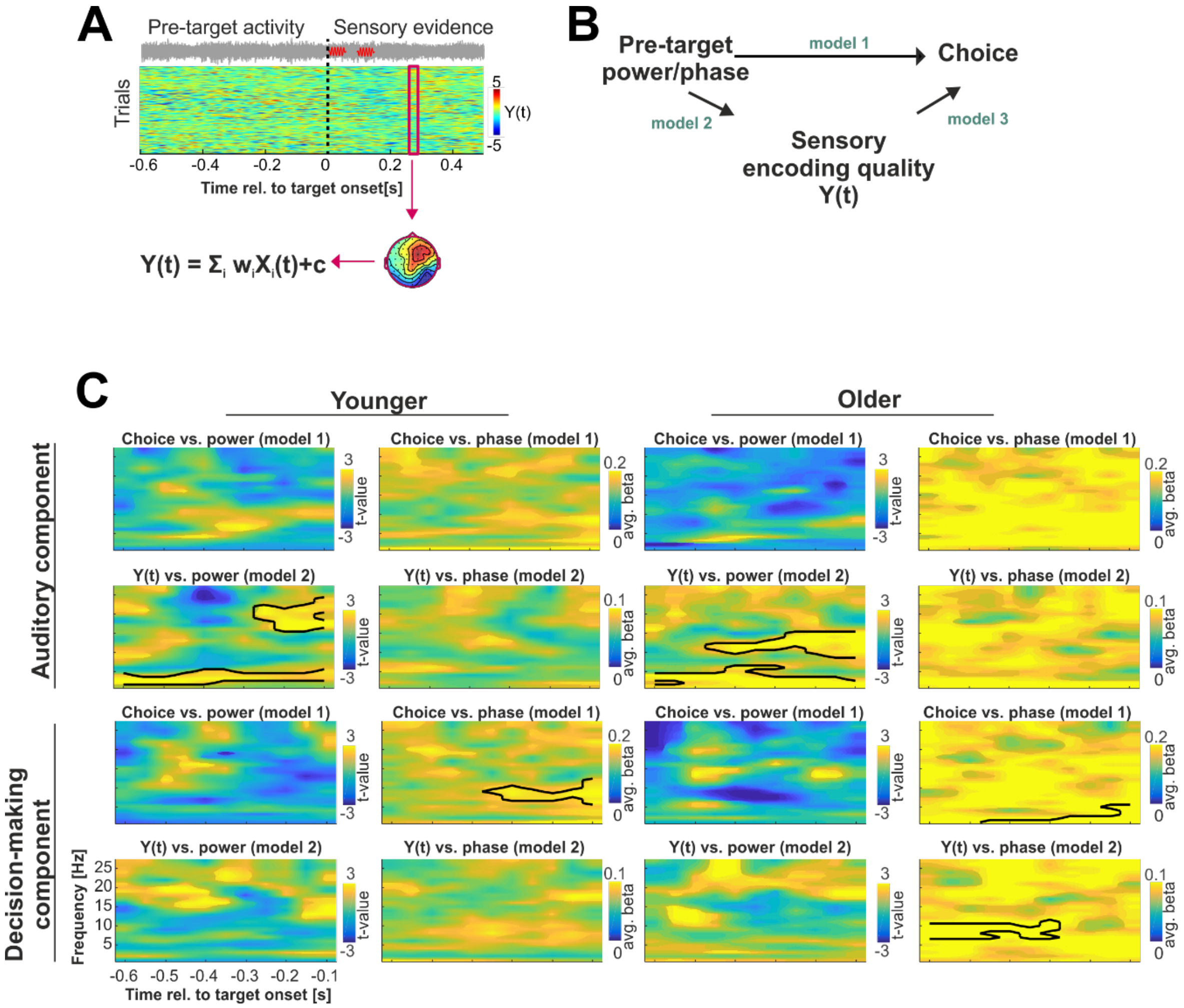

Figure 4. Linear modelling of pre-target activity on sensory evidence and choice within auditory and decision-making networks. (A upper panel) Single trial activity for one participant is shown. The red box highlights a classifier time window. (A lower panel) One-dimensional scalp projections carrying task relevant sensory evidence, Y(t) are derived from the single trial EEG data, X(t) and are defined by spatial weights, w(t), an a constant, c. (B) Models by which pre-stimulus activity could shape perceptual choice (c.f. Methods). (C) Group-level regression statistics for models 1 and 2, for both age groups and components. Significant time-frequency clusters are highlighted by black contours (at p<0.05; FDR corrected across models and comparisons).

For the auditory EEG component, we found no significant relation between pre-target power or phase on choice in either group (model 1; based on a significance level of $p < 0.05$, FDR corrected across models, Figure 4C). However, there were significant relations between pre-target power and sensory evidence (model 2): in the younger group at low frequencies (2-6Hz, -0.6s to -0.1s; $T_{sum} = 66$, $p = 0.001$) and the beta band (16-36Hz, -0.3s to -0.1s, $T_{sum} = 77$, $p = 0.002$). The same effects were observed in the older group, albeit at slightly different frequencies: low frequency (2-7Hz, -0.6s to -0.1s, $T_{sum} = 128.6$, $p < 0.001$) and alpha/beta band (10-16Hz, -0.45s to -0.1s, $T_{sum} = 9.6$, $p = 0.001$). No relation between phase and sensory evidence was found in either group. The relation between sensory evidence and choice (model 3) was significant in the younger group (t(12) =3.3, $p = 0.006$) and approached significance in older group (t(11) = 2.1, $p = 0.054$).

These results could be seen to suggest that pre-stimulus influences emerge systematically at lower frequencies in the older group. However, the existence of a significant cluster at a specific frequency does not demonstrate that this effect is significant only at that specific frequency. We hence used a bootstrap test to directly probe whether the group-level peak frequencies for each cluster differed significantly between groups. This was not the case for either cluster (low frequency cluster: difference in peaks = 0Hz, 95% bootstrap confidence interval (CI) [-9, +9] Hz, $p = 0.199$; alpha/beta cluster: difference in peaks = 7Hz, CI [-13, +13] Hz, $p = 0.173$).

3.3.6 Influence of Pre-Target Activity within the decision-making component

Repeating the same comparison for the late EEG component revealed a significant relation between pre-target phase and choice in the younger group around the alpha band (model 1; 7-14Hz, -0.4s to 0.1s, $T_{sum} = 5$, $p = 0.003$; Figure 4C) and at low-frequencies in the older group (1-5Hz, -0.4s to -0.1s, $T_{sum} = 4.5$, $p = 0.003$). Here we found some mild evidence that the respective peak frequencies may differ with age, as the difference was statistically significant (difference in peaks = 7Hz, CI [-8,+9] Hz, $p = 0.049$).

Furthermore, there were no significant relations between power and choice in either group (model 1 for power) and there were no significant relations between power and sensory evidence (model 2). However, in the older group there was a significant relation between alpha phase and evidence (model 2; 8-12Hz, -0.6s to -0.3s, $T_{sum} = 3.1$, $p = 0.002$), while no such effect was observed in the younger group. Additional mediation analysis revealed no significant mediation effects of phase on choice through evidence in either age group (at $p < 0.05$), and neither age group showed a significant relation between sensory evidence and choice (model 3; younger adults: t(12) = 1.1, $p = 0.27$; older adults: t(11) = 1.9, $p = 0.0741$), suggesting that the statistical relation between alpha phase and sensory evidence in the older group reflects a process not directly driving perceptual decisions.

Given that we found some evidence for pre-stimulus influences on choice to emerge at different frequencies in younger and older participants, we also asked whether this difference in peak frequency is related to the observed changes in amplitudes or latencies of the evoked potentials (c.f. Figure 2). Specifically, we obtained leave-one-out estimates of the group-level peak frequencies for the pre-stimulus effects and AEP amplitudes and latencies in response to background onset. We then used these six AEP characteristics as predictors for the pre-stimulus peak frequencies across the sample of young and old participants. Together, the AEP characteristics provided significant predictive power ($r^2 = 0.81$, $F = 16.8$, $p < 10^{-5}$), suggesting that changes in the timing and amplitude of evoked responses are indeed related to the observed changes in relevant pre-stimulus frequencies.

3.4 Discussion

We investigated the consistency of how pre-stimulus activity influences auditory frequency discrimination performance in young and older participants. In both groups the power of pre-stimulus activity influenced the encoding of sensory evidence reflected by early evoked components, while the phase influenced choice formation in later-activated EEG components. Importantly, for the early EEG components we did not find evidence for a systematic difference in the time scales of the perceptually relevant pre-stimulus activity. In the later-activated EEG component we found a trend for perceptually relevant rhythmic activity to arise from slower frequencies in the ageing brain. At the same time our data replicate previous findings of a significant age-related slowing of AEP latency, modulations of AEP amplitudes, and a flattening of the spectral profile of EEG activity.

3.4.1 Pre-stimulus influences on perception

In both groups we found that perceptual performance was influenced by rhythmic brain activity prior to the task-relevant stimulus. Our results hence confirm previous research showing that pre-stimulus brain activity influences perception in general (Florin et al., 2017; Henry et al., 2014; Henry & Obleser, 2012; Iemi et al., 2017; S. J. Kayser et al., 2016; Ng et al., 2012; Pinheiro et al., 2017; Samaha et al., 2017; Samaha & Postle, 2015; VanRullen, 2016).

In a previous study focusing on young subjects only we dissociated two mechanisms by which pre-stimulus activity influences auditory perception and mapped these onto distinct neural generators (S. J. Kayser et al., 2016). Specifically, we found that low frequency and alpha/beta power shaped the encoding of relevant sensory information in early-activated EEG components, which likely emerge from auditory cortical networks. In addition, the phase of alpha band activity emerging from later-activated fronto-parietal EEG components directly influenced the decision process. Here we replicated these results in a group of elderly participants characterized by no or mild hearing loss, in a paradigm where the overall task performance was equated between groups. Thereby the present data lend additional support to the hypothesis that multiple and distinct rhythmic processes control perceptual decisions and suggest that the relevant time scales of neural activity are largely conserved along the life span. Furthermore, they demonstrate that the relation of pre-stimulus brain activity and perception is not mandatorily affected by a general increase in neural response latencies with age.

3.4.2 Age-related changes in the timing of brain activity

In our data we found systematic age-related differences in the P1-N1-P2 evoked components of auditory evoked responses. Older adults' P1 and N1 component amplitudes were significantly larger compared to younger adults, yet their P2 peaks were reduced. These findings are consistent with previous reports of age-related changes in AEP amplitude (Anderer et al., 1996; Czigler et al., 1992; Harkrider et al., 2005; Henry et al., 2017; Rufener et al., 2014; Tremblay et al., 2003), which may be attributed to age-related changes at the cellular level (Caspary et al., 2008; de Villers-Sidani et al., 2010; Hughes et al., 2010) or neuronal synchrony (S. Anderson et al., 2012; Harris & Dubno, 2017). Furthermore, we also found an age-related slowing of the N1 and P2 peak latencies, an effect consistently reported in ageing research (Henry et al., 2017; Tremblay et al., 2004).

We also found that the spectral profile of ongoing EEG activity was significantly flatter in the older participants. This is in line with previous reports which propose a mediating role of spectral flattening in cognitive decline (Tran et al., 2016; Voytek et al., 2015), possibly resulting from a decrease in neuronal synchrony (Podvalny et al., 2015; Pozzorini et al., 2013; Voytek et al., 2015; Waschke et al., 2017), increases in spontaneous activity (S. L. Hong & Rebec, 2012), or changes in the excitation inhibition balance (Caspary et al., 2008; Price et al., 2017). Our participants passed a cognitive screening assessing a wide variety of cognitive abilities (reasoning, attention, working memory, abstraction, orientation, language), suggesting that the observed changes in spectral slope in the present data do not reflect cognitive decline itself but either compensatory mechanisms or basic changes in cellular physiology.

Previous EEG studies on stimulus-selective AEP components have suggested age-specific changes in the behavioural relevance of short- and long-latency components (Snyder & Alain, 2005, 2007). For example, so called object-related negativity potentials (ORN's) were found to consistently emerge at latencies of about 150 and 250ms post-stimulus in younger and older listeners, but were absent at yet longer latencies in the elderly. Furthermore, perceptual performance was best predicted by ORN's at different latencies across age groups (Snyder & Alain, 2005, 2007). These findings are in contrast to the present study, where we consistently observed stimulus-selective discriminant components from short (around 150ms) to long (up to 500ms) latencies across age groups. This difference could result from methodological approaches: the previous studies used the same fixed EEG electrodes to compare ORN's between groups, while we performed electrode-wide classification analysis, which allows for different electrode configurations to yield stimulus-selective EEG components for each time point and subject. Our results thereby suggest that stimulus-selective EEG activations emerge at multiple latencies in both younger and older listeners, but may differ between groups in their precise timing or topographies.

3.4.3 Do pre-stimulus influences change with age?

Our main focus was on whether pre-stimulus influences on perception are comparable between young and older participants. While the statistical clusters of significant effects seemed to shift towards lower frequencies in the older group, direct statistical tests did not provide clear evidence for a systematic shift of pre-stimulus effects towards lower frequencies in the elderly. In particular, within the early-activated ("auditory") EEG component there was no evidence for peak frequencies to differ between groups. Given a likely origin of this early EEG component in sensory-specific brain regions in the temporal lobe (S. J. Kayser et al., 2016), this suggests that the processes of early sensory encoding are conceptually conserved with age, despite a slowing of the respective evoked responses. Within the later-activated ("decision-making") EEG component pre-stimulus effects on choice were more variable, and we observed a trend towards lower peak frequencies in the older group. This reduction in peak frequency was significantly related to changes in the amplitude and latency of evoked responses between groups. This later-activated EEG component likely captures high-level cognitive and decision making processes, as suggested by its longer latency relative to target onset and the fronto-parietal topography (S. J. Kayser et al., 2016). Our data hence suggest that pre-stimulus influences on auditory perception are largely conserved across the age span, but may become more variable with age for those processes reflecting higher-level cognitive processes (McGovern et al., 2017; Sander et al., 2012; Zanto & Gazzaley, 2014).

This conclusion is also supported by our finding that there was an influence of alpha phase on sensory evidence in the late EEG component that was significant only in the older group. This phase-effect did not directly influence subjects' choice, and hence did not bear direct influence on behaviour. However, the stronger relation between alpha phase and sensory encoding may suggest that in the elderly subjects the encoding of the task-relevant sounds in fronto-parietal regions was affected by a reduced attentional commitment (Henry et al., 2017; Strauss et al., 2015; Wöstmann et al., 2015, 2016). This reasoning is based on the notion that enhanced alpha power reflects reduced attention (Thut et al., 2012; Wöstmann et al., 2016) and the stronger selection of sensory information by modulating the excitability of sensory cortices (Iemi et al., 2017; C. Kayser et al., 2015; Strauss et al., 2015). Increased alpha power is necessary to actually observe phase effects and hence the stronger phase-dependent gating of sound encoding in the elderly may reflect a reduced engagement of attention. In auditory perception, the enhancement of alpha activity is often inversely related to signal intelligibility and may reflect compensatory mechanisms during challenging listening conditions (Becker et al., 2013; Henry et al., 2017; McMahon et al., 2016; Obleser et al., 2012; Obleser & Weisz, 2012; Scharinger et al., 2014; Steinmetzger & Rosen, 2017; Wostmann et al., 2015). Hence, differences in the relation of alpha activity and sensory encoding may reflect age-specific strategies of dealing with hearing in noise, and the underlying perceptual and cognitive strategies (McGovern et al., 2017).

One possibility is that the sample size in the present study was not sufficient to reveal systematic shifts in the relevant frequencies, or that such effects are smaller than the frequency resolution employed here. On the other hand, it could also be that the mechanisms and time scales by which pre-stimulus activity shapes sensory encoding remain indeed the same, despite an overall change in the relative amplitude of different frequency bands (Babiloni et al., 2006; Cummins & Finnigan, 2007; Rondina et al., 2016; Vlahou et al., 2014). Support for the latter conclusion comes from studies demonstrating a similar modulation of alpha band activity by acoustical structure and task demands in young and elderly participants (Erb & Obleser, 2013; Tune et al., 2018; Wostmann et al., 2015), and from a study demonstrating a similar modulation of behavioural performance by stimulus-entrained delta-band activity in young and older participants (Henry et al., 2017). Furthermore, while many studies confirm age-related changes in the power of individual frequency bands with age, it remains unclear whether the peak frequencies of well-known brain rhythms change with age (X. Hong et al., 2015; Klimesch, 1999; McEvoy et al., 2001; Vlahou et al., 2014). In those studies reporting differences the effects are often at the edge of significance (X. Hong et al., 2015; McEvoy et al., 2001) or absent (Vlahou et al., 2014). As a result, further studies are required to more finely dissociate the various neural generators of pre-stimulus influences on perception in general, and their potential age-related changes in particular.

3.5 Conclusion

The present data demonstrate conceptually similar influences of rhythmic pre-stimulus activity on sensory encoding in young and older healthy listeners. This consistency in pre-stimulus effects arises largely despite systematic changes in the overall spectral profile of EEG activity and a general slowing of auditory evoked responses in the older participants, raising questions as to how these two processes are biophysically related. At the same time, we observed a trend towards a distinct influence of the timing of alpha and delta/theta band activity in later-activated EEG components with age, which calls for a more systematic assessment of the relation between rhythmic brain activity, sensory encoding and cognitive strategies in ageing.

Chapter 4 Age-related differences in the neurophysiological correlates of audio-visual enhancement in speech-in-noise discrimination

4.1 Introduction

As we get older we tend to find listening to a speaker in noisy environments more challenging (Babiloni et al., 2006; de Villers-Sidani et al., 2010; Pichora-Fuller et al., 2017; Sommers et al., 2005), due to age-related changes in bottom-up (S. Anderson et al., 2013; Clinard et al., 2010; Clinard & Cotter, 2015; Grose & Mamo, 2012; Harris & Dubno, 2017; He et al., 2007; Mahajan et al., 2017; Paraouty et al., 2016; Wallaert et al., 2016) and top-down processes (Dully et al., 2018; Henry et al., 2017; M. D. Nunez et al., 2015; Zanto & Gazzaley, 2014). In such scenarios the possibly unreliable auditory speech signal is enhanced by the presence of visual cues provided by articulatory facial movements (Sumby & Pollack, 1954). Articulatory movements are engaged approximately 100-300 ms prior to voice onset (Chandrasekaran et al., 2009; Schroeder et al., 2008). Therefore, it has been postulated that visual speech cues enhance comprehension by reducing the uncertainty of auditory speech through semantic and/or lexical priming (Peelle & Sommers, 2015; van Wassenhove et al., 2005). Despite generally poorer speech-in-noise recognition in older adults, the benefit that visual enhancement serves in facilitating their speech comprehension appears to be comparable to that of younger adults (Gordon & Allen, 2009; Maguinness et al., 2011; Sommers et al., 2005), if not greater (Sekiyama et al., 2014; Sheldon et al., 2008). Additionally, visual enhancement scales with degree of hearing loss (Puschmann et al., 2019) and with SNR (Ross et al., 2007). However, it has been reported that this is only the case when visual cues are reliable; when visual cues are made unreliable through blurring (Gordon & Allen, 2009; Maguinness et al., 2011), or are used ineffectively (Sommers et al., 2005), visual enhancement is reduced in older adults in particular. Older adults may therefore depend more on visual speech during challenging listening situations, possibly as a result of reduced sensory acuity in the auditory domain, or deficits in attentional control or attentional stimulus selection.

In searching for the neurophysiological signatures of AV speech integration, studies typically report that AV integration influences the amplitude and temporal profiles of AEPs namely the N1 – P2 complex. Successful AV integration typically results in suppressed and faster N1 and P2 peaks (Alsius et al., 2014; Baart, 2016; Baart et al., 2014; Frtusova et al., 2013; Ganesh et al., 2014; Kaganovich & Schumaker, 2014; Klucharev et al., 2003; Stekelenburg & Vroomen, 2007; Treille et al., 2014; van Wassenhove et al., 2005). In older adults, the N1 component in AV conditions is enhanced (Frtusova et al., 2013; Winneke & Phillips, 2011) and earlier (Frtusova et al., 2013) compared to younger adults. Stimuli used to reveal such effects usually involve McGurk-like stimuli involving phonemic utterances (for summary see Baart, 2016), although some studies have used complete words(Bhat et al., 2014; Frtusova et al., 2013; Shahin et al., 2012; Winneke & Phillips, 2011). However, studies often lack a range of target vocal stimuli in terms of the range of words used and/or the phonetic qualities (e.g. phoneme at voice onset) of the target speech stimuli, thus losing ecological validity. Many studies have also used acoustic masking signals such as multi-talker babble (Gordon & Allen, 2009; Sommers et al., 2005) and noise (Bernstein et al., 2004; Eskelund et al., 2011; Sekiyama et al., 2014) to enhance the multisensory benefit (Shahin et al., 2012; Winneke & Phillips, 2011, 2009). However, it remains unclear how acoustic SNR and the informativeness of the visual content interact to shape the neural correlates of speech-in-noise enhancement, and how these change with age.

