Ageing and multisensory integration:

A review of the evidence, and a computational perspective

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Abstract

The processing of multisensory signals is crucial for effective interaction with the environment, but our ability to perform this vital function changes as we age. In the first part of this review, we summarise existing research into the effects of healthy ageing on multisensory integration. We note that age differences vary substantially with the paradigms and stimuli used: older adults often receive at least as much benefit (to both accuracy and response times) as younger controls from congruent multisensory stimuli, but are also consistently more negatively impacted by the presence of intersensory conflict. In the second part, we outline a normative Bayesian framework that provides a principled and computationally informed perspective on the key ingredients involved in multisensory perception, and how these are affected by ageing. Applying this framework to the existing literature, we conclude that changes to sensory reliability, prior expectations (together with attentional control), and decisional strategies all contribute to the age differences observed. However, we find no compelling evidence of any age-related changes to the basic inference mechanisms involved in multisensory perception.

Keywords

Multisensory integration, multisensory perception, aging, computational models, Bayesian causal inference

1. Introduction

We exist in a world that is infinitely variable. Any object within it can be characterised according to a great number of properties: size, mass, position, velocity, transparency, temperature, elasticity, viscosity. It is only by estimating these properties that an organism can respond effectively to its environment. To this end, humans—like most other organisms—have evolved an array of senses with a variety of capabilities. Crucially, these senses do not operate in isolation, but combine with and complement each other. For example, our sense of hearing is generally sufficient for understanding another person's speech in a quiet room, but quickly becomes less useful as the environment becomes more challenging, such as in a noisy bar. In these cases, the addition of visual information (in the form of lip-reading) can make the difference between understanding your conversation partner and not (MacLeod & Summerfield, 1986; Schwartz et al., 2004; Sumby & Pollack, 1954). This process of combining multiple senses is referred to broadly as multisensory integration, and it is central to our ability to interact with the world around us.

Our central nervous system's ability to perform this process does not remain static across the lifespan (Murray et al., 2016). Older adults have been shown to perceive and respond to multisensory stimuli differently from younger people. For instance, they experience some multisensory perceptual illusions more frequently than younger control participants (Bedard & Barnett-Cowan, 2015; Chancel et al., 2018; DeLoss et al., 2013; Hirst et al., 2019). There is also evidence, based on race model analyses of response times, that older adults can sometimes receive greater benefits from multisensory signals (Laurienti et al., 2006; Peiffer et al., 2007). However, research to date has been mainly directed towards specific paradigms and phenomena (e.g. perceptual illusions), assessed across various sensory modalities and cognitive contexts. The aim of this review is to move beyond these phenomenological findings to develop an initial computational understanding of how ageing affects multisensory processing.

The review falls into two parts. In Part A, we review previous research relating to ageing and multisensory processing, organised by experimental paradigm. Please note that the intention of this review is not to provide an exhaustive account of multisensory processing research in ageing populations, but to outline key methodologies and findings (for other reviews of multisensory ageing research, please see e.g. Baum & Stevenson, 2017; de Dieuleveult et al., 2017; Freiherr et al., 2013). In Part B, we propose a computational framework that outlines formally the ways in which ageing might impact the computations involved in multisensory processing, briefly apply this framework to some of the existing literature outlined in Part A, and consider the limited but growing body of computational research on multisensory integration and ageing.

2. Part A: Review of previous research into multisensory integration and ageing

In this first part we summarise existing research into the effects of ageing on multisensory integration, grouped broadly into two experimental approaches. The first set of studies focuses on the integration of congruent signals. These studies assess multisensory integration in terms of faster responses (under speeded conditions) and/or greater accuracy (under unspeeded conditions). The second set of studies instead focuses on multisensory signals that are brought into conflict. Here, multisensory integration is assessed in terms of crossmodal biases (or perceptual illusions) that arise when conflicts between signals are small, or intersensory interference (e.g. longer response times) that is observed when conflicts are large.

2.1. Integrating congruent multisensory signals (multisensory enhancement)

One approach to investigating multisensory integration is to present participants with stimuli that are entirely congruent (at least for features that are task-relevant). In a spatial task, for example, the sound and flash will come from the same place; in a speeded detection task, all cues will appear simultaneously. In such paradigms, the measure of interest is the degree to which multisensory stimulus presentation improves performance, compared with unisensory signals presented in isolation (performance differences between congruent and incongruent stimuli are discussed later in the review). Here, we group these multisensory enhancement studies into two categories: those where the primary measure of performance is response speed, and those where the primary measure is accuracy.

2.1.1. Speeded paradigms (response time enhancement)

Response time enhancement paradigms assess the degree to which the synchronous presentation of two or more sensory signals improves response speed, compared to a unisensory signal presented alone. The stimuli used in these studies are usually suprathreshold, and they often use a classical redundant target approach in which simple unisensory (e.g. a flash of light or a beep) and multisensory (e.g. a simultaneous flash and beep) stimuli are presented at random intervals; observers are instructed to respond as quickly as possible to any stimulus, irrespective of sensory modality. Alternatively, an easy decision task, where response accuracy is near ceiling level for all participants (e.g. “indicate whether stimuli appeared on the right or left”), may also be used. Multisensory benefit in such paradigms can be quantified using a ‘race model’ (Colonius & Diederich, 2006; Miller, 1982) wherein the distribution of multisensory response times is compared to a distribution representing the fastest unisensory response times. If the multisensory distribution is faster than the unisensory distribution predicts, the race model is said to be violated, which is considered evidence of multisensory enhancement.

Older adults sometimes show greater multisensory enhancement of response times than younger controls in redundant target paradigms: Peiffer et al. (2007) found that the older age group had larger race model violations in an audiovisual speeded response task (see also Diaconescu et al., 2013, for a similar effect without a race model), and Mahoney et al. (2011) demonstrated the same for visual-somatosensory stimuli. A later series of studies by Mahoney and colleagues also demonstrated associations between the size of this visual-somatosensory race model violation in older adults and measures such as static balance (Mahoney, Holtzer, & Verghese, 2014; Mahoney et al., 2019), physical activity (Mahoney et al., 2015), and gait (Mahoney & Verghese, 2018), and showed that it is unaffected by stimulus location (Mahoney, Wang, et al., 2014). However, Murray et al. (2018) found that the age-related increase in (audiovisual) race model violation only held true for a subset of their participants, and Mahoney et al. (2011) report no such age difference for audiovisual or auditory-somatosensory stimuli. Furthermore, Couth et al. (2018) demonstrated that greater race model violations in older adults are correlated with longer unisensory response times, suggesting these age differences may be partially due to more ‘room for improvement’ in the older group.

The same analyses may also be applied to tasks that require a decision. For example, Laurienti et al. (2006) instructed participants to indicate, under speeded conditions, the colour of a stimulus based on auditory, visual, or audiovisual cues. Older adults again showed greater race model violations in this task. Results are mixed for spatial discrimination tasks, in which participants must give a speeded response indicating the location of a (unisensory or congruent multisensory) stimulus: Zou et al. (2017) found that older adults received more multisensory response time benefit, as did Diederich et al. (2008), but others have shown that this may not hold true for stimuli that are more naturalistic (Stephen et al., 2010) or presented peripherally (Wu et al., 2012).

Despite the apparent uncertainty about whether older adults benefit *more* from multisensory stimuli in this speeded response-time enhancement paradigms, it is very clear that they are not at all impaired in this function, compared with younger adults.

2.1.2. Unspeeded paradigms (accuracy enhancement)

As well as facilitating faster response times, congruent multisensory stimuli can also improve performance in tasks where the primary outcome measure is accuracy. In such tasks, the reliability of the least one of the unisensory signals must be sufficiently low that there is substantial room for improvement when an extra sensory modality is added. Stimuli are therefore often degraded in some way, masked by noise, or just naturally unreliable for the task (e.g. sound cues for location, or visual cues to speech). Generally, these paradigms involve dividing attention across multiple sensory modalities (i.e. participants must pay attention to all relevant information), but it is sometimes the case that participants are instructed to selectively attend to one modality.

In one audiovisual localisation study, Dobreva et al. (2012) asked participants to make saccades towards randomly presented unisensory and bisensory targets. The researchers report that the presentation of congruent visual signals significantly improved the precision of sound localisation in both the horizontal and vertical planes, and that this improvement was substantially more pronounced in older adults. Similarly, Roudaia et al. (2018) showed that the presence of a congruent auditory cue can improve the detection of a moving visual target within an array of distractors. However, in this case older adults were found to benefit less from the added auditory information than the younger controls.

The majority of research into the interaction between ageing and multisensory accuracy enhancement focuses on audiovisual speech integration, especially in the context of competing background noise, which has been shown to have a greater impact on comprehension in older age groups (Dubno et al., 1984; Killion et al., 2004; Wong et al., 2009). As the presence of lip movement information is known to substantially improve speech detection (Bernstein et al., 2004) and comprehension (MacLeod & Summerfield, 1986; Schwartz et al., 2004; Sumby & Pollack, 1954) in noisy environments, multisensory integration has the potential to "offer a fountain of youth for older ears" (Winneke and Phillips, 2011).