Besides these neural correlates of audio-visual speech in early evoked responses, studies have also shown effects in later components reflecting higher order processes, such as attentional control, stimulus selection or the mapping of sensory information to internal representations. For example, the EEG P3 component is affected by passive letter-sound integration (Andres et al., 2011; Stekelenburg et al., 2018) and is modulated by the presence of visual contextual information (Hernández-Gutiérrez et al., 2018; Hessler et al., 2013; Irwin et al., 2017, 2018; Starke et al., 2017). The P3 component is subject to age-related changes, such as a shift in the topography (Anderer et al., 1996; Friedman, 2012; Ortiz et al., 1990) and latency (Friedman, 2012; van Dinteren et al., 2014). Another component affected by the congruency of audio-visual speech is the N400 (Lebib et al., 2004) (Kaganovich et al., 2016)(Van Petten et al., 1999), which may index the mapping of contextual representations (for review see Duncan et al., 2009). With progressing age the N4 amplitude is reduced and delayed (Gunter et al., 1992, 1996) (Cameli & Phillips, 2000). Similar as for the earlier evoked responses, the interaction of visual context, acoustic SNR and age remains unknown.

In the current study, we investigated the neural correlates of AV speech perception in noisy listening conditions, in younger and older adults. Specifically, we compared behavioural and EEG data from younger (<30 years) and older (>65 years) listeners with no, or only mild hearing loss, obtained during an AV speech-in-noise paradigm. We tested for main effects and interactions between age group (younger, older), information condition (AV_{inf}, AO_{inf}), and noise level (low noise, high noise) in both the behavioural and EEG data. For comparison with previous studies, we also quantified age-related changes in the amplitude and timing of auditory evoked responses to background noise onset, and the spectral slope of the overall EEG signal. We employed a stimulus set consisting of 84 concrete and abstract monosyllabic nouns with varying voice onset times to overcome limitations of more artificial stimulus sets used in previous work.

4.2 Materials and Methods

4.2.1 Participants

Data was collected from 20 younger (9 male; median age= 21.5, min = 18, max = 28) and 18 older (4 male; median age = 68, min = 61, max = 79) adult participants. Younger and older sample sizes were chosen a priori to be in line with those used in previous, similar behavioural and EEG studies (e.g. Maguinness et al., 2011; Winneke and Phillips, 2011). Participants had no more than mild age-related hearing loss, as measured by the Better Hearing Institute Quick Hearing Questionnaire (Kochkin & Bentler, 2010), THI (where applicable; McCombe et al., 2001), and PTA procedures. The PTA procedure was presented via MATLAB (2015b; The MathWorks Inc., Natick, MA) and was designed in accordance with guidelines from the BSA (British Society of Audiology, 2012). We tested participants' hearing thresholds at frequencies of 250Hz, 500Hz, 1000Hz, 2000Hz, 4000Hz and 8000Hz individually for each ear. Median hearing thresholds were 11.3 dB and 19.5 dB for younger and older adults respectively, averaged across frequencies and ears. Sound levels were calibrated using a Bruel&Kjaer sound-level meter. Participants also had (near) normal or corrected-to-normal visual acuity, as measured using a Colenbrander mixed contrast card set (Colenbrander & Fletcher, 2005) at 63cm and 100cm viewing distances (approximate computer distance). Older participants were additionally screened for cognitive impairment using the MoCA (Nasreddine et al., 2005), D2 test of attention (Brickenkamp & Zillmer, 1998), and the Dspan memory test (Dspan; Turner and Ridsdale, 2004).Scores reported for the D2 test of attention are the concentration performance (CP) score, and the total number of items processed minus the total number of errors (TN-E). Dspan scores are reported as the total number of items recalled forwards plus the total number of correct items recalled backwards. Younger adults were not subjected to these additional cognitive tests as they self-reported that they did not have any form of cognitive impairment, and we had no reason to believe any of the younger participants were experiencing early-onset age-related cognitive decline. Group-level auditory, visual and cognitive test scores are shown in **Table 2**. Screening scores that were completed by both groups were tested for age-related differences using Mann-Whitney U tests, and were found to be significantly different (BHI QHQ, p = 0.001; PTA, VAS63HC, VAS63LC, VAS100HC, and VAS100LC, p < 0.001). Three subjects in total were excluded from further analysis: one younger participant had incomplete audiometric data, and one younger and one older adult did not complete the experimental task. Thus, data analysis was computed on data from 18 younger adults and 17 older adults. Participants indicated no history of mental/neuropsychological disorders, stroke, or trauma to the eyes, ears or brain. Participants gave written informed consent and received £6/hour payment plus travel expenses for participating. This study is in accordance with the Declaration of Helsinki and was approved by the local ethics committee (College of Science and Engineering, University of Glasgow).

				VAS 63cm		VAS 100cm	
	PTA (dB)	**BHI QHQ**	**THI**	**HC**	**LC**	**HC**	**LC**
Younger	11.19 [4.81,18.34]	4.5 [1,12]	18 (N=1)	107.5 [100,112]	99 [92,107]	107 [99,114]	101 [93,105]
Older	20.35 [12.63,46.58]	15 [1,58]	10 [2,18] (N=2)	98 [87,108]	91 [83,101]	100 [91,106]	89 [81,100]

	MoCA	**D2**		**Dspan**
		CP	**TN-E**	
Older	29 [25,30]	216 [167,271]	522 [360,606]	96 [82,132]

Table 2. Auditory, vision and cognitive test scores. Screening scores for younger and older participants who passed screening. Hearing scores are derived from pure tone audiometry (PTA), Better Hearing Institute Quick Hearing Questionnaire (BHI QHQ), and Tinnitus Handicap Inventory (THI). THI was administered only as applicable, thus n is reported. Note that one elderly participant had a self-reported BHI QHQ score of 46.58 (indicating severe hearing loss); this participant was not excluded due to an acceptable PTA score. Visual acuity test scores VAS) are from Colenbrander mixed contrast tests. Cognitive test scores are derived from Montreal Cognitive Assessment (MoCA), D2 test of Attention (D2) and digit span (Dspan) tests. Dspan test scores are calculated as the total number of correct items recalled forwards plus the total number of items recalled backwards. D2 test scores reported are the concentration performance (CP) score, and the total number of correct items processed minus the total number of error (TN-E), and are reported as raw scores due to the absence of norm data for adults aged >60. Scores correspond to median across all participants in each age group. Square brackets indicate minimum and maximum scores.

4.2.2 Audio-visual stimuli

The stimulus material consisted of 84 target monosyllabic nouns, spoken by a trained, male, native British actor. Target words were chosen from the MRC Linguistics Database (Coltheart, 1981), had a mean length of 4 letters, and were rated high in familiarity (min = 492, max = 618 , mean = 562, s.d. = 30) and high (min = 600, max = 670, mean = 618, s.d. = 16) or low (min = 234, max = 400, mean = 328, s.d. = 41) in concreteness (see **Table 5**). Each target word corresponded to one of seven onset phoneme types (approximant, affricate, fricative, vowel, rhotic, nasal, or plosive), with 12 target words in each category, and were articulated labially (n = 25) or non-labially (n = 59). Target words were embedded in acoustic noise simulating a 'cocktail-party' environment and consisted of a random sample from a one-minute-long multi-talker babble sound clip. The babble clip was created by taking the inverse of the superposition of 11 individual, normalized clips of single-speaker speeches (5 female, 6 male). The noise level for each participant was titrated around their 70% correct threshold for auditory speech-perception-in-noise. We manipulated auditory intelligibility over two levels in the main experiment: low noise and high noise, wherein the average SNR ratio across subjects was approximately -7.31 dB [younger = -7.6 dB, older = -7.18 dB] and -8.14 dB [younger = -8.43 dB , older = -8.01 dB] for each noise level respectively. Acoustic target stimuli were accompanied by audio-visually informative (AV_{inf}) and audio-only informative (AO_{inf}) visual stimuli. During AV_{inf} trials, the target acoustic stimuli were presented with congruent videos showing the actors enunciating the target word. In AO_{inf} trials, the acoustic target stimuli were accompanied by a neutral video of the actor showing a neutral facial expression without any articulatory facial movements. Stimulus recording took place within a sound-attenuated recording booth. Videos were digitized using a Sony PMW-EX1 camcorder at a frame rate of 25 frames per second, at 1280 × 720 pixels. Videos were later resized to 784 x 610, spanning an onscreen size of 23 x 16.5 cm thus subtending 15.41 x 11.09 degrees of visual angle, and at a viewing distance of 85cm. From the video recording, target words were digitized with 16-bit resolution at a sampling frequency of 48,000 Hz.

4.2.3 Experimental procedure

Following informed consent, participants completed 10 training trials before their hearing-in-noise thresholds were measured using three interleaved two-down-one-up staircase procedures. The task in the staircase procedure was a two-alternative forced choice task based on single auditory target words embedded in noise. The target words used in the staircase procedure were acoustic versions of those presented in the main experiment. Noise level scaling varied based on participants' performance until a reliable level was reached.

The experimental task a 4-alternative forced choice audio-visual speech-perception-in-noise discrimination task. Participants were presented with single spoken target words embedded within a noisy background and had to discriminate which word they heard from a choice of four words (see Figure 5A). Each trial started with a fixation cross lasting between 300ms and 700ms. After fixation, stimulus onset consisted of the simultaneous presentation of the first auditory stimulus sample of the selected target word plus noise and the first frame of the selected visual stimulus (either the corresponding AV_{inf} video or a pseudo-randomly selected AO_{inf} neutral video). Each stimulus lasted, on average, 2.676 s ± 0.222 s (min = 2.26 s, max = 3.26 s). Participants were then presented with four unique words, consisting of the target word plus three words chosen pseudo-randomly from the remaining non-stimulus words. Participants were prompted to select the word they perceived using the keys V, B, N ,and M on a standard computer keyboard, corresponding to the position of the words as they appeared on the computer screen. Trials were separated by an inter-trial period uniformly distributed between 1500-2000ms following participants' response. Participants experienced all 84 words in each condition (AV_{inf} and low noise, AV_{inf} and high noise, AO_{inf} and low noise, AO_{inf} and high noise), which were presented across 3 blocks. Each block contained 112 trials and each participant completed 336 trials in total. Trials were pseud-randomized across information and SNR conditions, and were subsequently divided into 3 blocks of 112 trials. The experiment was controlled using MATLAB (Mathworks) using the Psychophysics Toolbox Version 3 (Brainard, 1997). Acoustic stimuli were presented binaurally using Sennheiser HD 280 PRO headphones, while visual stimuli were presented on a 21-inch Hansol 2100A CRT monitor, at a refresh rate of 75 Hz. A chin rest was used to stabilize participants' viewing distance.

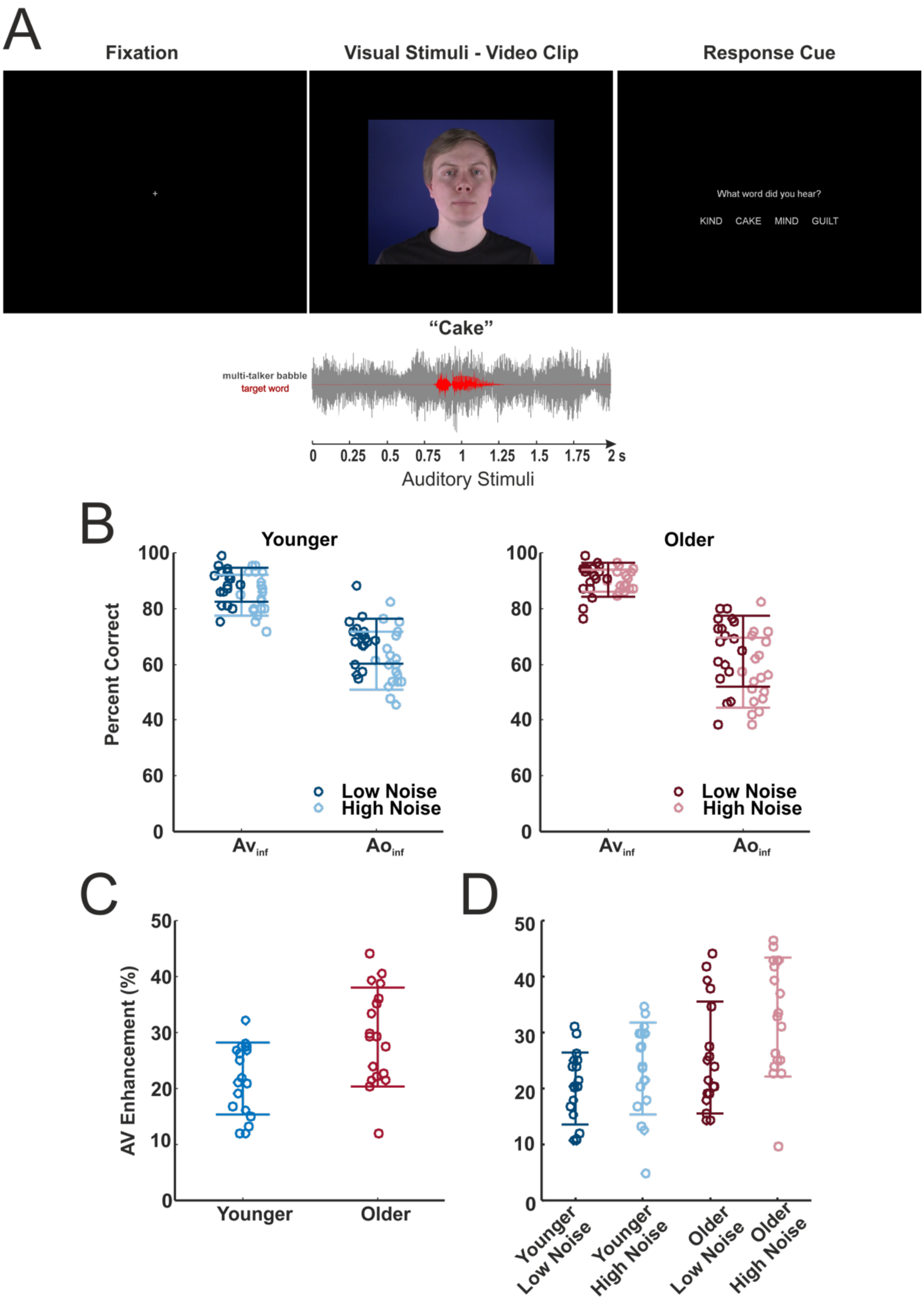

Figure 5. Audio-visual paradigm and task performance. (A) Audio-visual paradigm. Following fixation, monosyllabic spoken nouns were presented within a continuous multi-talker babble background. On half of the trials, the visual stimuli enunciated the target word presented (i.e. was audio-visually informative; AV$_{inf}$) and on the other half remained neutral but still dynamic (i.e. auditory informative only; AO$_{inf}$). We varied the level of noise around participants' own 70% correct thresholds for auditory speech-in-noise perception, such that the noise level was high on half of the trials, and low on the other half. (B) Group-level task performance as a function of age group, information condition, and noise level. Performance across all trials was comparable between age groups. Performance as greater in AV$_{inf}$ conditions compared to AO$_{inf}$, and was greater in low noise compared to high noise. (C) Group-level AV enhancement as a function of age group. Older adults showed significantly greater AV enhancement compared to younger adults. (D) Group-level Av enhancement as a function of age group. AV enhancement was greater in high noise conditions compared to low noise, and this effect was consistent between age groups.

4.2.4 EEG recording and pre-processing

EEG signals were recorded using an active 64-channel BioSemi system (BioSemi B.V., Netherlands) with Ag-Agl electrodes mounted on an elastic cap and placed according to the 10/20 system. Signals reflecting ocular muscle activity were derived from four electrodes placed at the outer canthi and below each eye. Data were recorded at a sampling rate of 500Hz and low-pass filtered online up to 208Hz. Electrode offsets were kept below 25mV.

Pre-processing was carried out offline in MATLAB using the FieldTrip toolbox (Oostenveld et al., 2011) and custom-built functions. Data were first band-pass filtered between 1-70Hz and subsequently resampled to 150Hz. We used Independent Components Analysis to remove ocular (Debener et al., 2010), and muscle artifacts (Beirne & Patuzzi, 1999; Hipp & Siegel, 2013). Horizontal, vertical and radial EOG signals were computed to detect further ocular artifacts, where trials were rejected if EOG signals exceeded 3 SDs above the mean high-pass-filtered EOG (Keren et al., 2010). Based on these criteria, 3% of trials were rejected, on average. EEG signals were re-referenced to the common average for further analysis.

4.2.5 Analysis and statistical methods

4.2.5.1 Behavioural data

Participants' performance was computed as a percentage of correct responses. A four-factor mixed analysis of variance (ANOVA) was performed to compare the mean effects of age group (younger, older; between subjects), information condition (AV_{inf}, AO_{inf}; within subjects), articulation type (labial, non-labial; within subjects), and noise conditions (low noise, high noise; within subjects) and their interactions on response accuracy. Effect size (r) is calculated as the square root of the F-statistic divided by F-statistic plus the residual degrees of freedom (Field, 2013).

To assess the extent to which the informativity of the visual stimuli influenced performance, we computed a measure of AV enhancement. AV enhancement is typically calculated as the influence the visual modality has on performance (i.e. (AV -A)/(1-A), where A is performance in a unisensory auditory condition) or vice versa (i.e. (AV-V)/(1-V), where V is performance in unisensory visual condition). The trials in the current study were always multisensory trials, with informativity of the visual stimuli being manipulated, thus we quantified AV enhancement as the difference between AV_{inf} and AO_{inf} in line with approaches taken by Sekiyama et al. (2014) and Ross et al. (2007). AV enhancement was computed by age and by age and noise.

To assess the potential relationship between behavioural AV enhancement and cognitive status in older adults, robust Spearman correlations (r_s; Pernet et al., 2013) were computed between AV enhancement and Dspan, CP score, and TN-E score. Bootstrapped 95% confidence intervals are reported.

4.2.5.2 Pre-target evoked responses and power spectral density

We computed AEPs in response to the onset of the noisy acoustic background based on trial-averaged data over a 3x3 grid of central channels (FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, CP2). Individual participants' P1, N1 and P2 component median peak latencies and amplitudes were then extracted by taking the median of participants' max-/minimal amplitude and corresponding latency within pre-defined, component-specific, time-windows (P1, 42 ms to 142 ms; N1, 122 ms to 237 ms; P2, 162 ms to 302 ms). Peak AEP amplitudes and latencies were compared between age groups using a non-parametric Wilcoxon rank-sum tests, with effect sizes (r) calculated following (Field, 2013).

We then computed PSD estimates using Welch's method, averaged across all channels in a pre-target time window of -0.6s to 0s relative to target word onset. PSD estimates were normalized by removing individual participants' mean PSD from their own spectra and were fit using a linear regression models to extract PSD slopes over frequencies between 1Hz and 25Hz whilst excluding alpha power between 7 and 14 Hz (Tran et al., 2016; Voytek et al., 2015). PSD slopes were compared between age groups using a non-parametric Wilcoxon rank-sum tests, with effect sizes (r) calculated following (Field, 2013). Furthermore we tested whether observed changes in ERP latency and amplitude were related to changes in PSD slope using robust Spearman rank correlations with bootstrapped 95% confidence intervals (r_s; (Pernet et al., 2013).

4.2.5.3 Evoked activity to target word onset: testing differences in amplitude

Our aim was to assess the stability of evoked activity signatures reflecting AV enhancement between younger and older adults. Therefore, we tested for main effects and interactions in a three-factor mixed design (information condition x noise level x age group) using spatio-temporal cluster-based permutation tests (S. J. Kayser et al., 2015; Maris & Oostenveld, 2007) across all channels and in a time window of -0.1s to 1s relative to target word onset. The procedure computed a two-tailed t-test for each channel and controlled for multiple comparisons. The cluster test statistic (T_{sum}) was computed by summing the t-value of adjacent channels where $p < 0.05$ during clustering, with a required cluster size of at least 2 significant neighboring channels and based on 2000 iterations.

We tested the neurobehavioural correlation of AV enhancement by computing Spearman correlations with bootstrapped 95% confidence intervals (r_s) between the noise-averaged behavioural AV enhancement and AV enhancement as reflected in the EEG signal for each age group. To represent neural AV enhancement we extracted the maximal amplitude within the significant spatio-temporal clusters derived from the neural information condition x age group interaction, averaging over significant channels at the peak latency.

4.2.5.4 Evoked activity to target word onset: testing differences in latency

We tested for age-related differences in the latencies of differences in evoked activity reflecting AV enhancement using a bootstrapping procedure based on 1000 iterations. On each iteration a random sample of subjects was taken from each age group (younger adults, n = 18; older adults, n=17). One-sided, paired t-tests were computed at each EEG samples between -0.1 s and 1 s comparing AV_{inf} versus AO_{inf} time courses, averaged over channels in which a significant AV_{inf} versus AO_{inf} effect was observed in the respective age group during clustering. The earliest latency showing a significant AV_{inf} versus AO_{inf} difference was extracted, thus creating a distribution of 1000 ‘onset’ latencies for each age group. These distributions were compared using a two-sided independent samples t-test and a 95% confidence interval on the difference between the bootstrap younger and older latency distributions was calculated.

4.3 Results

4.3.1 Behavioural performance

Table 3 indicates percentage of correct responses as a function of age group, information condition, and noise level, as well as AV enhancement as a function of age, averaged over noise conditions, and as a function of age and noise condition. Behavioural performance as a function of information condition and noise level for younger and older adults are displayed in **Figure 5**B. **Figure 5**C shows AV enhancement for both age groups, while AV enhancement is shown as a function of age and noise condition in **Figure 5**D.

	Younger			**Older**		
	AV$_{inf}$	**AO$_{inf}$**	**AV enhancement**	**AV$_{inf}$**	**AO$_{inf}$**	**AV enhancement**
Noise-averaged	86.7 [6.4]	64.9 [8.8]	21.8 [6.4]	90.2 [4.5]	60.9 [11.9]	29.2 [8.9]
Low noise	88.5 [6.2]	68.4 [8]	20 [6.4]	90.4 [6]	64.8 [12.8]	25.6 [10]
High noise	84.8 [7.3]	61.3 [10.3]	23.6 [8.2]	89.9 [4]	57.1 [12.5]	32.8 [10.5]

Table 3. Behavioural performance. Mean and standard deviation (in square brackets) response accuracy (%). AV$_{inf}$ and AO$_{inf}$ refer to audio-visual informative and auditory informative only information conditions. AV enhancement was computed at the subject level and then averaged by age group; hence some rounding error exists.

Table 4 indicates percentage of correct responses as a function of age, information condition, and articulation type. Also displayed is visual predictability as a function of age (averaged over noise conditions and information conditions), as a function of age and noise condition (averaged over information conditions), and as a function of age and information condition (averaged over noise condition). Behavioural performance is displayed in Figure 6A for younger and older adults. Figure 6B shows AV enhancement by age and articulation type, while visual predictability (labial – non-labial) is shown as a function of age and noise condition in Figure 6C.

	Younger			Older		
	Labial	Non-labial	Visual Predictability	Labial	Non-labial	Visual Predictability
Across conditions	69.8 [8.7]	78.3 [6.6]	-8.5 [3.9]	70.7 [8.9]	77.7 [7.8]	-7 [0.049]
AV	86.0 [8.3]	87 [6.9]	-1 [7.9]	90.8 [6.4]	89.9 [4.6]	0.9 [5.6]
AO	53.8 [12.8]	69.6 [0.081]	-15.8 [9.2]	50.1 [13.5]	65.5 [11.8]	-15.4 [6.3]
Low Noise	72.3 [10]	81.2 [5.5]	-8.9 [7]	72.8 [9.4]	75.7 [9]	-3.9 [5.3]
High Noise	67.4 [9.2]	75.4 [8.2]	-8 [6.6]	68.5 [10]	75.7 [7.4]	-4.2 [7.9]

Table 4. Behavioural performance by articulation type.Mean and standard deviation (in square brackets) response accuracy (%). AV_{inf} and AO_{inf} refer to audio-visual informative and auditory informative only information conditions. Visual predictability was calculated as the difference between labial and non-labial performance and was computed at the subject level and then averaged by age group; hence some rounding error exists.

Main effects and interactions of age group, information condition, articulation type, and noise conditions on response accuracy were tested by way of a four-factor mixed ANOVA. No significant main effect of age group was observed ($F_{(1, 33)} = 0.007$, $p = 0.933$) indicating similar performance between younger and older adults across noise level, articulation type, and information conditions. A significant main effect of noise level was found $F_{(1, 33)} = 49.467$, $p < 0.001$, $r = 0.774$), wherein more accurate performance was observed for low noise compared to high noise. A significant main effect of information condition was observed ($F_{(1, 33)} = 381.025$, $p < 0.001$, $r = 0.959$), wherein participants performed more accurately in the AV_{inf} trials compared to AO_{inf} trials. Lastly, a significant main effect of articulation type was found ($F_{(1, 33)} = 171.295$, $p < 0.001$, $r = 0.916$), wherein more accurate performance was observed generally for non-labial (i.e. least visually predictive) nouns compared to labial nouns. The information condition × noise level interaction was significant ($F_{(1, 33)} = 12.973$, $p = 0.001$, $r = 0.531$), revealing a larger difference between AV_{inf} and AO_{inf} conditions (and thus larger AV enhancement) in high noise compared to low noise. A significant information condition x articulation type interaction was also observed ($F_{(1, 33)} = 32.752$, $p < 0.001$, $r = 0.706$), suggesting that, behaviourally, there is larger AV enhancement for labial nouns compared to non-labial nouns. The age group x information condition interaction was significant ($F_{(1,33)} = 8.005$, $p = 0.008$, $r = 0.442$), revealing a greater difference between AV_{inf} and AO_{inf} trials in older adults compared to younger adults.

We found no significant interactions between age group × noise level ($F_{(1, 33)} = 0.892$, $p = 0.352$), or between age group × information condition × noise level ($F_{(1, 33)} = 0.049$, $p = 0.826$). We also did not find significant interactions between articulation type x age group interaction ($F_{(1, 33)} = 0.013$, $p = 0.909$), or age group x information condition x articulation type interaction ($F(_{1, 33)} = 0.003$, $p = 0.959$). We did not observe a significant noise level x articulation type interaction ($F_{(1,33)} = 0.009$, $p = 0.926$), which suggests that behavioural enhancement due to the visual predictability of the target word is consistent as a function of task difficulty. Furthermore, we observed no significant effects for the noise condition x articulation condition x age ($F_{(1, 33)} = 0.155$, $p = 0.696$), noise condition x articulation type x information condition ($F_{(1, 33)} = 0.297$, $p = 0.589$), noise x articulation x information x age ($F_{(1, 33)} = 0.15$, $p = 0.701$) interactions.

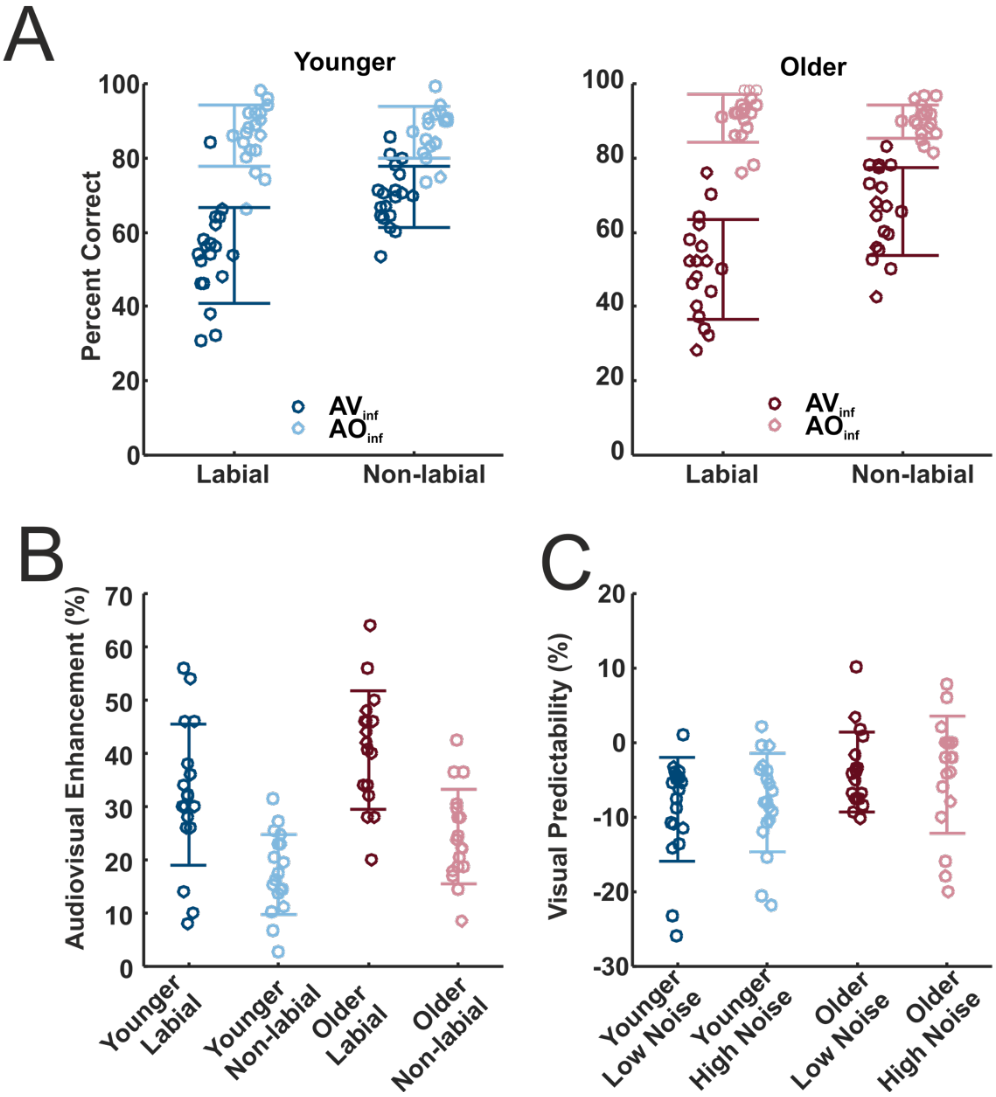

Figure 6. Articulation-type-related behavioural performance. (A) Group-level task performance as a function of age group, information condition, and articulation type. Performance as greater generally for non-labial (least visually predictive) nouns compared to labial nouns. (B) Group level AV enhancement (AV$_{inf}$ minus AO$_{inf}$ performance) as a function of age group and articulation type. AV enhancement is greater for labial words compared to non-labial words, and is consistent between age groups. (C) Group level visual predictability (labial minus non-labial performance) as a function of age group and noise level. Behavioural enhancement due to the visual predictability of the target word is consistent as a function of noise level, information condition and/or age-group.

In the ageing group, AV enhancement was not related to cognitive status, and no significant correlations were observed between AV enhancement and Dspan score (r_s = -0.177 [-0.684, 0.3663], p = 0.497), TN-E score (r_s = 0.01 [-0.517, 0.469], p = 0.981), or CP score (r_s = 0.01 [-0.504, 0.45], p = 0.959).

4.3.2 Age-related changes in pre-target AEPs and PSD

With the aim of replicating previous reports of an age-related slowing of sensory-evoked activity, we computed AEP time-courses in response to background noise onset (**Figure 7**A) and compared the amplitude **Figure 7**B) and latency (**Figure 7**C) of the P1, N1, and P2 components between age groups. The peak amplitude of the N1 component was significantly larger in older adults (younger median = -0.88, older median = -1.902 s, Z = 3.251, p = 0.001, r = 0.549), whereas no significant age-related differences in amplitude were found in the P1 or P2 components (P1, younger median = 0.862, older median = 0.814, Z = -0.313, p = 0.753, r = -0.053; P2, younger median = 3.049, older median = 3.782, Z = -1.171, p = 0.241, r = -0.198). The latencies of the N1 and P2 peaks were significantly delayed in adults (N1, younger median = 0.137 s, older median = 0.197 s, Z = -3.671, p < 0.001, r = -0.62; P2, younger median = 0.247 s, older median =0.262 s , Z = -2.904 , p = 0.003, r = -0.491). No significant age-related difference in P1 peak latency was observed (younger median = 0.107 s, older median = 0.102 s, Z = 1.133, p = 0.256, r =191).

Previous research has reported age-related differences in the power spectra of ongoing brain activity between younger and older adults (Klimesch, 1999; McNair et al., 2019; Tran et al., 2016; Voytek et al., 2015). Thus, we analysed the spectral slope of ongoing brain activity of the EEG signal (**Figure 7**D). The PSD slopes of the older adults were significantly flatter than those of the younger adults (younger median = -0.389 dB, older median -0.211 dB, Z = -4.373, p < 0.001, r = -0.739).

We also tested whether, across subjects, the observed changes in AEP latency and amplitude correlated with changes in spectral slope. Differences in PSD slope correlated significantly with differences in AEP latency for the N1 (r_s = 0.391 [0.048, 0.654], p = 0.02) and P2 components (r_s = 0.364 [0.02, 0.675], p = 0.032, reduced slope corresponding to longer latency) but not the P1 component (r_s = -0.146 [-0.482, 0.216], p = 0.402). Differences in PSD slope also correlated with the amplitudes of the N1 (r_s = -0.522 [-0.707, -0.251], p = 0.001) and P2 (r_s = 0.373 [0.057, 0.611], p = 0.027) peaks, with a flatter PSD spectrum correlating with stronger evoked responses. There was no correlation with the P1 amplitude

(r_s = 0.226 [-0.118, 0.504], p = 0.192). Our results show that these two distinct features, namely AEP dynamics and PSD slope, are related.

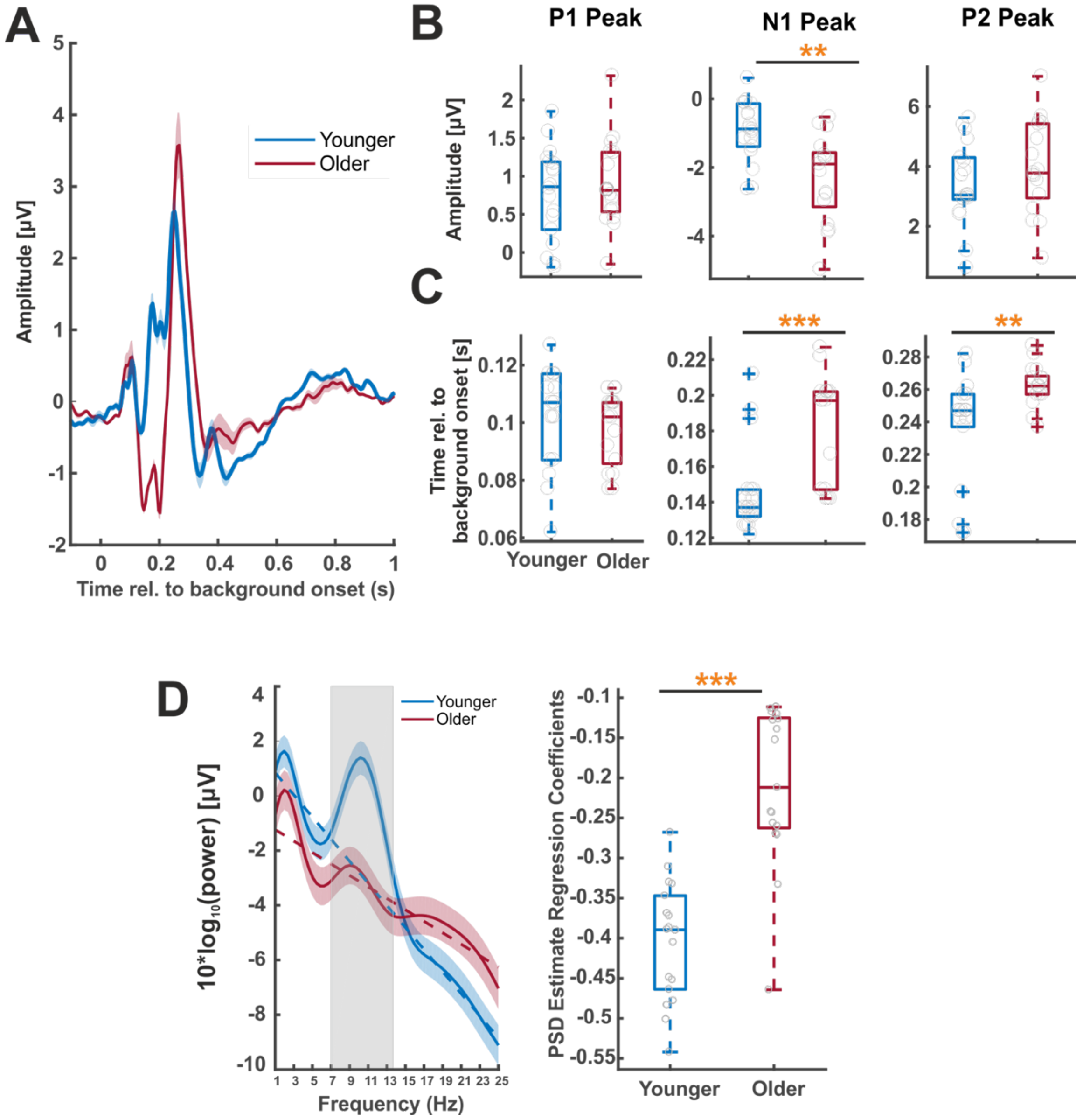

Figure 7.Auditory evoked responses to background onset and pre-stimulus power spectral density. (A) Grand-average AEPs with standard error (SEM) over central channels (FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, CP2). Both younger and older subject display a clear P1-N1-P2 potential. (B) A comparison of AEP peak amplitudes between groups revealed an age-related suppression of N1 peak amplitude. (C) Component peaks were also compared in terms of latencies, revealing an age-related delay in N1 and P2 peaks. (D left panel) Group-averaged PSD estimates (smooth curves) and fitted regression slopes (dashed lines) for frequencies up to 25 Hz, averaged over all channels. Slopes were computed whilst ignoring alpha power between 7 and 14 Hz (indicated by shaded area). (D right panel) PSD slopes were flatter for the older adults. Grey circles indicate individual subject data. Yellow asterisks indicate significance as follows: **p < 0.01, ***p < 0.001.

4.3.3 Age-related differences in late evoked responses

In comparing evoked responses to target word onset between younger and older adults, significant age-related differences emerge between 360 to 520 ms following target onset (**Figure 8**A). Two significant clusters were found within this time window: younger adults showed more negative evoked activity over fronto-central channels (T_{sum} = -796.393, p = 0.002), and more positive evoked activity over posterior channels (T_{sum} = 678.697, p = 0.005), compared to older adults (**Figure 8**B). No significant differences were found between AV_{inf} and AO_{inf} condition (**Figure 8**A, center panel), or between low noise and high noise (**Figure 8**A, right panel), when averaged across age groups (at $p < 0.05$).

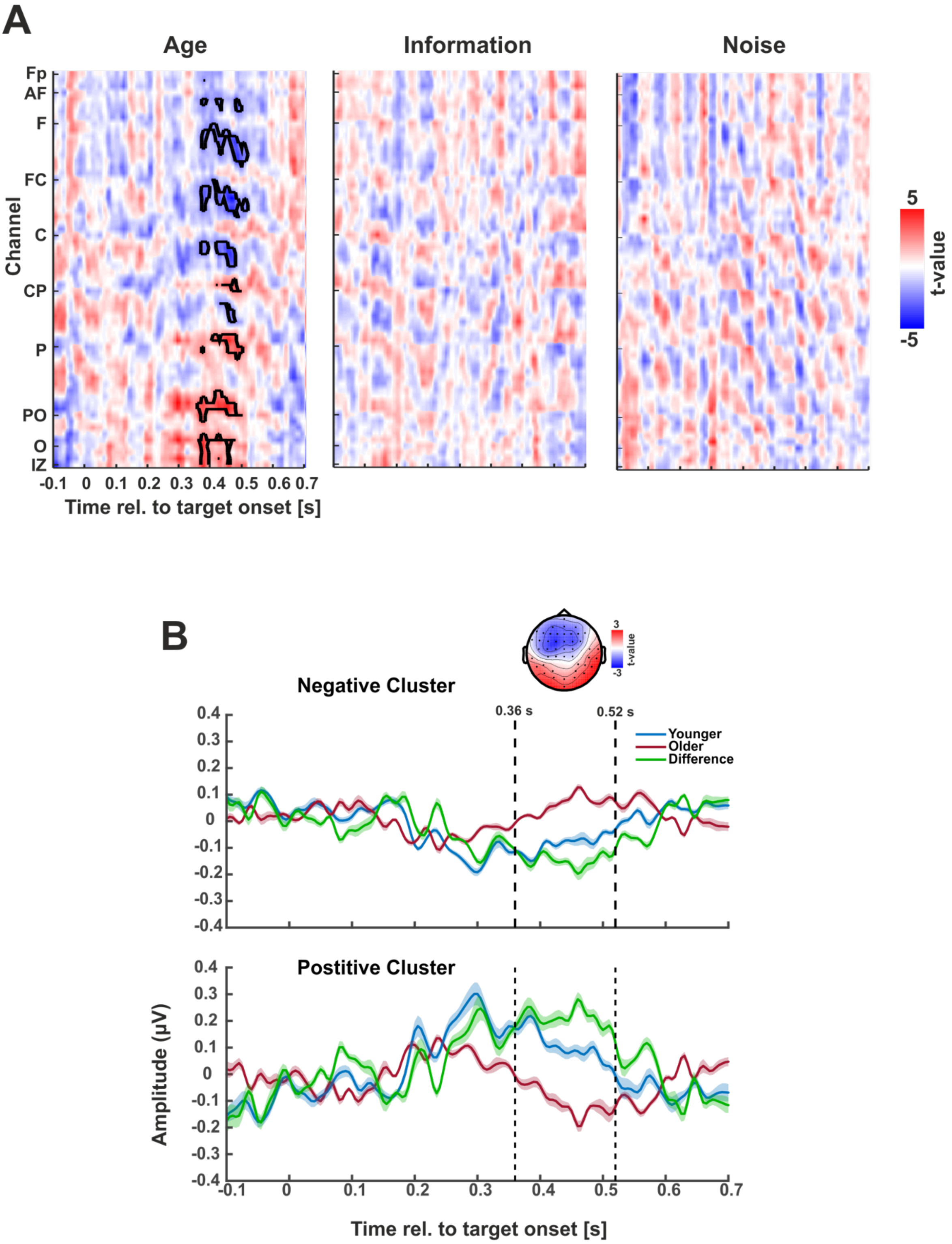

Figure 8.T-maps and time-courses of neural main effects in evoked activity in response to target word onset. (A) T-maps for age group, information condition, and noise level contrasts based on cluster-based premutation tests. Significant age-related differences were observed in two clusters representing fronto-central negativity, and parieto-occipital positivity between 360 ms and 520 ms. Significant clusters are outlined in black. No significant contrasts were observed in comparing information condition or noise level. (B) Time-courses and scalp topography of the significant clusters found in the younger vs. older contrast. Time courses are grand-averages of evoked activity with standard error over significant channels highlighted in panel A. Evoked activity is shown as the difference between age groups in green, younger adults in blue, and older adults in red. Perforated lines indicate the temporal extent of the significant clusters.