Tye-Murray et al. (2010; 2016), using build-a-sentence tests that required participants to identify target words in a sentence presented with background noise, found that intact visual information is indeed useful for older adults, and that it improves sentence comprehension to a similar degree in both age groups. Other work, including an earlier consonant discrimination study by the same group (Sommers et al., 2005), and sentence repetition (Helfer, 1998) and word recognition (Anderson Gosselin & Gagné, 2011) tests by others, confirm this similarity. Age differences do appear to emerge when the task becomes more challenging, however. Dey and Sommers (2015) report reduced visual enhancement of speech comprehension in older adults, but only when the task was to identify lexically hard words (those with many close alternatives). Similarly, in the context of extremely challenging listening environments (SNR of -12 dB and lower), Stevenson et al. (2015) found that younger participants exhibited far more multisensory benefit in whole-word recognition; performance was comparable across age groups for a less challenging but otherwise equivalent phoneme recognition task (see also the congruent audiovisual stimuli in Huyse et al., 2014).

Furthermore, older adults seem to be less able to utilise information in heavily degraded stimuli. Tye-Murray et al. (2010), for example, found that an extremely-low-contrast video stimulus facilitated comprehension less in the older age group. Gordon and Allen (2009) report even more extreme age differences, with older adults receiving almost no benefit from blurred visual signals that improved comprehension substantially in the younger age group (though see Legault et al., 2010), while Maguinness et al. (2011) showed that pixilating the visual stimulus can impair older adults' audiovisual speech comprehension even when the auditory stimulus is intact and clear.

In sum, older and younger adults appear to benefit to a similar degree from the addition of extra (cross-sensory) information in tasks where the added stimulus is relatively reliable and extra distractors are limited. However, older adults become less able to exploit extra information contained within heavily degraded stimuli, or when the context involves suppressing substantial amounts of irrelevant information.

2.2. Integrating conflicting multisensory signals

Many lab-based assessments of multisensory integration behaviour rely not on congruent stimuli, as have been discussed so far, but on stimuli that provide conflicting information. These measures are usually selective attention paradigms (i.e. respond to stimuli in one sensory modality while ignoring distractors in another) and fall broadly into two categories. First, when the conflict between two signals is small, they may still be integrated. This leads to crossmodal biases, in which observers' perceptual estimate in one sensory modality is biased towards the estimate obtained from the other sensory modality; these biases are the key mechanism for several prominent multisensory perceptual illusions. For example, when a sound is presented simultaneously with a spatially displaced visual distractor, the apparent location of the sound can change – a phenomenon known as the ventriloquist effect. Second, when the conflict is sufficiently large that the stimuli are not integrated, it can still be possible to measure effects on response time and accuracy caused by the presence of a cross-sensory distractor.

2.2.1. Small conflicts – Crossmodal biases and perceptual illusions

The sound-induced flash illusion (SIFI) is commonly used to investigate properties of multisensory perception in the temporal domain. First described by Shams et al. (2000), though mechanistically similar to an auditory-induced flicker effect discussed much earlier (e.g. Shipley, 1964), the SIFI occurs when one or more visual stimuli (e.g. flashes) are presented simultaneously with a conflicting number of auditory stimuli (e.g. beeps). In such situations, participants often perceive a number of flashes that is actually consistent with the number of beeps. For example, when presented with a single flash accompanied by two beeps, participants will often report perceiving two flashes. This occurs because, in humans, the temporal reliability of auditory stimuli is far greater than visual (we can detect *when* something happened far better by hearing than by seeing). Therefore, when conflicting auditory and visual temporal signals are integrated, the sensory system gives greater weight to the more reliable auditory information. Several studies have reported that older adults are significantly more susceptible to the sound-induced flash illusion (DeLoss et al., 2013; Hirst et al., 2019; McGovern et al., 2014; Setti, Burke, et al., 2011), though this effect is equivocal and seems to depend on the specific properties of the stimuli (DeLoss & Anderson, 2015; McGovern et al., 2014; Parker and Robinson, 2018; Setti et al., 2014; Sun et al., 2020). Scurry et al. (2019) report equivalent age differences for an audiovisual duration perception illusion.

Bedard and Barnett-Cowan (2015) instead tested for age differences in perception of the stream/bounce effect, another timing-critical audiovisual illusion. In this illusion, two visual stimuli are seen to converge, and the probability of them being perceived as bouncing off each other (rather than moving past each other without interacting) may be increased by the presentation of a sound at the point of overlap. Older adults were found to be susceptible across a wider range of audiovisual asynchronies. Roudaia et al.'s (2013) findings generally agree, but the authors also note that the age difference is not especially robust and can be entirely reversed by certain stimulus manipulations. See Brooks et al. (2018) for a more thorough review of the effects of ageing on audiovisual temporal perception.