Significant differences in AV enhancement between younger and older adults were found between 265 ms to 420 ms following target onset (**Figure 9**A left panel). A significant negative cluster was observed over central channels (T_{sum} = -223, $p < 0.001$, **Figure 9**B left panel), suggesting that older adults have greater positivity in AV enhancement-related evoked activity over these sites compared to younger adults. To examine this effect in more detail, we compared evoked activity between AV_{inf} and AO_{inf} conditions separately in younger (**Figure 9**A center panel) and older adults (**Figure 9**A right panel). A significant negative cluster was observed over fronto-central channels between 360 ms to 420 ms (T_{sum} = -428.002, $p = 0.032$, **Figure 9**B center panel), suggesting that AV enhancement in younger adults is reflected in late evoked negativity. In older adults however, a positive cluster was found over central electrodes between 255 ms and 425ms (T_{sum} = 957.546, $p = 0.002$, **Figure 9**B right). AV enhancement in older adults, therefore, is reflected in late evoked positivity. Behavioural and neural AV enhancement were not significantly correlated in either younger or older adults (younger, $r = -0.364$ [-0.678, 0.138], $p = 0.138$; older, $r = -0.142$ [-0.616, 0.366], $p = 0.586$).

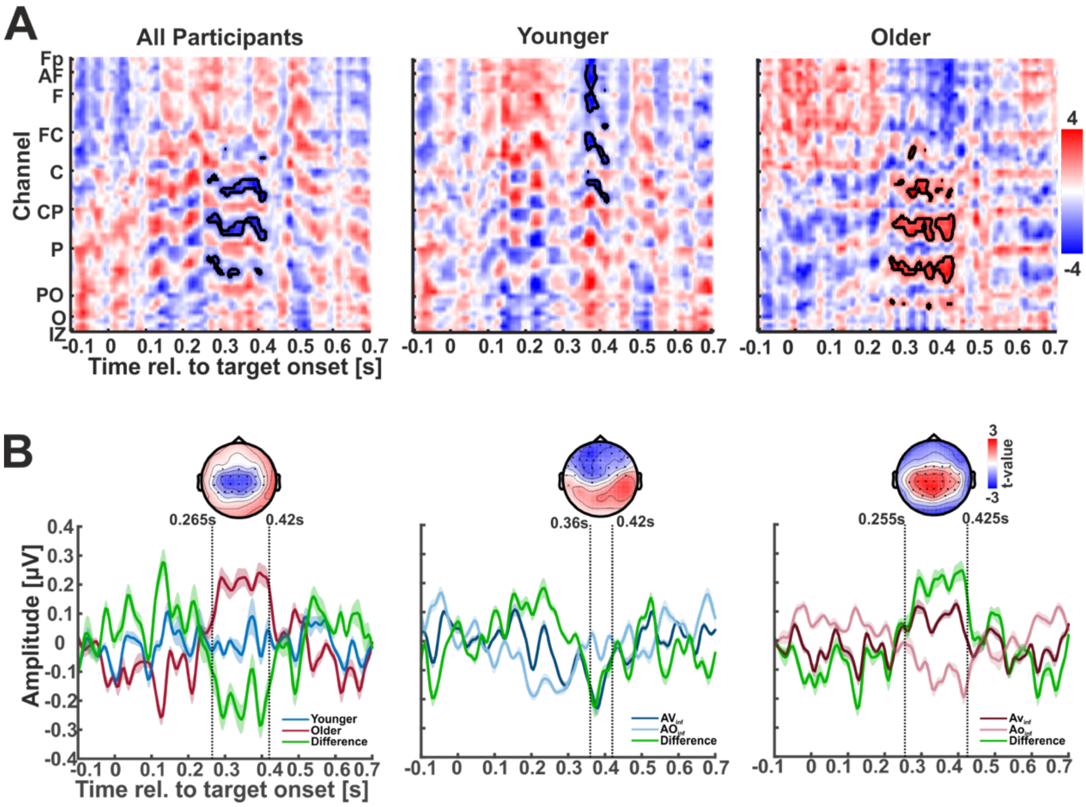

Figure 9. T-maps, time-courses and topographies of the AV_{inf} vs. AO_{inf} contrasts (i.e. the neural signature of AV enhancement). (A) T-maps reflecting neural AV enhancement are shown for all participants, younger participants, and older participants separately. Across all participants, a negative cluster is observed centro-parietal channels between 265 ms and 420 ms. This contrast emerges as negative activity over fronto-central channels between 360 ms and 420 ms in younger adults, and as positive activity over centro-parietal channels between 255 ms and 425 ms in older adults. Significant cluster are outlined in black. (B) Time-courses and scalp topography of the significant clusters found displayed in panel A. Time courses are grand-averages of evoked activity with standard error over significant cluster-specific channels. In the left panel evoked activity is shown in blue for younger adults and red for older adults. AV_{inf} and AO_{inf} is represented in dark and light blue respectively in the central panel, and in dark and light red respectively in the right panel. Difference waves between age groups or information condition are always shown in green. Perforated lines indicate the temporal extent of the significant clusters being represented.

No significant interaction effect between age and noise level on evoked activity was observed (at $p < 0.05$). Furthermore, no significant differences in evoked activity between low noise and high noise conditions were observed for younger and older adults separately (at $p < 0.05$,**Figure 10**).

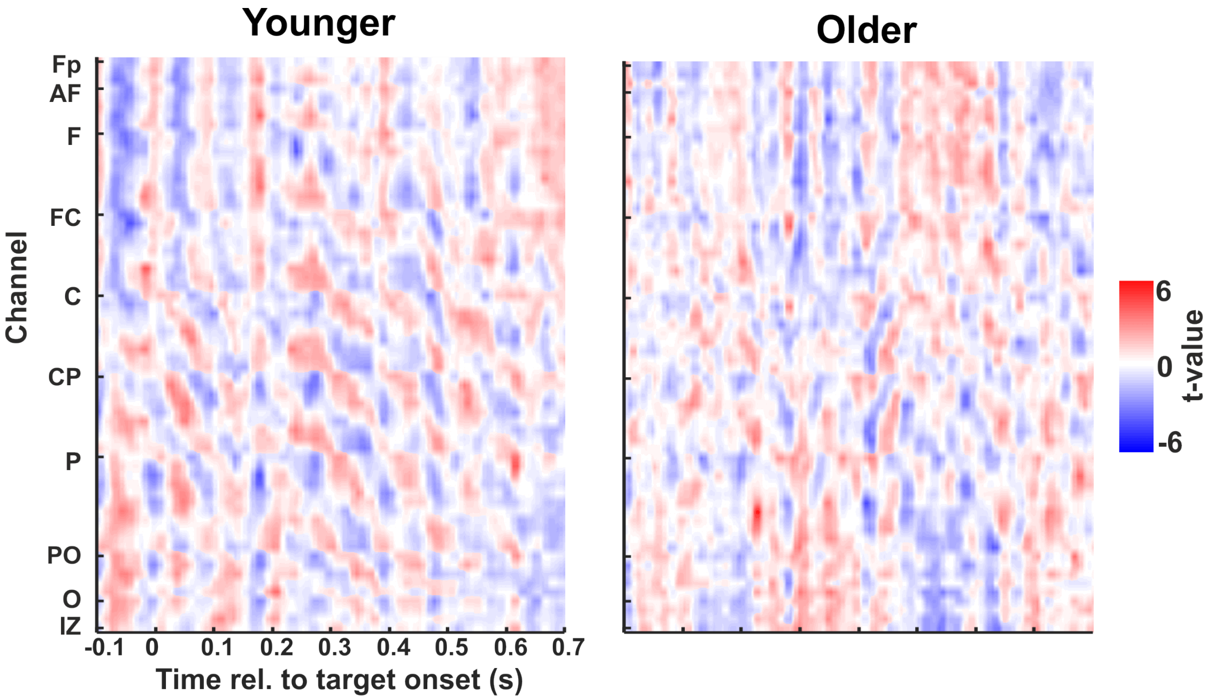

Figure 10.T-maps for the low noise vs. high noise contrast by age group. No significant effects were observed in either age group.

4.3.4 Late evoked activity emerges earlier in older adults

We observed a significant difference in earliest AV enhancement-related evoked activity latency (two sample t-test: $t(1984) = 82.989$, $p < 0.001$, $d = 3.724$). Younger adults' AV enhancement-related evoked activity were delayed by a mean of 0.086 s in comparison to older adults (Bootstrapped 95% confidence interval of the difference in latency: [0.010 s, 0.135 s]).

4.4 Discussion

In the current study we have investigated the consistency of evoked activity underlying AV speech integration in a speech-in-noise discrimination task in younger and older adults.

4.4.1 Age-differences in visual influences on behavioural performance

We observed significantly greater performance for visually-informative stimuli across participants, with older adults showing significantly greater improvement in performance for audio-visually informative stimuli compared to acoustically informative stimuli. Since the degree of AV enhancement does not correlate with cognitive status, and that our participants had only mild age-related impairment in hearing and visual capabilities, the behavioural AV enhancement observed in older adults is likely due to compensatory strategies in AV speech perception rather than as a result of cognitive or sensory impairment.

In ageing studies, there are reports that performance in AV conditions between younger and older adults is comparable (Sekiyama et al., 2014; Winneke & Phillips, 2011), or poorer in older adults (Sommers et al., 2005). However, it is more common practice to compare visual enhancement (or some measure of visual influence) between age groups to investigate the magnitude of the benefit visual speech has in AV conditions over AO conditions. It is hypothesized that since auditory acuity and attentional resources become more limited with age, older adults depend more on visual speech in AV speech settings for comprehension compared to younger adults, providing that viewing conditions are good.

Previous results have been inconsistent concerning the influence ageing has on AV enhancement. Both Sekiyama et al. (2014) and Maguinness et al. (2011) found that AV enhancement was greater in older adults compared to younger adults, which aligns with the results of the current study. Other studies, however, report that AV enhancement is comparable between age groups (Gordon & Allen, 2009; Sommers et al., 2005; Winneke & Phillips, 2011). In particular, Sommers et al. (2005) found no difference in enhancement provided by AV speech-in-noise stimuli when controlling for age differences in lip-reading ability. In addition, they found that older adults' speech discrimination performance was less accurate in AV conditions compared to younger adults, despite titrating noise level in participants individually and screening for impairments to visual and hearing abilities.

We also observed significantly poorer performance for high noise conditions compared to low noise across participants, and a greater difference between information conditions when there is high noise compared to low noise. Ross et al. (2007) found that visual gain increases up to an SNR of -12 dB, and thereafter visual gain decreases, thus describing the relationship between SNR and visual as curvilinear. The SNRs used in the current study were approximately -7.31 dB and -8.14 dB for the low noise and high noise conditions respectively, thus this result is in line with those of Ross et al. (2007), however further work is needed in comparing the SNR-visual-gain profile between younger and older adults as this could offer insight into the age-related differences in visual discussed above. We found that the interaction between noise and information condition was consistent across age groups (via the absence of an age group x information condition x noise level interaction).This was to be expected since noise levels were titrated around participants' own 70% correct speech-in-noise discrimination threshold.

4.4.2 Influence of visual predictability on behaviour

Behaviourally, we found that word discrimination accuracy was greater for target words with non-labial onset phonemes (assumed to be least visually predictive) compared to target words with labial-onset phonemes (assumed to be most visually predictive). We also found that behavioural AV enhancement varied as a function of visual predictability, wherein AV enhancement was greater for labial target words, compared to non-labial target words. These effects were consistent across age groups.

The lack of age-related differences in behaviour is unsurprising in this case given the divergence of reports of age-related differences in the extent of the benefit afforded by AV speech (Gordon & Allen, 2009; Maguinness et al., 2011; Sekiyama et al., 2014; Sheldon et al., 2008; Sommers et al., 2005). It was expected that AV enhancement would be greater when the initial phoneme target words was visually predictive, since previous research has found that speech discrimination is enhanced by visual speech compared to auditory speech alone (Bernstein et al., 2004). Within a predictive coding framework, this enhancement occurs because the visual speech signal serves as a primer in reducing the uncertainty of the upcoming voiced signal (Peelle & Sommers, 2015; van Wassenhove et al., 2005).

However, what was unexpected was the finding of poorer performance in discriminating target words with labial initial phonemes. Individual differences in lip-reading ability have been reported (Auer & Bernstein, 2007; Bernstein et al., 2000); however, in this case we did not test participants' lip-reading abilities in the current study and thus cannot say whether lip-reading difficulties led to poorer performance in the labial condition and/or reliance on non-labial articulatory features within the target stimuli. Furthermore, in our analyses we have categorized visual predictability based on stable patterns of articulatory movements (Fisher, 1968; Owens & Blazek, 1985; Woodward & Barber, 1960) that do, or do not, involve labial articulation of the initial phoneme of the target word. This makes the assumption that the initial phoneme is indeed predictive of subsequent voicing, however, in terms of identification, research has shown that consonants are discriminated easiest at the end of an utterance (van Son et al., 1994). Furthermore, phoneme confusability is predictive of word discrimination accuracy (Mattys et al., 2002). It is perhaps the case that in the current design, initial phonemes are not the most task-relevant phonetic feature, and accurate performance may instead be driven by (with possible reliance on) phonetic features in other positions (e.g. vowels; Fogerty et al., 2012; Fogerty and Humes, 2010; Richie and Kewley-Port, 2008).

Lastly, we observed that the influence of visual predictability on behaviour was consistent as a function of listening difficulty (noise level), and this effect was stable across information conditions and age groups. This suggests either that the influence of visual predictability is robust under difficult listening conditions, and thus a consistent strategy can be applied regardless of acoustic reliability, or that the differences in SNR ratio between the low and high noise conditions were not low enough to elicit differential processing strategies. In this case the former is most likely given that we observe significant differences in word discrimination, and AV enhancement, between noise levels.

4.4.3 Age-related differences in early EEG activity

In our data we expected to observe age-related differences in the P1-N1-P2 evoked components of auditory evoked responses in two portions of the trial. Firstly, in alignment to background onset (and first visual frame), and in alignment to target word onset. Considering the former, we found an age-related suppression of the N1 peak amplitude, which is inconsistent with previous findings reporting N1 peak enhancement in older adults (Anderer et al., 1996; Harkrider et al., 2005; Henry et al., 2017; McNair et al., 2019; Rufener et al., 2014; Tremblay et al., 2003).The studies cited here used only auditory stimuli, whereas the current study contained audio-visual stimuli on every trial (through not always audio-visually informative), thus N1 peak suppression in this case may be a result of age-differences in attentional control. Furthermore, we found an age-related slowing of the N1 and P2 peak latencies, an effect replicated consistently in ageing research (Henry et al., 2017; McNair et al., 2019; Tremblay et al., 2004).

We also found that the profile of pre-target power spectral density of ongoing EEG activity was significantly flatter in older adults. This replicates our previous findings (McNair et al., 2019) and is in line with previous reports which propose a mediating role of spectral flattening in cognitive decline (Tran et al., 2016; Voytek et al., 2015). Our participants passed a battery of cognitive screening assessments designed to test a variety of cognitive abilities, suggesting that changes in spectral slope in the present data do not reflect cognitive decline per se but either compensatory mechanisms or basic changes in cellular physiology (Caspary et al., 2008; R. Gao et al., 2017; S. L. Hong & Rebec, 2012; Podvalny et al., 2015; Pozzorini et al., 2013; Voytek & Knight, 2015; Waschke et al., 2017).

The second vein of inquiry of this study in relation to early AEPs considers activity in response to target word onset. Previous studies have reported suppressed and earlier N1 –P2 peak latencies and/or amplitudes in AV conditions (Alsius et al., 2014; Baart, 2016; Baart et al., 2014; Frtusova et al., 2013; Ganesh et al., 2014; Kaganovich & Schumaker, 2014; Klucharev et al., 2003; Stekelenburg & Vroomen, 2007; Treille et al., 2014; van Wassenhove et al., 2005), and an age-related potentiation of the N1 (Frtusova et al., 2013) and P2 peak (Winneke & Phillips, 2011) and reduction in latency of the N1 peak

(Frtusova et al., 2013; Winneke & Phillips, 2011, 2009). We did not observe any significant age- or AV-related effects within the early portion (i.e. < 255 ms) of post-target activity. The aim of our analyses was not to investigate the presence of evoked responses per se, but to investigate the contrasts between conditions of interest (namely information and noise conditions) and between age groups. However, the observance of age-related differences in behavioural AV enhancement suggests that age-related differences in early AEPs should also occur. Therefore, that we do not observe significant effects in these contrasts suggests two possibilities: that early evoked activity in the current sample remains consistent across information and noise conditions and age group, or that condition/age-group –related differences in early evoked activity exist but are not observable due to features of the current experimental design.

Amplitude and latency modulation of early auditory components by sensory modality and age group are extensively replicated but are inconsistently reported, an effect most likely due to paradigm-specific demands. However, early auditory activity correlates well with behavioural task performance (Frtusova et al., 2013; Starke et al., 2017; Stevenson et al., 2012; Treille et al., 2014), and given that we observe significant behavioural contrasts it is unlikely that the task-relevant neural correlates would remain consistent. It remains that such effects do not survive or are not observable due to design features. One possibility is that the current sample size was not sufficient to reveal systematic differences in early evoked activity. In the majority of studies published in this field, ERP analyses are carried out on single or small groups of channels chosen a-priori (e.g. Stekelenburg and Vroomen, 2007; van Wassenhove et al., 2005; Winneke and Phillips, 2011) and in a short time window focused on early latencies (usually 300 ms or less; e.g. Shahin et al., 2018; Stekelenburg and Vroomen, 2007; Winneke and Phillips, 2011). Few studies in AV research investigate the development of event-related activity over time using whole-scalp statistical methods (e.g. Besle et al., 2004; Boyle et al., 2017; Roa Romero et al., 2015). In the current study we used a whole-scalp approach in a wide time window, using cluster-based permutation procedures (S. J. Kayser et al., 2015; Maris & Oostenveld, 2007; I. S. Rao & Kayser, 2017) in avoiding a-priori assumptions regarding the (in-)consistency of neural activity topographically (Cabeza, 2002; Davis et al., 2008; McNair et al., 2019) and temporally (Bieniek et al., 2013; McNair et al., 2019; Price et al., 2017; Salthouse, 1996). It is therefore possible that weaker effects (but not significant in this case) exist, but do not survive multiple comparison correction during the cluster-permutation procedures. Future research could address this by adopting EEG-analyses which avoid spatio-temporal a priori assumptions and the multiple comparison problem, such as discriminant analyses (Boyle et al., 2017; S. J. Kayser et al., 2016; McNair et al., 2019; Parra et al., 2005; Philiastides, 2006; Ratcliff et al., 2009).

4.4.4 Differential late activity could index differential predictive coding

Though we did not observe significant contrasts in early evoked activity, we found significant age-related differences later in the trial. In comparing younger versus older adults, we observed a negative difference in EEG amplitude over fronto-central channels, and a positive difference at posterior channels at 360 ms to 520 ms. Older adults tend to recruit anterior areas in compensation for increased noise in sensory systems and decreased support for memory processes, even when behavioural performance is comparable (Davis et al., 2008; Reuter-Lorenz & Cappell, 2008). In EEG research, anterior-posterior shifts in topography have been observed in late evoked potentials (Anderer et al., 1996; Friedman, 2012; Ortiz et al., 1990).

Our results also revealed a significant negative difference between younger and older adults in the evoked activity representing the difference between AV and AO conditions at 265 ms to 420 ms over central channels. Further investigation into this effect revealed AV-related attenuation of the signal over fronto-central channels in younger adults between 360ms and 420 ms, and enhancement over central channels between 255 and 425 in older adults. This is in line with previous research which demonstrate AV influences on late ERP components such as the P3 (Andres et al., 2011; Hernández-Gutiérrez et al., 2018; Hessler et al., 2013; Irwin et al., 2017, 2018; Starke et al., 2017; Stekelenburg et al., 2018) and N4 (Duncan et al., 2009; Kaganovich et al., 2016; Lebib et al., 2004; Van Petten et al., 1999) components. The P3 component indexes memory processes in mapping incoming sensory information onto matching internal representations (Polich, 2012). Increasing memory load is associated with reduced amplitude over frontal sites (Segalowitz et al., 2001), however P3 topography is typically task-dependent. The N4 component is elicited in response to assessing congruence in mapping incoming sensory information to contextual cues. In AV speech paradigms, N4 amplitude increases when target stimuli and contextual information are incongruent (Duncan et al., 2009).

It is possible that that since we observe age-related differences in neural AV enhancement polarity and topography it can be concluded that older and younger adults engage different task-relevant predictive strategies in target discrimination (S. J. Kayser et al., 2016; McNair et al., 2019). In younger adults we observe AV-related negativity over anterior sites. This differs from the canonical central topography of the N400, however there are reports of a frontal N4 response in lexical priming (Coulson et al., 2005), and in tasks engaging recognition memory (for review see Kutas and Federmeier, 2011), wherein N4 amplitude scales with word familiarity (Curran, 2000). In older adults we observe AV-related positivity over centro-parietal channels, which is in line with the canonical P3 topography. The latencies of evoked activity reflecting AV enhancement are markedly different between two age groups also. Significant AV_{inf} versus AO_{inf} contrasts in older adults emerge as early as 255 ms and endure until 425 ms, while in younger adults effects are seen later and over a smaller duration of 360 ms to 420 ms. We found that bootstrap distributions of onset latencies for these effects were significantly different, suggesting that cognitive processing reflected by AV enhancement in late-latency activity occurs earlier in older adults compared to younger adults. This is inconsistent with previous results that show that evoked potentials are delayed in healthy ageing (Friedman, 2012; Gunter et al., 1992, 1996; van Dinteren et al., 2014). It is however, consistent with Raij et al.'s (2000) findings that phonetic auditory and graphemic visual activity converge around 225 ms after stimulus onset and interact in multisensory brain areas (temporo-parietal junction and superior temporal sulci) up to latencies of 535 ms.

It could be hypothesized that, in support of a predictive coding perspective, the late activity we observe in the current study are likely to be top-down signatures of memory processes engaged in updating mental representations of audio-visual speech (Polich, 2012), and/or of prediction error (Kutas & Hillyard, 1989; Swaab et al., 2012). This hypothesis would suggest a prediction strategy based on mental representation maintenance in working memory is used by older adults, and a strategy based on lexical priming in semantic memory is used by younger adults. Support for this comes from the observance of P3 and N4-like effects in older and younger adults respectively, and through a lack of neurobehavioural correlation in AV enhancement, which suggests that the late-evoked activity observed is not a signature of sensory encoding but possibly of higher-order processing. Our finding of systematic changes in the overall spectral profile of EEG activity and a general slowing of early auditory evoked responses in the older participants (in response to background onset), discussed earlier, could suggest that differential functional strategies in sensory encoding could have a knock-on-effect on subsequent cognitive strategies. Future research should address this hypothesis by varying memory processes and load in AV speech paradigms.

4.5 Conclusion

The present data demonstrate age-related differences in EEG signatures underlying visually-informative AV speech discrimination. Behaviourally, we find that overall, younger and older adults performed comparably, but older adults derived greater AV enhancement than younger adults. Younger adults show later, more frontal, and more negative activity in late evoked activity compared to older adults, however these effects do not correlate with behaviour AV enhancement. Age-related differences in the profiles of late evoked activity, suggest differential cognitive processing strategies, likely involving differential memory processes, between age groups, which calls for a more systematic assessment in varying and/or controlling for memory processing a load in AV speech perception.

4.6 Supplementary material: target word list

Word	Sound type	Articulation type	Word length	Word duration (s)	Concreteness category	Concreteness rating	Familiarity rating
ACT	vowel	non-labial	3	2.66	low	379	566
AGE	vowel	non-labial	3	2.9	low	390	582
AID	vowel	non-labial	3	2.78	low	372	536
AIM	vowel	non-labial	3	2.46	low	324	549
APE	vowel	non-labial	3	2.98	high	654	547
BEAT	plosive	labial	4	2.3	low	361	536
BOAT	plosive	labial	4	2.74	high	637	584
CAKE	plosive	non-labial	4	2.78	high	624	594
CAUSE	plosive	non-labial	5	3.06	low	287	557
CHAIR	affricate	non-labial	5	2.38	high	606	617
CHAIR	affricate	non-labial	5	2.38	high	606	617
CHALK	affricate	non-labial	5	2.5	high	634	560
CHANCE	affricate	non-labial	6	3.02	low	254	563
CHARM	affricate	non-labial	5	2.54	low	352	514
CHEAT	affricate	non-labial	5	2.7	low	329	549
DART	plosive	non-labial	4	2.5	high	608	496
EAR	vowel	non-labial	3	2.46	high	640	560
EASE	vowel	non-labial	4	3.1	low	305	519
EGG	vowel	non-labial	3	2.78	high	613	608
END	vowel	non-labial	3	2.7	low	320	592
EYE	vowel	non-labial	3	2.9	high	634	611
FACT	fricative	labial	4	3.26	low	332	593

FEET	fricative	labial	4	2.9	high	642	611
GLOVE	plosive	non-labial	5	2.9	high	607	575
GUILT	plosive	non-labial	5	2.74	low	299	559
HATE	fricative	non-labial	4	2.78	low	335	552
HEAD	fricative	non-labial	4	2.7	high	603	611
ICE	vowel	non-labial	3	3	high	621	564
INK	vowel	non-labial	3	2.9	high	608	542
JAW	affricate	non-labial	3	2.8	high	617	529
JAW	affricate	non-labial	3	2.8	high	617	529
JOIN	affricate	non-labial	4	2.38	low	292	544
JOKE	affricate	non-labial	4	2.5	low	388	580
JOKE	affricate	non-labial	4	2.5	low	388	580
JOY	affricate	non-labial	3	2.78	low	300	545
KEY	plosive	non-labial	3	2.5	high	612	603
KIND	plosive	non-labial	4	2.78	low	323	575
KNIFE	nasal	non-labial	5	2.9	high	612	573
KNOW	nasal	non-labial	4	2.86	low	274	605
LAND	fricative	non-labial	4	2.5	high	604	574
LEAST	fricative	non-labial	5	2.98	low	275	529
MAKE	nasal	labial	4	2.58	low	299	618
MILK	nasal	labial	4	2.5	high	670	588
MIND	nasal	labial	4	2.26	low	333	591
MOOD	nasal	labial	4	2.62	low	234	541
MOUSE	nasal	labial	5	2.5	high	624	520
MYTH	nasal	labial	4	3.02	low	334	514

NAG	nasal	non-labial	3	2.26	low	293	492
NEED	nasal	non-labial	4	2.58	low	314	589
NONE	nasal	non-labial	4	2.34	low	288	569
NOSE	nasal	non-labial	4	2.8	high	628	584
PLAN	plosive	labial	4	2.54	low	357	571
PLUM	plosive	labial	4	2.5	high	632	547
RAIN	rhotic	non-labial	4	2.6	high	600	604
RAT	rhotic	non-labial	3	2.4	high	624	548
RATE	rhotic	non-labial	4	2.58	low	308	527
REACH	rhotic	non-labial	5	3.06	low	368	577
RICE	rhotic	non-labial	4	2.94	high	608	548
RIGHT	rhotic	non-labial	5	2.82	low	361	599
ROCK	rhotic	non-labial	4	2.54	high	600	583
ROLE	rhotic	non-labial	4	2.5	low	335	524
ROPE	rhotic	non-labial	4	2.54	high	608	539
ROSE	rhotic	non-labial	4	2.86	high	608	556
RULE	rhotic	non-labial	4	2.66	low	286	534
RUSH	rhotic	non-labial	4	2.82	low	350	546
SAVE	fricative	non-labial	4	2.86	low	314	559
SHAME	fricative	non-labial	5	2.66	low	287	534
SOUP	fricative	non-labial	4	2.42	high	615	576
TERM	plosive	non-labial	4	2.46	low	374	575
THREAD	fricative	non-labial	6	2.78	high	607	522
THROW	fricative	non-labial	5	2.78	low	400	548
VOTE	fricative	labial	4	2.7	low	389	567

WANT	approximant	labial	4	2.7	low	302	606
WEALTH	approximant	labial	6	2.78	low	370	557
WEAR	approximant	labial	4	2.5	low	360	536
WEED	approximant	labial	4	2.54	high	600	542
WEST	approximant	labial	4	2.78	low	355	563
WILD	approximant	labial	4	2.9	low	381	572
WILL	approximant	labial	4	2.3	low	275	584
WINE	approximant	labial	4	2.54	high	621	570
WISE	approximant	labial	4	2.86	low	268	533
WOOD	approximant	labial	4	2.42	high	606	574
WOOL	approximant	labial	4	2.54	high	608	540
WORM	approximant	labial	4	2.34	high	611	498

Table 5. Target word stimuli list. List of monosyllabic nouns used as target stimuli and accompanying statistics. Sound type, articulation type, concreteness ratings and familiarity ratings were derived from the MRC Linguistics Database (Coltheart, 1981)

Chapter 5 Neurophysiological correlates of phonemic visual predictability in audio-visual speech-in-noise discrimination in younger and older adults

5.1 Introduction

Seeing visual speech helps us to discriminate auditory speech-in-noise faster (Klucharev et al., 2003) and more accurately (Bernstein et al., 2004). Speech is a complex, hierarchically organized stimulus; to parse an excerpt of acoustic speech, the listener must segment the signal in constituent parts such as phrases, words, syllables, and phonemes (Giraud & Poeppel, 2012a). EEG research has investigated the cortical oscillatory tracking (entrainment) of the temporal components of speech by cortical oscillatory activity. AV speech enhances entrainment and comprehension (Crosse et al., 2015; Hyojin Park et al., 2016; Zion Golumbic et al., 2013) within multiple feature-dependent frequency bands (Keitel et al., 2018). Keitel et al. (2018) report that entrainment to phonetic features occurs within alpha-band activity (8-12.4 Hz) in the right hemisphere, while syllables and words are reported to be tracked within low frequency (delta, theta) activity. Furthermore, irregularity of speech rate reduces the fidelity of auditory delta-band entrainment (S. J. Kayser et al., 2015).

Different phonemic categories have been found to elicit distinct patterns in evoked activity. Khalighinejad et al. (2017) found that AEP amplitude fluctuated as a function of the phonemic features of the presented speech targets at multiple timescales between 50 ms and 400 ms. Differences in the spatio-temporal profile of evoked activity are often markedly different for different phoneme classes (fricative, plosive, nasal, vowel, etc.), with key differences emerging between phonemes engaging labial articulatory cues and less predictable, non-labial phonemes (Khalighinejad et al., 2017; Mesgarani et al., 2008, 2014). Generally speaking, N1 and P2 AEP peaks reflecting, early sensory encoding processes, are suppressed and earlier in light of predictive visual information (Stekelenburg et al., 2013; Stekelenburg & Vroomen, 2007, 2012), specifically when dynamic labial articulations are predictive of upcoming speech targets (Arnal et al., 2009; Besle et al., 2004; Klucharev et al., 2003;

Stekelenburg & Vroomen, 2007; van Wassenhove et al., 2005). Modulation of N4 peak, on the other hand, is reflective of predictive coding in matching sensory phonetic (Lebib et al., 2004), lexical (Kaganovich et al., 2016), and semantic information (Van Petten et al., 1999) with internal schema, and its amplitude is enhanced when word stimuli are predicted (Kutas & Federmeier, 2011; Lau et al., 2008).

It remains unclear, however, whether and how neural AV enhancement might vary as a function of the visual predictability of speech targets. Additionally, it is unclear whether such effects would be stable across the lifespan. Previous work has studied the behavioural and neural correlates of phonemic perception by using either McGurk-style syllabic utterances (Besle et al., 2004; Stekelenburg & Vroomen, 2007; van Wassenhove et al., 2005) or continuous speech (Khalighinejad et al., 2017; Mesgarani et al., 2008, 2014). Studies have not yet investigated the visual predictability of phonemes at word onset using a speech-in-noise word discrimination task.

The aim of the current chapter was to separate target words based on the visual predictability of the initial phoneme (labial, non-labial) and then quantify the influence of phoneme type on the behavioural benefit of visual predictability and its associated ERP correlates. Thus, the current chapter is an extension to the analyses presented in Chapter 4. Our goal was to study the neural correlates underlying the visual predictability of AV speech under noisy listening conditions in younger and older adults. Using the same datasets collected from the AV speech-in-noise paradigm described in Chapter 4, we tested for the additional behavioural and neural main effects of articulation type (labial, non-labial), and its interaction with age group (younger, older), information condition (AV_{inf}, AO_{inf}), and noise level (low noise, high noise).

5.2 Analysis and statistical methods: auditory evoked responses to stimuli onset

The current chapter is an extension of the analyses reported in Chapter 4, thus only methodological details specific to this chapter are reported here. See Chapter 4 for details regarding participants, stimuli, experimental procedure, and EEG recording and pre-processing processes.

Our aim was to derive ERP signatures reflecting the visual predictability of target word initial phonemes. To this end, we tested for main effects and interactions in the four-factor mixed design age group x information type x noise condition x articulation type, using spatio-temporal cluster-based permutation tests (Maris & Oostenveld, 2007) across all channels and in a time window of -0.1s to 1s relative to target word onset. The procedure computed a two-tailed t-test for each channel and controlled for multiple comparisons. The cluster test statistic (T_{sum}) was computed by summing the t-value of adjacent channels where $p < 0.05$ during clustering, with a required cluster size of at least 2 significant neighboring channels and based on 2000 iterations.

We computed two measures in assessing the influence of visual information on performance (and also neural activity later). Firstly we calculated AV enhancement as the difference between AV_{inf} and AO_{inf} , as per Chapter 4 (McNair & Kayser, 2019). Secondly, we calculated visual predictability of the target word stimuli by the word’s onset phoneme as the difference between visually predictive (labial) and non-predictive (non-labial) conditions.

5.3 Results

5.3.1 Visual predictability is reflected in late evoked activity in older adults only

To investigate the main effect of articulation type of target word onset, we compared evoked time courses between words with labial versus non-labial initial phonemes across noise level, information condition, and age group. Significant articulation-related differences emerged in the form of a negative cluster between 345 to 380 ms following target onset over frontal channels ($T_{sum} = -322.313$, $p = 0.031$, **Figure 11**A). Target words with non-labial onset phonemes therefore induced more negative deflections in evoked activity compared to target word with labial onset phonemes (**Figure 11**B).

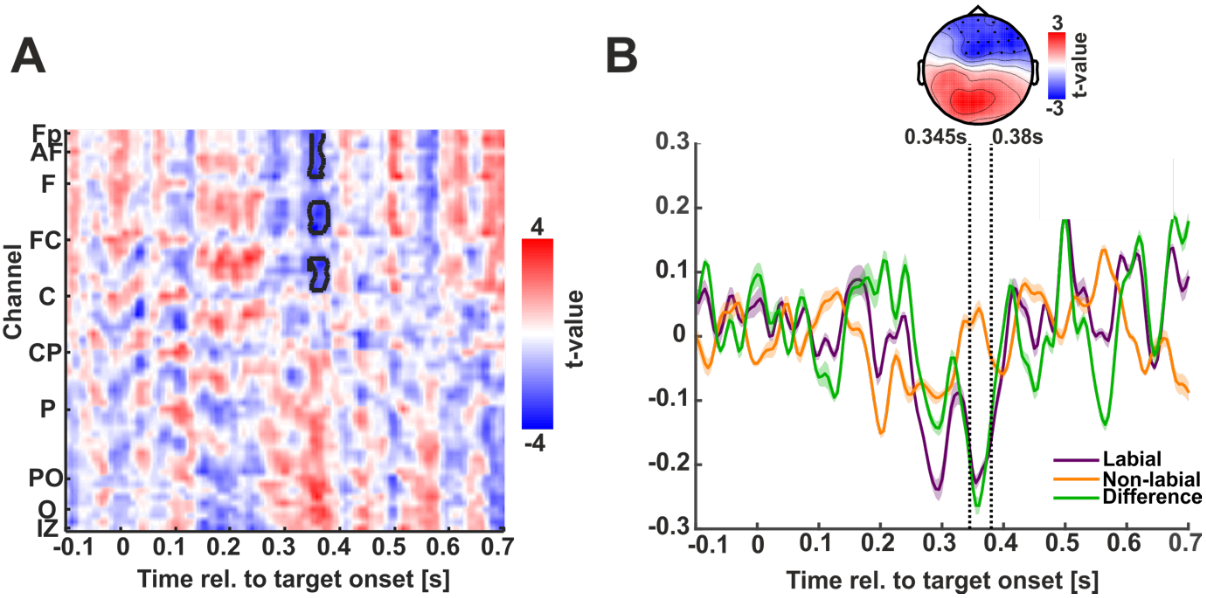

Figure 11.T-maps, time-courses and topography of the neural main effect of articulation type in response to target word onset. (A) T-map for labial vs. non-labial contrast based on cluster-based premutation tests. Significant articulation-related differences were observed in a cluster representing fronto-central negativity between 345 ms and 380 ms. Significant clusters are outlined in black. (B) Time-courses and scalp topography of the significant cluster displayed in panel A. Time courses are grand-averages of evoked activity with standard error over significant channels. Evoked activity is shown as the difference between articulation types (labial minus non-labial) in green, labial in purple, and non-labial in orange. Perforated lines indicate the temporal extent of the significant clusters.

To examine this effect further we tested the interaction between articulation type and age group by comparing the difference in articulation-related evoked responses (labial minus non-labial, thus reflecting activity underlying visual predictability) between younger and older age groups. A significant difference in activity representing visual predictability was found between younger and older adults (T_{sum} = 337.357, p = 0.029, **Figure 12**A left) between 245 to 315 ms. In this case, younger adults show more positive activity over frontal channels compared to older adults (**Figure 12**B, left). Age-related idiosyncrasies in articulation-evoked response patterns were further tested by comparing labial versus non-labial evoked responses for both age groups separately. No significant differences were observed in younger adults (at $p < 0.05$, **Figure 12**A center), however older adults show a more negative evoked deflection (**Figure 12**B, right) over fronto-central channels between 260ms and 380ms (T_{sum} = -765.866, $p < 0.001$, **Figure 12**A right). Taking these results together, we observe a neural signature representing the visual predictiveness of target word onset phoneme which is specific to older adults.

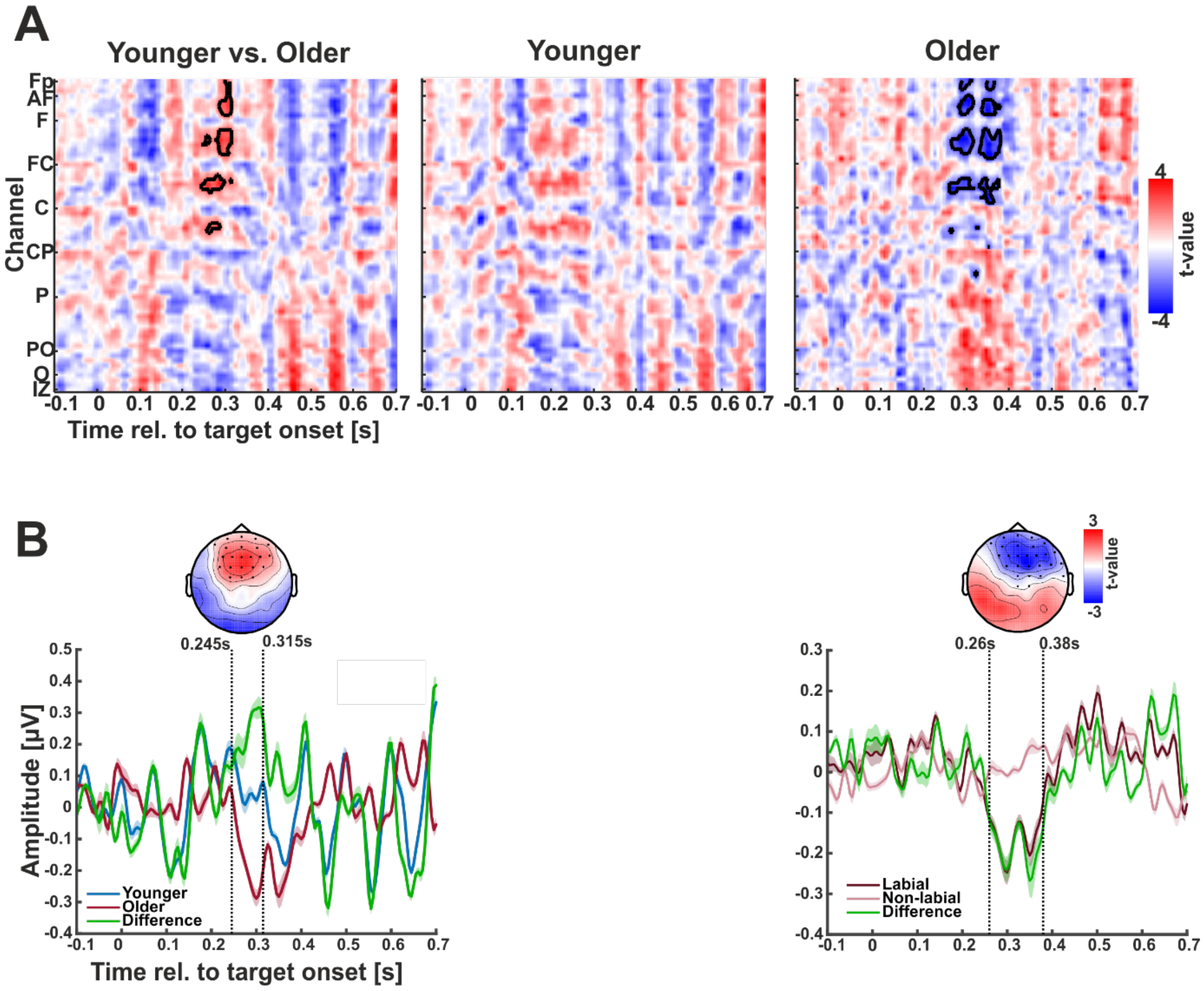

Figure 12.T-maps, time-courses and topographies of the labial vs. non-labial contrasts (i.e. the neural signature of visual predictability of target words). (A) T-maps reflecting visual predictability are shown for the younger vs. older contrast (left), younger participants (center) and older participants (right) separately. Across all participants, a positive cluster is observed in fronto-central channels between 245 ms and 315 ms. This contrast emerges as negative activity over fronto-central channels between 260 ms and 380 ms in older adults, however no significant contrasts were observed in younger adults. Significant cluster are outlined in black. (B) Time-courses and scalp topography of the significant clusters as displayed in panel A. Time courses are grand-averages of evoked activity with standard error over significant cluster-specific channels. In the left panel evoked activity is shown in blue for younger adults and red for older adults. Labial and non-labial evoked activity is represented in dark and light red respectively in the right panel. Difference waves between age groups or articulation condition are shown in green. Perforated lines indicate the temporal extent of the significant clusters being represented.

5.3.2 Visual predictability does not vary as a function of AV enhancement in evoked activity

We tested for an articulation type x information condition interaction by comparing time courses reflecting AV enhancement (AV_{inf} - AO_{inf}) between labial and non-labial articulation conditions both across all participants **Figure 13**A), and in younger and older participants separately (**Figure 13**C). No significant clusters were identified (at $p < 0.05$), suggesting that AV enhancement-related evoked responses are unaffected by the type of the target onset phoneme. Similarly, no significant clusters were observed (at $p < 0.05$) in testing the articulation type x information condition x age interaction (**Figure 13**B), which was computed by comparing the differences in articulation-related AV enhancement between age groups (i.e. $\text{Younger}_{\text{(labial AV - labial AO) - (non-labial AV - non-labial AO)}}$ versus $\text{Older}_{\text{(labial AV - labial AO) - (non-labial AV - non-labial AO)}}$). Together, this suggests that though visual predictability has a distinct event-related profile in older adults, AV enhancement-related activity is unaffected by visual predictability.

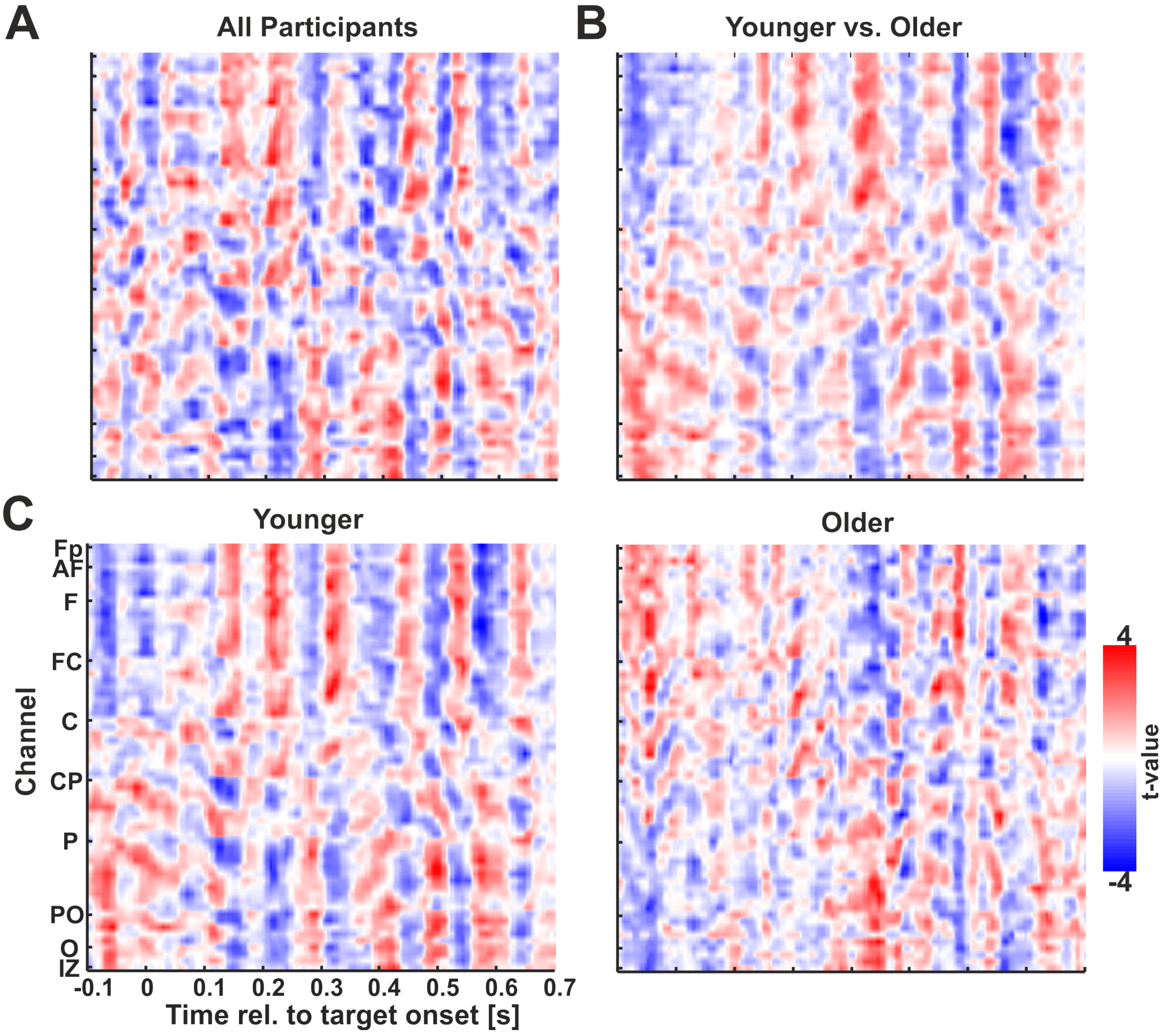

Figure 13.T-maps for the contrasts of differences in articulation-related AV enhancement (i.e. (labial AV_{inf} – labial AO_{inf}) – (non-labial AV_{inf} – non-labial AO_{inf})) across all participants (A), between age groups (B), for each age-group separately (C). No significant contrasts were observed in any case.

To investigate the interaction between information condition and articulation type further, we compared event-related time courses for information condition (AV_{inf} versus AO_{inf}) for each articulation type and age group separately. No significant clusters were observed in either the labial (**Figure 14**A) or non-labial (**Figure 14**B) articulation conditions in younger adults. In older adults, however a significant positive cluster over parieto-occipital channels was found in labial-related evoked activity (**Figure 14**D) for older adults at 325 to 380 ms (T_{sum} = 261.758, p = 0.023, **Figure 14**C). Thus, more positive activity over posterior channels may be an index of visual enhancement of the auditory signal for visually predictive targets. A significant information-related cluster was also observed in older adults' non-labial evoked activity (**Figure 14**F). A positive cluster was found over centro-parietal channels at 260 to 420 ms (T_{sum} = 843.071, $p < 0.001$, **Figure 14**E). Therefore, more positive activity over central channels may index visual enhancement of speech when visual predictiveness of the target word is low.

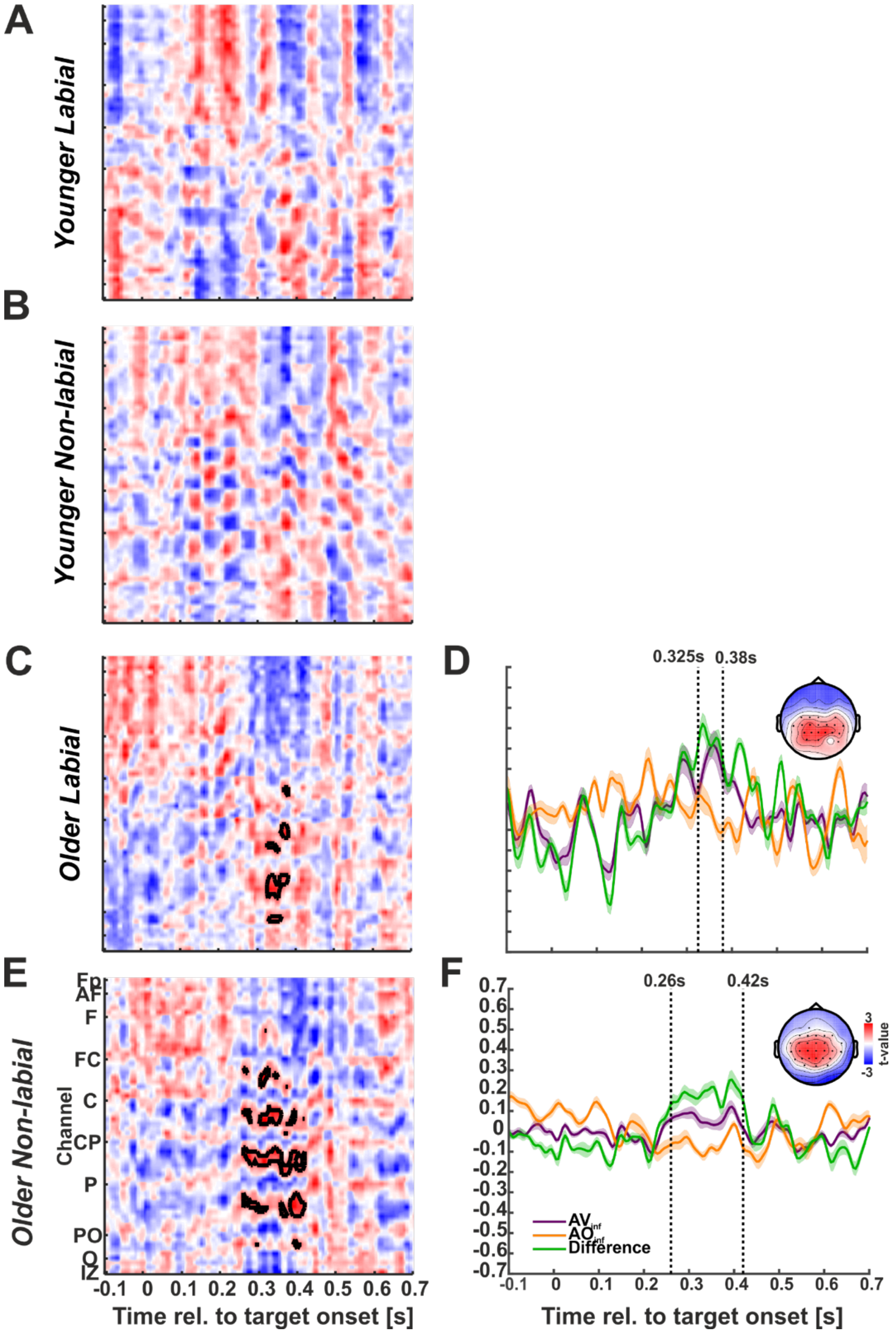

Figure 14.T-maps, time-courses and topographies of the AV$_{inf}$ vs. AO$_{inf}$ contrasts (i.e. the neural signature of AV enhancement) in evoked activity by articulation type and age group. (A-C, E). T-maps reflecting AV enhancement in evoked activity are shown for both age groups and articulations conditions separately. (D) Time-courses and scalp topography of the significant clusters in older adults' labial evoked activity, displayed in panel C. This contrast emerges as positive activity over centro-parietal channels between 325 ms and 380 ms. (F) Time-courses and scalp topography of the significant clusters in older adults' non-labial evoked activity, displayed in panel E. This contrast emerges as positive activity over centro-parietal channels between 260 ms and 420 ms.Difference waves between information conditions are shown in green, AV$_{inf}$ activity is shown in purple, and AO$_{inf}$ activity is shown in orange. Perforated lines indicate the temporal extent of the significant clusters being represented.

5.3.3 Neural correlates of visual predictability do not vary by task difficulty

AV enhancement, and the use of visual cues is greater when auditory signals are degraded (Puschmann et al., 2019; L. A. Ross et al., 2007). We therefore tested whether evoked signatures reflecting visual predictiveness (labial minus non-labial time courses) differed between low and high noise conditions (articulation type x noise condition interaction) both across all participants (**Figure 15**A), and in younger and older participants separately (**Figure 15**C), however no significant effects were observed (at $p < 0.05$). We also tested the articulation type x noise condition x age group interaction (**Figure 15**B) by comparing the noise-related differences in activity underlying visual predictability between age groups (i.e. $\text{Younger}_{(\text{low noise labial} - \text{low noise non-labial}) - (\text{high noise labial} - \text{high noise non-labial})}$ versus $\text{Older}_{(\text{low noise labial} - \text{low noise non-labial}) - (\text{high noise labial} - \text{high noise non-labial})}$), but no significant effects were observed (at $p < 0.05$). Therefore, we find no evidence that evoked activity underlying the visual predictiveness of speech differs as a function of listening difficulty and age.

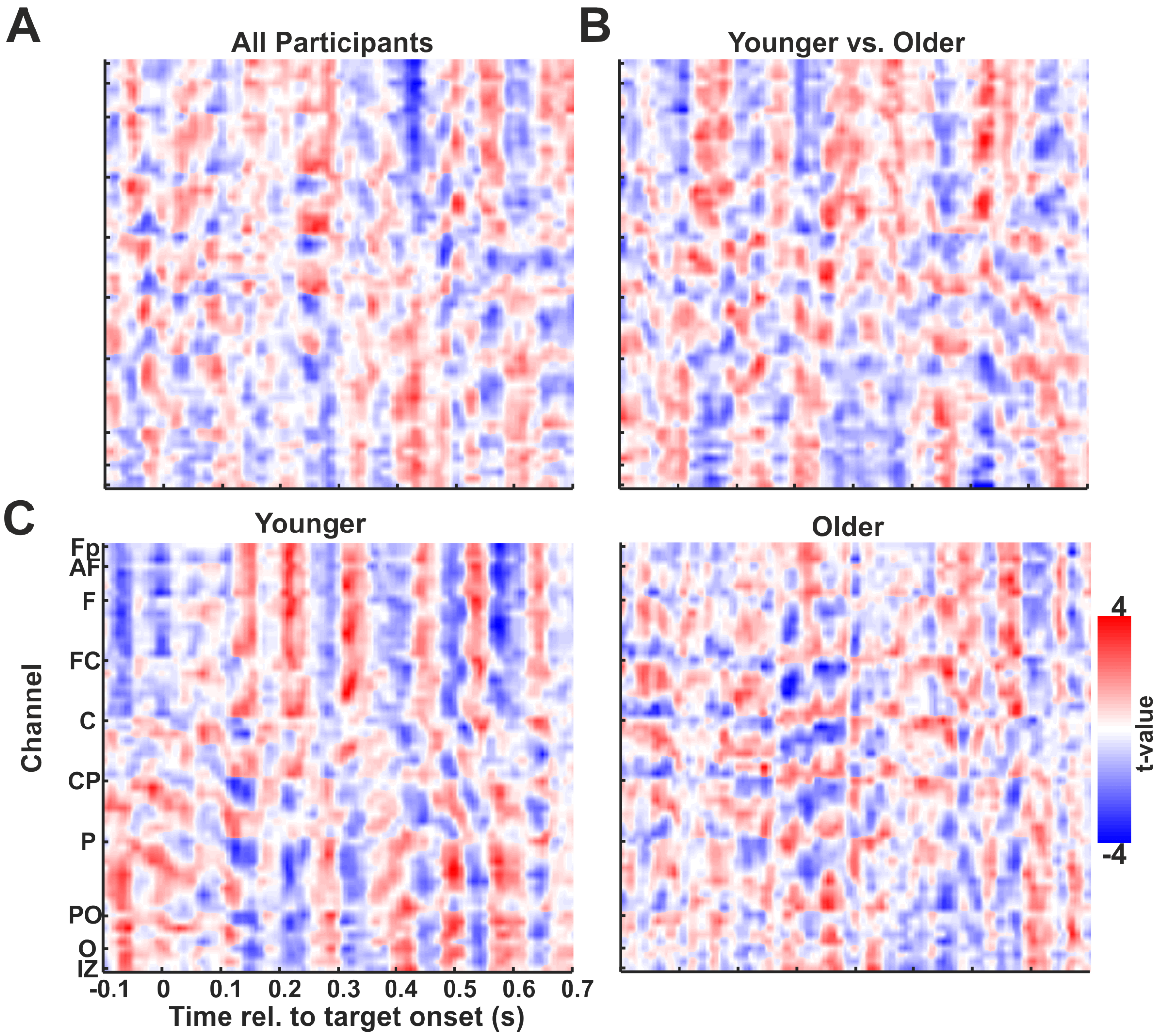

Figure 15.T-maps for the contrasts of noise-related differences in visual predictability in evoked activity (i.e. (low noise labial – low noise non-labial) – (high noise labial – high noise non-labial)) across all participants (A), between age groups (B), for each age-group separately (C). No significant contrasts were observed in any case.

5.4 Discussion

In the current chapter, we have investigated the consistency of evoked activity underlying the visual predictability of AV speech, using a speech-in-noise discrimination task in younger and older adults.

Visual predictability (labial - non-labial) was reflected by negative evoked activity over frontal channels between 345 ms and 380 ms, across all participants. Conversely, this indicates that evoked activity to non-labial initial phonemes is significantly more positive. Thus, what we observe here is a reduction in the amplitude of evoked activity in relation to visually predictive stimuli. Comparing visual predictability between younger and older adults, younger adults show more positive activity over frontal channels between 245 ms and 315 ms, compared to older adults. Younger adults do not exhibit a significant effect of visual predictability (labial vs. non-labial contrast), whereas older adults have more negative activity over fronto-central channels between 260 ms and 380 ms. Taking these results together, we observe a neural signature representing the visual predictiveness of target word onset phoneme which is specific to older adults.

These results suggest that late evoked activity is sensitive to articulatory features of lexical stimuli in older adults, and is consistent with previous research that shows AV suppression of evoked activity peaks. AV-related ERP suppression has been observed in relation to the N1 – P2 early auditory potential (Alsius et al., 2014; Baart, 2016; Baart et al., 2014; Frtusova et al., 2013; Ganesh et al., 2014; Kaganovich & Schumaker, 2014; Klucharev et al., 2003; Stekelenburg & Vroomen, 2007; Treille et al., 2014; van Wassenhove et al., 2005), and the later P3 component reflecting the mapping of auditory and visual representations to internal representations (Hernández-Gutiérrez et al., 2018; Hessler et al., 2013; Irwin et al., 2017, 2018; Klucharev et al., 2003; Starke et al., 2017). In line with our results, P3 peak suppression in AV speech is often demonstrated over fronto-central sites (Hernández-Gutiérrez et al., 2018; Hessler et al., 2013; Irwin et al., 2017, 2018; Starke et al., 2017). Most similar to our findings is that of Klucharev et al. (2003) who observed a reduction in amplitude between congruent versus incongruent spoken phonemes, peaking at 325 ms after stimulus onset. According to Van Wassenhove et al. (2005), in line with a predictive coding view under an analysis-by-synthesis framework, AV-related modulation of evoked activity is influenced by the predictability of visual speech and thereafter the redundancy of visual and auditory information. Specifically, modulation of the N1 – P2 component is reflective of prediction error following the mapping of sensory input against an internal predictor. Our results are in line with this interpretation and extend its scope beyond early auditory activity to later-occurring components which closely resemble P3 and N4, and thus top-down, activity.

Given that we do not observe behavioural labial versus non-labial contrasts between younger and older adults (see Chapter 4), it is likely that neural differences are reflective of compensatory mechanisms supporting accurate performance given healthy changes in cognitive function with age (Cabeza, 2002; Davis et al., 2008). In Chapter 4, we discussed age-related differences in AV enhancement, possibly reflecting differential cognitive strategies in predictive coding that are reliant on distinct memory processes. We needed to understand the interaction between visual predictability and AV enhancement in the neural data. AV enhancement-related evoked responses were unaffected by articulation type in either age group. Significant spatio-temporal profiles of AV enhancement were observed in older adults for labial and non-labial words separately, however when comparing these profiles no significant differences were observed. Similar effects are not observed in younger adults, despite significant AV_{inf} versus AO_{inf} contrasts observed in younger adults in Chapter 4suggests that such effects in this age group are made weaker when separating the data by articulation type, and thus are not significant here.

In neither age group does neural AV enhancement vary as a function of visual predictability. This is inconsistent with our behavioural findings, in which we observe heightened AV enhancement with increased visual predictability. Previous research (discussed above) suggests that this should result in heightened AV-related suppression of evoked activity. This does not necessarily suggest that such effects do not exist. One possibility is that potential weaker effects do not survive multiple comparisons owing to the spatio-temporal nature of our analysis approach. Analyses at the single-channel level would eliminate the spatial dimension, but inherently rely on a-priori assumptions about which channels most strongly reflect the neuroanatomical sources generating visual predictability-related and AV enhancement-related activity. These assumptions are complicated by evidence that visual enhancement has been associated with activity at multiple sites including superior temporal areas (Beauchamp et al., 2004; Nath & Beauchamp, 2012; Riedel et al., 2015; Van Atteveldt et al., 2014), inferior frontal and pre-motor areas (Arnal et al., 2009; Evans & Davis, 2015; Hasson et al., 2007; H. Lee & Noppeney, 2011; I. G. Meister et al., 2007; Skipper et al., 2009; Wright et al., 2003), and early auditory cortices (Besle et al., 2008; Chandrasekaran et al., 2013; Ghazanfar et al., 2005; C. Kayser et al., 2010; Lakatos et al., 2009; Zion Golumbic et al., 2013). Alternatively, LDA is increasing used in cognitive neuroscience to reduce the spatial dimension of EEG data to one-dimensional scalp projections maximally separating experimental conditions

(Boyle et al., 2017; S. J. Kayser et al., 2016; McNair et al., 2019; Parra et al., 2005; Philiastides, 2006; Ratcliff et al., 2009). Our previous work has demonstrated that clustering these projections can reveal systematic temporal patterns in the sensory-perceptual cascade (S. J. Kayser et al., 2016; McNair et al., 2019). Therefore, further work is required in reconciliating effects observed in task-relevant neuroanatomical sources, and in identifying their scalp-level correlates.

Lastly, we found that evoked activity reflecting visual predictability did not vary with listening difficulty, and this was consistent across information conditions and age groups. These results were to be expected as they are in line with our behavioural findings (see Chapter 4).

5.4.1 Conclusion

The present data demonstrate age-related differences in EEG signatures underlying visual predictability of AV speech. Behaviourally, we found that words with non-labial initial phonemes are discriminated from noise more accurately than non-labial words, while AV enhancement was greater for labial words, compared to non-labial words. Our behavioural results show that though older adults benefit more from AV speech in noisy settings compared to younger adults (see Chapter 4) this effect is not necessarily driven by the predictiveness of phonemes at word onset. Neurally, we found that visual predictability was reflected by late fronto-central negativity in older adults, but not in younger adults. However, we did not find evidence of an interaction between visual predictability and AV enhancement in terms of evoked activity, raising further questions about how visual predictability of speech is represented the brain’s electrophysiology.

Chapter 6 Discussion

This thesis aimed to address questions in two distinct areas of research in ageing and cognitive neuroscience. Firstly, given that the pre-stimulus state of cortical oscillations had been shown to predict behavioural and neural responses, we addressed the question of whether pre-stimulus oscillatory mechanisms change or remain consistent in the ageing brain. Secondly, previous research had shown that AV speech influences the amplitude and latency of evoked activity. Our research addressed the questions of whether/how AV enhancement and visual predictability of AV speech is represented in evoked activity in noisy listening conditions, and whether such EEG signatures remain stable with age.

In Chapter 3 we investigated the consistency of how pre-stimulus activity influences auditory frequency discrimination performance in young and older participants. In both groups the power of pre-stimulus activity influenced the encoding of sensory evidence reflected by early evoked components, while the phase influenced choice formation in later-activated EEG components. Importantly, for the early EEG components we did not find evidence for a systematic difference in the time scales of the perceptually relevant pre-stimulus activity. In the later-activated EEG component we found a trend for perceptually relevant rhythmic activity to arise from slower frequencies in the ageing brain. At the same time our data replicate previous findings of a significant age-related slowing of AEP latency, modulations of AEP amplitudes, and a flattening of the spectral profile of EEG activity.

In Chapter 4, we investigated the consistency of behaviour and evoked activity underlying AV speech integration in a speech-in-noise discrimination task in younger and older adults. Behaviourally, younger and older adults performed comparably. Performance was greater for AV_{inf} speech compared to AO_{inf} speech across groups and noise levels, and was poorer at low noise levels. AV enhancement was greater in high noise levels, across all participants, and older adults derived greater AV enhancement compared to younger adults (an effect that was consistent across noise levels). In terms of visual predictability, we found that behaviourally, word discrimination performance was greater for target words with non-labial initial phoneme, compared to labial initial phonemes. Furthermore, we found that AV enhancement was greater for labial target words, compared to non-labial target words, and was consistent across age groups. Neurally, we found that AV enhancement is represented by a centro-parietal P3-like activity in older adults and an N4-like fronto-central activity in younger adults, but found that this activity did not correlate with behavioural AV enhancement. Our results point to distinct patterns of late evoked activity underlying AV enhancement between younger and older adults, possibly representing distinct cognitive (memory) strategies in predicting upcoming target stimuli. At the same time our data replicate previous findings of a significant age-related slowing of AEP latency, modulations of AEP amplitudes, and a flattening of the spectral profile of EEG activity.

In Chapter 5 we investigated the consistency of evoked activity underlying the visual predictability of AV speech. We found that visual predictability was reflected by late fronto-central negativity in older adults, but not in younger adults. However, we did not find evidence of an interaction between visual predictability and AV enhancement in terms of evoked activity, raising further questions about how visual predictability of speech is represented the brain's electrophysiology. Our results point to distinct patterns of late evoked activity underlying visual predictability of visual speech, again possibly reflecting differential strategies in predictive coding.

6.1 Oscillatory activity

6.1.1 Pre-stimulus influences on perception remain consistent in ageing

In Chapter 3we investigated the consistency of how pre-stimulus activity influences auditory frequency discrimination in young and older adults. We found that in both age groups, perceptual performance was reliably influenced by oscillatory activity prior to the presentation of the task-relevant stimuli. This is consistent with a body of literature showing that pre-stimulus oscillatory brain activity can influence perception (Florin et al., 2017; Henry et al., 2014; Henry & Obleser, 2012; Iemi et al., 2017; S. J. Kayser et al., 2016; Ng et al., 2012; Pinheiro et al., 2017; Samaha et al., 2017; Samaha & Postle, 2015; VanRullen, 2016).

Furthermore, we replicate our previous finding delineating two mechanisms by which pre-stimulus oscillatory activity influences auditory pitch perception (S. J. Kayser et al., 2016). We found that oscillatory power of low frequency, alpha, and beta band activity shaped the encoding of task-relevant sensory information in early EEG components, likely reflecting emerging from auditory cortical networks. Additionally, the phase of alpha band activity influenced behavioural choice in a later-activated fronto-parietal EEG component. Therefore, we find that that multiple and distinct rhythmic processes control perceptual decisions and suggest that the relevant time scales of neural activity are largely conserved along the life span. Furthermore, our results demonstrate that the relation of pre-stimulus brain activity and perception is not mandatorily affected by a general increase in neural response latencies with age.

Furthermore, we observed that alpha phase influences sensory evidence in the late EEG component, but only in older adults. This component was not significantly related to behavioural choice, however it may suggest that in the elderly subjects the encoding of the task-relevant sounds in fronto-parietal regions was affected by a reduced attentional commitment (Henry et al., 2017; Strauss et al., 2015; Wostmann et al., 2015; Wöstmann et al., 2016). Support for this interpretation comes from research showing that enhanced alpha power is reflective of reductions in attention (Thut et al., 2012; Wöstmann et al., 2016) and of stronger selection of sensory evidence through the modulation of cortical excitability in sensory areas (Iemi et al., 2017; C. Kayser et al., 2015; Strauss et al., 2015), and that alpha power has been shown to increase with decreased acoustic reliability and thus may reflect compensatory mechanisms engaged due to more challenging listening conditions (Becker et al., 2013; Henry et al., 2017; McMahon et al., 2016; Obleser et al., 2012; Obleser & Weisz, 2012; Scharinger et al., 2014; Steinmetzger & Rosen, 2017; Wostmann et al., 2015). Furthermore, behavioural studies show that older adults tend to find difficulty in controlling attention (H. Meister et al., 2013; Passow et al., 2014) and ignoring irrelevant stimulus information (Chao & Knight, 1997; de Villers-Sidani et al., 2010; Gazzaley et al., 2005; Rossi-Katz & Arehart, 2009; Tun et al., 2002). Therefore, the differences we observe in the relationship between alpha band activity and the encoding of sensory information may be reflective of age-related differences in strategies used in parsing a noisy acoustic scene at sensory and cognitive levels, in light of age-related attentional decline (McGovern et al., 2018).

6.1.2 Oscillatory frequency changes with age

In Chapter 3 we reported age-related consistencies in two oscillatory mechanisms by which pre-stimulus influences perception: the power of low frequency, alpha, and beta band activity shaped the encoding of task-relevant sensory information in early EEG components, while the phase of alpha band activity influenced behavioural choice in a later-activated fronto-parietal EEG component. In the early-activated ("auditory") EEG component we observed no significant differences in peak frequencies between younger and older adults. However, we observed a trend in which oscillatory frequency was more variable and shifted more towards lower peak frequencies in older adults, though this shift was not found to be statistically significant. Together, these results suggest that though pre-stimulus influences on auditory pitch perception remain consistent between younger and older adults, they may be more variable as we get older for processes involving higher-level cognitive processes (McGovern et al., 2017; Sander et al., 2012; Zanto & Gazzaley, 2014).

Furthermore, in Chapter 3 and Chapter 4 we found that the spectral profile of ongoing EEG activity was significantly flatter in the older participants. This fits with previous studies reporting age-related reduction in power spectral density slopes (Tran et al., 2016; Voytek et al., 2015). Spectral flattening possibly occurs due to a decreased neuronal synchrony (Podvalny et al., 2015; Pozzorini et al., 2013; Voytek & Knight, 2015; Waschke et al., 2017), increased spontaneous activity (S. L. Hong & Rebec, 2012), or changes in the balance of inhibitory-excitatory neuronal function (Caspary et al., 2008; R. Gao et al., 2017). It has been reported that spectral flattening is a mediator of cognitive decline (Tran et al., 2016; Voytek et al., 2015). This is supported by studies which have found that alpha and theta activity are engaged differentially in the younger and older adult brain, both in cognitive performance and at rest (Cummins & Finnigan, 2007; Hartikainen et al., 1992; Kardos et al., 2014; Karrasch et al., 2004; McEvoy et al., 2001; Polich, 1997; Tóth et al., 2014; Vlahou et al., 2014; Volf & Gluhih, 2011; Widagdo et al., 1998). In both Chapter 3 and Chapter 4, participants passed a battery of cognitive assessments, testing a wide range of cognitive abilities including reasoning, attention, working memory, abstraction, orientation, and language. Therefore, our finding of an age-related spectral flattening does not reflect cognitive decline but rather compensatory mechanisms or changes in cellular physiology. Support for the latter comes from research showing that pathological changes such as the amyloid plaques and neurofibrillary tangles (Braak & Braak, 1991), and changes in cerebral blood flow (Beason-Held et al., 2013) can occur before the behavioural manifestations of cognitive decline.

6.2 Latency and amplitude of early evoked activity

In Chapter 3 and Chapter 4, we investigated the effects of ageing on the latency and amplitude on the P1-N2-P2 components of auditory evoked activity in response to background noise onset. In Chapter 3 we found that older adults' P1 and N1 component amplitudes were significantly larger compared to younger adults, yet their P2 peaks were reduced, whereas in Chapter 4, we only found an age-related suppression of the N1 peak amplitude. In both Chapter 3 and Chapter 4, we report an age-related slowing of the N1 and P2 peak latencies.

Our results in Chapter 3 are consistent with previous research which have observed enhanced P1 and N1 components in older adults, compared to younger adults (Anderer et al., 1996; Harkrider et al., 2005; Tremblay et al., 2003). Increases in ERP amplitude with age could be explained by an age-related reduction in inhibitory processes stemming from reduced GABA activity (Caspary, Milbrandt, & Helfert, 1995; Caspary, Ling, Turner, & Hughes, 2008; Caspary, Schatteman, & Hughes, 2005; de Villers-Sidani et al., 2010; Hughes, Turner, Parrish, & Caspary, 2010). Our findings in Chapter 4 of an age-related suppression of N1 peak amplitude is not consistent with this literature, however N1 suppression has been found in response to unattended, compared to attended, acoustic stimuli (Giard, 2000; Hillyard & Kutas, 1983; Näätänen, 1992). Therefore, age-related N1 suppression could be reflective of greater, or more effortful, suppression of background noise in older adults.

The ageing profile of the P2 component remains less clear, with reports of both enhancement (Amenedo & Díaz, 1998, 1999; Pfefferbaum et al., 1980) and diminution (Czigler et al., 1992; Henry et al., 2017; Rufener et al., 2014) with age. Furthermore, Anderer et al., (1996) report a non-linear relationship between P2 amplitude and age, with enhancement until around 60 years of age and diminution thereafter. In Chapter 3 we found an age-related reduction in P2 amplitude, which could be explained by changes in attentional control. Like the N1 component, the auditory P2 component has been shown to vary with attentional control and is reflective of the listeners' ability to filter irrelevant information (Crowley & Colrain, 2004; Lister et al., 2011; Rufener et al., 2014). Given that the AEP we investigated was in response to background noise (i.e. the stimulus to be ignored), it is possible that the age-related P2 modulation we observed is due to age-related differences in selective attention (Chao & Knight, 1997; Gazzaley et al., 2005; H. Meister et al., 2013; Passow et al., 2014; Tun et al., 2002).

As the brain ages cognitive and neural processes become slower (Bieniek et al., 2013; Price et al., 2017; Salthouse, 1996), resulting in N1 and P2 evoked responses that are typically delayed (Anderer et al., 1996; Bertoli et al., 2005; Harkrider et al., 2005; Harris et al., 2007; Henry et al., 2017; Pfefferbaum et al., 1980; B. Ross et al., 2007; Tremblay et al., 2002, 2003) in the aged brain. In Chapter 3 and Chapter 4, in concordance with these results, we also found that N1 and P2 components were significantly delayed in older adults, compared to younger adults. Age-related delays in auditory neural processing have been attributed to grey matter degeneration in A1 (Price et al., 2017), while declining hearing abilities have been attributed to functional changes such as poorer frequency tuning in A1 (Caspary et al., 2008; de Villers-Sidani et al., 2010; Kamal et al., 2013; J. G. Turner, 2005), desynchronized spiking (de Villers-Sidani et al., 2010; Kamal et al., 2013), and reductions in GABA (Burianova et al., 2009; F. Gao et al., 2015; Ling et al., 2005). Thus, delays in auditory evoked activity is likely a result of structural and/or functional changes in the ageing auditory pathway.

6.3 AV speech processing

6.3.1 AV influences on behavioural performance

Behaviourally, we observed significantly greater performance for visually informative stimuli across participants, with older adults showing significantly greater improvement in performance for audio-visually informative stimuli compared to acoustically informative stimuli. Since the degree of AV enhancement does not correlate with cognitive status, and that our participants had only mild age-related impairment in hearing and visual capabilities, the behavioural AV enhancement observed in older adults is likely due to compensatory strategies in AV speech perception rather than as a result of cognitive or sensory impairment. We also observed significantly poorer performance for high noise conditions compared to low noise across participants, and a greater difference between information conditions when there is high noise compared to low noise. Lastly, we found that the interaction between noise and information condition was consistent across age groups. Previous literature shows discrepancies in whether ageing has an influence on AV enhancement. Some studies have found that AV enhancement is greater in older adults than in younger adults, which is consistent with our findings (Maguinness et al., 2011; Sekiyama et al., 2014); however, other studies have shown that AV enhancement remains stable with age (Gordon & Allen, 2009; Sommers et al., 2005; Winneke & Phillips, 2011). Our results are also in accordance with research which has shown that visual gain increases as SNR decreases (L. A. Ross et al., 2007).

In terms of the visual predictability of audio-visual speech, we found that word discrimination accuracy was greater for target words with non-labial onset phonemes, compared to target words with labial-onset phonemes. We also found that, across age-groups, behavioural AV enhancement varied as a function of visual predictability, wherein AV enhancement was greater for labial target words, compared to non-labial target words. However, we unexpectedly found poorer performance in discriminating target words with labial initial phonemes. Lastly, we observed that the influence of visual predictability on behaviour was consistent as a function of listening difficulty (noise level), and this effect was stable across information conditions and age groups. In a predictive coding framework, it has been hypothesised that (audio-) visual enhancement occurs when visual speech can reduce the uncertainty of upcoming voiced stimuli through lexical or semantic priming (Peelle & Sommers, 2015; van Wassenhove et al., 2005). Therefore, our finding of greater AV enhancement for words with labial onset phonemes, compared to non-labial onset phonemes, is in accordance with this view. However, our finding of poorer overall discrimination of words with labial onset phonemes conflicts with this hypothesis and might be explained by differences in methodological approaches between the current research and previous literature. For example, lip reading abilities can influence the accuracy of AV speech perception (Auer & Bernstein, 2007; Bernstein et al., 2000), and was not assessed in the current research. Furthermore, we assume that the target word onset phoneme is the more task-relevant phonetic feature of the stimuli, which might not be the case considering previous research has found that some phonetic features are best discriminated at the end of utterances (van Son et al., 1994). Lastly, our finding of stability in the influence of target word visual predictability on AV enhancement between age groups conflicts with the predictive coding framework. However, this is unsurprising considering the discrepancies of reports of age-related differences in AV enhancement (Gordon & Allen, 2009; Maguinness et al., 2011; Sekiyama et al., 2014; Sheldon et al., 2008; Sommers et al., 2005).

In multisensory research, Bayesian probability models have been used to estimate the combination of multiple sensory inputs in multisensory environments. The linear cue combination model estimates an optimal linear combination of the cues based on their precision. Research diverges on whether age-related differences exist in the weighting of sensory cues, with some studies reporting similar weighting between younger and older adults (Braem et al., 2014; Brooks et al., 2015) while others report impaired weighting (Bates & Wolbers, 2014) or differential reweighting strategies wherein older adults place increasing weight on visual information (Alberts et al., 2019). We found that visually informative AV stimuli led to enhanced discrimination of speech-in-noise, compared to auditory-only informative AV stimuli, and we found that this enhancement was greater in older adults, compared to younger adults. Within a cue-combination framework, this suggests that informative visual information might be weighted more in the presence of degraded auditory input across age groups, and that older adults might weight informative visual information even more than younger adults. However, as we did not employ Bayesian modelling in our analysis approach, future research should test this objectively.

In the current research, any potential age-related differences in sensory cue-weighting should be a result of age-related differences in the cue-weighting processes themselves, rather than as a result of declining sensory or cognitive processes. Controlling for perceptual threshold between age groups has been shown to result in different cue-weighting strategies in older adults, compared to when the same physical stimuli is presented to both age groups (Brooks et al., 2015). To eliminate differences caused by sensory decline, our participants passed a battery of auditory and visual acuity tests and we controlled for perceptual threshold by scaling task difficulty (SNR) around participants' 70% correct speech-in-noise thresholds. Furthermore, ineffective cue weighting in older adults has been suggested to be due to an increase in sensitivity to irrelevant sensory information (Hugenschmidt et al., 2009). In Chapter 4 and Chapter 5, our participants passed a battery of cognitive tests which included measures of attentional capacity (e.g. MoCA and D2 test of attention). Taking all of this together, we can reasonably assume that any age-related differences in sensory cue-weighting, as reflected in age-related differences in AV enhancement, are a result of differences in cue-weighting processes themselves.

Causal inference models estimate multisensory integration via a weighted average of an estimate assuming that sensory cues are generated by the same source and an estimate assuming that sensory cues are generated by independent sources (Körding et al., 2007). Age-related differences in perception have been reported in situations involving temporal order judgement. For example, older adults have wider multisensory temporal binding windows (Bedard & Barnett-Cowan, 2016; Stevenson et al., 2018), are more susceptible to multisensory illusions dependent on temporal tracking (Bedard & Barnett-Cowan, 2016; De Boer-Schellekens & Vroomen, 2014; Hirst et al., 2018), and explicit judgments of temporal order (Bedard & Barnett-Cowan, 2016). Age-related differences in causal inference have been attributed to sensory decline (Jones et al., 2019; Hame Park et al., 2020) and changes in cognitive function (Allred et al., 2016; Cao et al., 2019; Dobreva et al., 2012; Körding et al., 2007; Hame Park & Kayser, 2019; Rohe & Noppeney, 2015; Wozny & Shams, 2011). Any differences in causal inference in the current study would be with regards to binding the auditory stimuli of the actor's voice together with the visual stimuli of the actor's face. Since, audio-visual speech perception is facilitated by wider temporal binding windows in older adults (Bedard & Barnett-Cowan, 2016; De Boer-Schellekens & Vroomen, 2014; Hirst et al., 2018; Stevenson et al., 2018), it is possible that that the behavioural (and neural) gains we observe, and the age-related differences we report, are correlates of increased temporal binding windows. However, as we did not systematically vary the temporal order of the auditor and visual stimuli, we cannot objectively confirm this.

6.3.2 AV influences on Neural Processes

In Chapter 4, we investigated the consistency of evoked activity underlying AV speech integration in noisy listening conditions. In comparing younger versus older adults, across all trials, we observed a negative difference in EEG amplitude over fronto-central channels, and a positive difference at posterior channels at 360 ms to 520 ms. Our results also revealed a significant negative difference between younger and older adults in the evoked activity representing the difference between AV and AO conditions (AV enhancement) at 265 ms to 420 ms over central channels. Further investigation into this effect revealed AV-related attenuation of the signal over fronto-central channels in younger adults between 360ms and 420 ms, and enhancement over central channels between 255 and 425 in older adults.

In Chapter 5we aimed to extend these findings by investigating whether evoked activity underlying the visual predictability of AV speech differed between age groups. We found that visual predictability of the initial phoneme of AV speech was reflected by negative evoked activity over frontal channels between 345 ms and 380 ms, across all participants. In comparing neural visual predictability between younger and older adults, we found that younger adults show more positive activity over frontal channels between 245 ms and 315 ms. Younger adults do not exhibit a significant effect of visual predictability (labial vs. non-labial contrast), whereas older adults have more negative activity over fronto-central channels between 260 ms and 380 ms. We did not find evidence that neural AV enhancement varies as a function of visual predictability in either age group. The following subsections explore how these results from Chapter 4 and Chapter 5 fit within the current ageing literature.

6.3.2.1 AV enhancement and visual predictability in late evoked activity

Previous studies have reported suppressed and earlier N1–P2 peak latencies and/or amplitudes in AV conditions (Alsius et al., 2014; Baart, 2016; Baart et al., 2014; Frtusova et al., 2013; Ganesh et al., 2014; Kaganovich & Schumaker, 2014; Klucharev et al., 2003; Stekelenburg & Vroomen, 2007; Treille et al., 2014; van Wassenhove et al., 2005). Furthermore, there is evidence of an age-related potentiation of the N1 (Frtusova et al., 2013) and P2 peak (Winneke & Phillips, 2011) and reduction in latency of the N1 peak (Frtusova et al., 2013; Winneke & Phillips, 2011, 2009). Therefore, our finding that age group contrasts in evoked activity reflecting AV enhancement, and visual predictability of speech, emerge at longer latencies, with the earliest significant effect reported at 245 ms and the latest at 520 ms. As discussed in Chapter 4 and Chapter 5, our main aim was not to investigate the existence of evoked potentials at certain latencies, but instead to examine whether contrasts in evoked activity existed between variables of interest (age groups, information condition, noise level, and articulation type). Thus, that we do not observe significant contrasts in early AEPs does not suggest that they do not exist, but instead are consistent between the groups/conditions being compared.

In Chapter 4 we found that AV enhancement was reflected by negative activity between 306 ms and 420 ms in younger adults, and by positive activity between 255 ms and 425 ms in older adults. These patterns of activity are consistent with P3-like activity and with previous research which demonstrate AV influences on late ERP components such as the P3 (Andres et al., 2011; Hernández-Gutiérrez et al., 2018; Hessler et al., 2013; Irwin et al., 2017, 2018; Starke et al., 2017; Stekelenburg et al., 2018) and N4 (Duncan et al., 2009; Kaganovich et al., 2016; Lebib et al., 2004; Van Petten et al., 1999) components. There is evidence that the P3 component is an index of processes involved in mapping incoming sensory information onto internal representations in working memory (Polich, 2012), and of decision-making (Dully et al., 2018). In AV paradigms, the P3 peak amplitude is suppressed in response to congruent AV stimuli in comparison to incongruent AV stimuli (Andres et al., 2011; Stekelenburg et al., 2018), and in comparison to AO stimuli (Hernández-Gutiérrez et al., 2018; Hessler et al., 2013; Irwin et al., 2018, 2017; Starke et al., 2017). The P3 amplitude is also sensitive to changes in working memory load (Segalowitz et al., 2001). Therefore, our finding that AV enhancement-related, and visual predictability – related, positivity in older adults possibly represents cognitive processes involved in mapping sensory information onto internal representations in working memory. The N4 component is believed to index the mapping of sensory input to contextual representations (for review see Duncan et al., 2009) in semantic processing, and is sensitive to semantic cloze probability (Kutas & Federmeier, 2011). The N4 peak is enhanced when AV stimuli is incongruent; an effect which has been shown for phonetic (Lebib et al., 2004), lexical (Kaganovich et al., 2016), and semantic congruence (Van Petten et al., 1999). Therefore, our finding that AV enhancement – related negativity in younger adults possibly represents cognitive processes involved in mapping of sensory input onto contextual representations in semantic memory.

6.3.2.2 Topography of late evoked activity

Support for differential strategies reflecting predictive coding between age groups comes from our finding of age-related differences in scalp topography of activity underlying AV enhancement and visual predictability. In younger adults, AV enhancement-related negativity had a fronto-central scalp distribution (Chapter 4), while in older adults both AV enhancement-related (Chapter 4) and visual predictability-related positivity (0) were centro-parietally distributed.

In younger adults we observe AV-related negativity over anterior sites. This differs from the canonical central topography of the N4, however there are reports of a frontal N4 response in lexical priming (Coulson et al., 2005), and in tasks engaging recognition memory (for review see Kutas and Federmeier, 2011), wherein N4 amplitude scales with word familiarity (Curran, 2000). In older adults we observe AV-related positivity over centro-parietal channels, which is in line with the canonical P3 topography. Furthermore, that we observe differences between younger and older adults in AV-enhancement and visual predictability-related evoked activity could also be attributed to age-related compensatory mechanisms.

In Chapter 4 and Chapter 5 we observed symmetrical scalp topographies for AV enhancement and visual predictability-related evoked activity in both younger and older adults. We also observed an age-related anterior to posterior shift in topography along the coronal plane. These results are inconsistent with the HAROLD model of compensatory patterns of neural recruitment in the ageing brain. The HAROLD model suggests that an increase in bilateral recruitment of pre-frontal brain regions acts as a compensatory mechanism in neurocognitive decline. For example, an age-related reduction in specificity has been found in in the fusiform face area during face processing tasks (Burianová et al., 2013; Zebrowitz et al., 2016). In auditory speech perception, older adults do not show the same hemispheric specificity typical in younger adults in the processing of slowing changing speech cues (Keller et al., 2019). Much of this research has measured neural activity using fMRI, however there is evidence of HAROLD-like shifts in the topography of early evoked activity (the N1-P1 complex) underlying speech perception (Bellis et al., 2000). Since we observed age-related differences in evoked activity profiles at later latencies, we interpret our results in terms of age-related differences in late semantic processing. There is evidence that semantic processing itself might not follow a HAROLD trajectory, and instead might follow a trajectory along the coronal plane (M. T. Diaz et al., 2014; Methqal et al., 2017). Therefore, it is unlikely that the age-related changes we observed in the scalp topography of AV enhancement and visual predictability of AV speech is a result of compensatory mechanisms under the HAROLD model.

The PASA model (Davis et al., 2008), on the other hand, describes a shift in neural recruitment along the coronal plane. Grady et al. (1994) observed an age-related recruitment of the pre-frontal cortex in response to reduced activity in the visual cortex due to the decline of sensory processing functions in the occipital and temporal cortices. However, these effects are not limited to visual processing, but have also been observed in tasks involving attention (Cabeza et al., 2004; Madden et al., 2002) , working memory (Grossman et al., 2002; Rypma & D'Esposito, 2000), and episodic memory (N. D. Anderson et al., 2000; Cabeza et al., 1997, 2004; Daselaar et al., 2003; Dennis et al., 2007; Grady et al., 2002; Madden et al., 1999). While the PASA model has been investigated mostly in studies investigating cognitive function itself, there is evidence of PASA in speech and multisensory processes. In a speech-discrimination-in-noise paradigm, Wong et al. (2009) found reduced auditory cortex activity and increased pre-frontal and pre-cuneus activity in older adults when compared with younger adults, particularly in the noisiest listening conditions. They found that age-related increases in frontal brain regions was positively correlated with behavioural accuracy, suggesting that such activity is reflective of compensatory mechanisms supporting perception. Furthermore, Diaconescu et al. (2013) found that the detection of semantically congruent multisensory events resulted in increased activity in parietal and medial pre-frontal brain areas 100 ms following stimulus onset exclusively in older adults. The age-related increase in activity in these areas was predictive of faster behavioural detection of the multisensory events and was mediated by age-related decreases in pre-frontal grey matter volume. Therefore, PASA compensatory mechanisms in multisensory integration could be a result of reductions in pre-frontal grey matter integrity.

Though the shifts in topographies we observed along the coronal plane are in the opposite direction to the PASA model, our results are in accordance with the findings of Nyberg et al. (2010), who found an age-related under-recruitment of frontal regions during a semantic categorisation task when participants were tested longitudinally. Furthermore, Morcom and Henson (2018) found that increased pre-frontal activation was not reflective of supportive, compensatory mechanisms, but rather a reflection of reduced specificity and reduced efficiency in frontal neural processes in both short-term memory maintenance and long-term memory encoding functions. This suggests that the PASA model, on its own, might not fully represent the full extent and function of age-related shifts in neural activity along the coronal plane, and does not fully consider the task-dependent nature of this mechanism. Indeed, the CRUNCH model posits that compensatory activity is only of benefit to older adults when cognitive load is kept low, and becomes less effective with increasing cognitive load (Reuter-Lorenz & Cappell, 2008). This suggests that there is a limit to the benefit of compensatory neural recruitment can afford, which is bound by age-related changes in cognitive capacity.

6.4 Modelling age-related cognitive and neurobiological changes

One question that arises from this discussion on age-related differences in the neural correlates of cognitive processes in predictive coding is how do these findings fit within the various theories of ageing? Several models have been suggested in an attempt to describe how ageing influences sensory, cognitive, neural processing.

Firstly, the common cause hypothesis argues that age-related changes in sensory and cognitive processes occur simultaneously and are attributable to wide-spread changes in the ageing nervous system (Baltes & Lindenberger, 1997; Christensen et al., 2001; Lindenberger & Baltes, 1994). Lindenberger and Baltes (1994) investigated the relationships between visual and auditory acuity and various measures of cognitive function (including perceptual speed, memory, fluency and reasoning functions). They found that visual and auditory acuity explained 93.1% of the age-related variance in intelligence. Furthermore, in a large sample study, Baltes and Lindenberger (1997) found that individual differences in cognitive function linked to sensory function increased from younger adulthood (25 to 69 years) to older adulthood (over 70 years). Additionally, the strength of the association between sensory functioning and measures of fluid intelligence increased with age. More recently, Olderbak et al. (2015) found that visual acuity and self-reported physical health are related to performance in face-matching and face-memory tasks. Furthermore, they found that a common factor explained some of the age-related variance in these measures, and that the relationship between visual acuity and physical health could be explained by fluid cognition. The precise common cause of shared variance of sensory and cognitive functions in ageing remains under investigation and may be task dependent. Studies have suggested that the common cause is the ageing of a physiological process or set of processes (Baltes & Lindenberger, 1997; Lindenberger & Baltes, 1994), of the central nervous system (Anstey et al., 1997), or of general physiology (Anstey & Smith, 1999). In considering the current thesis, the participants that were recruited for each study were screened for impaired hearing, vision, and cognitive function. The data analysed in Chapter 3, Chapter 4, and Chapter 5 were derived from participants who passed the screening, thus resulting in older adult samples which had no significant sensory or cognitive impairments, and which were homogenous with respect to these domains. Furthermore, our sample of participants may have had a particularly high cognitive and/or neural reserve and were thus less susceptible to the effects of ageing on sensory, cognitive and neural processes (Kaup et al., 2011). In Chapter 3, we found no evidence of an association between AV enhancement and cognitive status, nor evidence of associations amongst cognitive measures, however in this thesis we were limited in being able to fully investigate whether any age-related differences in behavioural and neural metrics were associated with sensory acuity or cognitive function, as per the common cause hypothesis, due to the homogeneity of sensory and cognitive function within our samples.

Secondly, there are models which argue that reduced quality and/or quantity of sensory input, through reduced sensory acuity, has a knock-on declining effect on cognition (sensory deprivation hypothesis and information degradation hypothesis). In support of the information degradation hypothesis, studies have shown that memory for auditory language is poorer when the auditory stimulus is degraded, compared to when the stimulus is heard clearly. For example, McCoy et al. (2005) compared the recall of spoken words presented within sentences of varying approximation to English, in a running memory task, between older adults with good hearing and those with mild to moderate hearing loss. Older adults with poorer hearing recalled fewer non-final words than those with good hearing, despite performing comparably when recalling the final 3 words of the sentences. This implies that age-related changes in peripheral hearing processes can create higher cognitive load in terms of long-term memory function. In younger adults, Piquado et al. (2010) found that masking spoken words with noise not only impaired the recall of the masked words, but also words presented prior to the masked words. The authors argue that degradation disrupts working memory processes whereby associative links between words are weakened, thus reducing working memory capacity. However, studies have also shown that older adults show an overall poorer recall of spoken words, even when perceptual performance is equated between age groups (Murphy et al., 2000; Schneider et al., 2002).

In all studies within this thesis, participants were required to discriminate acoustic targets embedded within masking noise. It is possible that the age-related differences we observe in each study are a result of differential compensatory mechanisms recruited to support the processing of degraded sensory information. In Chapter 3, participants discriminated the pitch of tones embedded within a noisy cacophony, and while we found that while the ways in which pre-stimulus oscillatory activity influences behavioural choice remained consistent across age groups, there were age-related differences in the oscillatory frequency bands within which these influences operated, namely a shift from alpha/beta activity towards the lower frequency bands. Since alpha activity is often inversely related to signal intelligibility, differential engagement of neural resources within alpha band activity might reflect distinct strategies used to process the noisy stimuli by each age group (Becker et al., 2013; Henry et al., 2017; McMahon et al., 2016; Obleser et al., 2012; Obleser & Weisz, 2012; Scharinger et al., 2014; Steinmetzger & Rosen, 2017; Wostmann et al., 2015). In Chapter 4 and Chapter 5, participants discriminated audio-visual target words embedded within multi-talker babble noise, and we found age-related differences in behavioural and late evoked measures of AV enhancement (Chapter 4) and visual predictability (0) of AV speech. Based on the differences in polarity and latency of evoked activity between age groups, we attribute these differences to the engagement of differential strategies of predictive coding, based on distinct, age-differential memory processes, in attempting to reduce the uncertainty of upcoming stimuli (Andres et al., 2011; Duncan et al., 2009; Hernández-Gutiérrez et al., 2018; Hessler et al., 2013; Irwin et al., 2017, 2018; Kaganovich et al., 2016; Lebib et al., 2004; Starke et al., 2017; Stekelenburg et al., 2018; Van Petten et al., 1999).

Evidence in support of the sensory deprivation hypothesis, however, is more scarce. Humes et al. (2013) computed several principal components factor analyses on a variety of psychophysical measures (threshold sensitivity, gap detection, temporal order identification, and temporal masking across multiple sensory domains) and cognitive tasks (via the Wechsler Adult Intelligence Scale). The authors found that age, a component reflecting global sensory processing, and a component reflecting global cognitive function were correlated; however, the correlation between age and global cognitive function disappeared after controlling for global sensory processing. Structural equation modelling confirmed global sensory processing as a mediator of age-related changes in global cognitive function. Since all participants had good sensory acuity and since task difficulty in all experimental tasks were scaled to participant's 70% correct thresholds, we cannot conclude that age-related differences in behavioural or neural metrics are due to degraded sensory input as a result of reduced sensory acuity, as per the Sensory Deprivation hypothesis.

Lastly it has been suggested that deterioration of cognitive abilities influences sensory processing via top-down control (cognitive load on perception hypothesis); however, there is little evidence of this in an ageing population. In a longitudinal study, Kiely et al. (2012) tested older adults', aged 50 years and over, hearing thresholds four times over a period of 11 years. They found that age and cognitive impairment, along with hypertension and baseline age, were significant, independent predictors of the rate of decline in hearing threshold. Despite the lack of evidence in the older adult population, several studies have demonstrated an influence of cognitive load on perception. Another study investigated age-related differences in the perception of foreign-accented speech and its underlying cognitive processes (Ingvalson et al., 2017). Younger and older adult participants judged which of two presented spoken phrases was the most accented, and their cognitive status was measured via a battery of tests assessing auditory working memory, processing speed, task-switching, receptive vocabulary and inhibitory control. Overall, older adults' performance was poorer in discriminating accents compared to younger adults, and further age-related differences were found in the cognitive processing strategies involved in the perception of foreign-accented speech. While younger adults' accent-discrimination accuracy was found to be associated with a main effect of working memory and an interaction between auditory acuity and processing speed, older adults' performance was associated with a main effect of working memory and interactions between hearing acuity and cognitive flexibility and between hearing acuity and inhibitory control. In studies focussing on younger adults, increasing working memory demands often leads to impairments in speech perception (Chiu et al., 2019; Hunter & Pisoni, 2018; Mitterer & Mattys, 2017), training to improve working memory capacity has shown to improve speech perception-in-noise (Ingvalson et al., 2015).

In relation to the current thesis, since all analysed data were derived from participants with good cognitive function, we cannot make any objective conclusions regarding the influence of cognitive decline on sensory processing. It is possible that age-related differences in oscillatory (Chapter 3) and evoked signatures (Chapter 4 and Chapter 5) of auditory/audio-visual perception-in-noise is reflective of top-down influences on perception. Thus, the same argument that could be made regarding the information degradation hypothesis, could be made regarding the cognitive load on perception hypothesis. In the work contained in this thesis, is has not been possible to determine whether age-related differences in behavioural and neural measures of auditory and audio-visual perception are reflective of mechanisms supporting the processing of degraded sensory information or those supporting the deficits resulting from declining cognitive function. For example, in Chapter 4 and Chapter 5, we describe age-related differences in the neural correlates of AV enhancement and the visual predictability of speech. We attribute these differences to the engagement of differential strategies of predictive coding in attempting to reduce the uncertainty of upcoming stimuli. Predictive coding theorizes that top-down processes generate mental models in order to make predictions about the nature of upcoming stimuli, while bottom-up processes feedforward prediction errors to update these models (Friston, 2018; R. P. N. Rao & Ballard, 1999). Within this framework it is possible that there is an interplay between models that suggest that degraded sensory information influences cognitive and neural processing and models that suggest that changes in top-down processing influences sensory encoding. Declining sensory acuity would, theoretically, result in the collection of less reliable sensory evidence on which prediction error would be assessed. Declining top-down processes may either generate less accurate models and would thus return greater prediction error, or may engage additional cognitive and neural resources in an attempt to reduce prediction error. Future research should attempt to delineate these processes and assess their relative contribution to age-related differences in AV speech processing.

6.5 Limitations

In this thesis we screened our older adults participants for signs of mild cognitive impairment, as well as declines in visual and auditory acuity. This was done in an attempt to ensure that these participants could be considered under the umbrella of healthy ageing. However, healthy ageing cannot always be guaranteed as dementia-related pathology can be present without showing any behavioural or cognitive symptoms (Beason-Held et al., 2013; Braak & Braak, 1991). Furthermore, some degree of sensory, cognitive and neural decline is to be expected with age, and thus screening out individuals who do not perform comparably to younger adults may then result in an older adult sample that is not representative of the wider population. Individual differences in cognitive reserve have been reported, however several predictive factors (and thus risk factors for age-related dementia) include lifestyle (Scarmeas & Stern, 2003), education (Farfel et al., 2013), and occupational complexity and attainment (Boots et al., 2015; Ghaffar et al., 2012). The majority of our older adult participants were highly educated, having attained some form of further or higher education (Scottish Higher National Certificate/Diploma, or undergraduate degree), and approximately one quarter of our older sample had attained a postgraduate qualification (masters degree or PhD). All participants were in good physical and mental health at the time of taking part. Therefore, our older adults sample is unlikely to be fully representative of the wider population of older adults in Scotland demographically. Specifically, due to a higher-than-average educational attainment, our older sample may have had a higher neural and/or cognitive reserve compared to the typical older adult. However, the extent to which cognitive and neural reserve contributes to pre-stimulus influences on auditory pitch perception, or on differences in the latency and amplitude of evoked activity underlying AV speech perception, has yet to be determined.

As well as sampling bias, another limitation is that we only used cross-sectional designs across all experiments in this thesis. Therefore, cohort effects such as educational attainment and differences in lifestyle are not controlled for and therefore may pose as potential confounding variables. For example, individual differences in cognitive reserve may influence the compensatory strategies engaged in AV speech processing, for. Some discrepancies in findings have been found in comparing cross-sectional versus longitudinal designs. Nyberg et al. (2010) reported differential effects in the age-related recruitment of frontal regions in longitudinal versus cross-sectional designs. Together this suggests that longitudinal research is required to further investigate the influence of various lifestyle factors as potential confounds, as well as in replicating results found in cross-sectional designs.

There are also limitations imposed by our choice of neuroimaging technique. While EEG excels in its temporal resolution, its spatial resolution is very limited. Therefore, we are unable to precisely attribute any of the effects we report in this thesis to a specific location in the brain. This would be particularly useful in identifying which brain areas are specifically engaged in the early “auditory” and later “decision-making” components reported in Chapter 3. Furthermore, in being able to locate the source of evoked activity reflecting AV enhancement and visual predictability in Chapter 4 and Chapter 5 respectively, we would be able to assess more accurately whether and what kind of compensatory mechanisms are engaged. Also, we have not been able to assess whether our older sample displays evidence of dedifferentiation, which would be possible by localising brain activity to specific areas. An alternative approach which would make these investigations possible, would be to use neuroimaging techniques which have better spatial resolution such as fMRI or MEG. Notably, MEG shares a similar temporal resolution to EEG, but has greater spatial resolution.

Lastly, the spatio-temporal nature of EEG usually means that researchers must make a choice on whether to analyse channels (or a subset of channels) across the whole scalp, and thus carry out correction for multiple comparisons, or to analyse single (or group-averaged) channels, and thus make a priori assumptions on which channels best represent task-relevant activity. In Chapter 4 and Chapter 5, we use a whole-scalp approach meaning that it is possible that weaker effects existed in our analyses that did not survive multiple comparison correction. Weaker effects were lost may have been observed had the spatial dimension of the data been reduced. One approach which considers the whole scalp, but which eliminates the multiple comparison problem is to reduce the spatial dimension of the EEG data to a singleton dimension through a linear combination of EEG signals using LDA as we did in Chapter 3. This way we can derive a one-dimensional, single trial representation of cognitive function. Several studies have shown that information about sensory encoding and cognitive processing can be derived from such neural signals (Gherman & Philiastides, 2015; S. J. Kayser et al., 2016; McNair et al., 2019; Philiastides et al., 2014; Philiastides & Sajda, 2006). Applied to AV speech perception, this could be a promising method of extracting evoked activity which maximally separates information or articulation conditions, but it has yet to be applied to this field.

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