There have, to date, been few attempts to measure similar age differences in the spatial domain. In one such study, we assessed older adults' responses to ventriloquist stimuli under both speeded and unspeeded conditions (Jones et al., 2019). We found that, in both cases, the strength of the ventriloquist effect was comparable across age groups, despite some evidence of unisensory reliability differences. However, incongruent stimuli had a disproportionate effect on response times in the older age group, the implications of which we discuss later in the review. Park et al. (2020) also tested older adults using an (unspeeded) ventriloquist paradigm, and found very similar results: no differences in the strength of the illusion, despite age-related impairments to unisensory reliability.

One of the most common paradigms for assessing multisensory speech perception is the McGurk-MacDonald effect (McGurk and MacDonald, 1976). In this illusion, a visual phoneme (e.g. /ga/) presented simultaneously with an incongruent auditory phoneme (e.g. /ba/) may result in an illusory percept that does not match either of those presented (e.g. /da/). Older adults' responses to this effect vary depending on the specifics of the stimuli and task, but regularly deviate from those seen in younger age groups. For example, Cienkowski and Carney (2002) found that the age groups were similarly susceptible to the illusion, but older adults' integrated percepts were biased more towards the visual stimulus (a finding supported by Sekiyama et al., 2014). Huyse et al. (2014) experimented with adding auditory and visual noise to McGurk-MacDonald stimuli. They found that, while amplitude-modulated auditory noise substantially increased younger adults' tendency to fuse incongruent percepts, the same was not true for the older group. Also, in agreement with the findings discussed earlier regarding degraded stimuli, the age groups were similarly capable at lip reading intact (unisensory) visual stimuli, but older adults performed significantly worse when these stimuli were blurred. Finally, Setti et al. (2013) found that older adults were more susceptible to McGurk-McDonald stimuli embedded within sentences, despite performing the same as younger adults in unisensory conditions.

Other researchers have investigated the presence of crossmodal biases when presenting visual, haptic (touch), and proprioceptive (limb position) cues. For example, Riemer et al. (2019) assessed whether older adults differed in their perception of the rubber hand illusion. In this paradigm, a participant is induced to perceive a rubber hand as part of their body by the experimenter applying continuous, synchronous visual and tactile cues to the (visible) rubber hand and the (concealed) real hand simultaneously. They found that older adults were similarly susceptible to the illusion, despite evidence of impaired proprioception. However, in a paradigm that induced illusory movement via visual, haptic, and proprioceptive (muscle vibratory) cues, Chancel et al. (2018) found that multisensory stimulation led to stronger illusory percepts (compared with unisensory) in the older age group only. Finally, Higgen et al. (2020) found that younger adults were significantly better at determining the congruence of visual and haptic patterns presented at perceptual threshold levels.

Multisensory processing is also crucial for navigation and locomotion, which rely on effective integration of visual, proprioceptive, haptic, and vestibular cues. Deshpande & Patla (2007) assessed the effect of perturbations to vestibular signals (induced via electrical stimulation) on older adults' walking trajectories, and found that they were less able to reweight the signals to prioritise the (unperturbed) visual information. Berard et al., (2012) used a similar paradigm but instead perturbed the visual signal (via a virtual reality display), and found an equivalent effect: older adults were less able to prioritise the unperturbed vestibular and postural cues.

To summarise, the evidence generally suggests that older adults are more susceptible to most illusions that are induced by presenting multisensory stimuli with small levels of conflict. The one major outlier in this regard is the ventriloquist effect, where age differences are not apparent.

2.2.2. Large conflicts – Cross-sensory distraction and interference

Other paradigms instead use multisensory cues with conflicts that are sufficiently large to not be integrated at a perceptual level. In such cases, the irrelevant (non-target) stimulus may still have an impact on behavioural responses. This may be partially due to limits in attentional resources: if an observer is distracted by a stimulus in another sensory modality, they are likely to respond less quickly or accurately to a target of interest.

In many cases, older adults do appear to be more susceptible to cross-sensory distraction. In a simulated driving study, Pitts and Sarter (2018) asked participants to detect unisensory or simultaneous bi-, and tri-sensory stimuli whilst maintaining a continuous driving position. Older participants were both less able to accurately detect the multisensory stimuli, and more likely to deviate in driving position following stimulation. Similarly, in a paradigm that paired visual (vertical) motion stimuli with auditory that increased or decreased in pitch, Puschmann et al. (2014) found that incongruent visual stimuli led to significantly increased error rates in older adults' responses to the auditory stimulus. The authors also report that incongruent auditory stimuli led to disproportionately impaired response times to the visual stimuli. In a variety of other paradigms, visual distractors have been shown to disproportionately affect older adults during motor (Mevorach et al., 2016), auditory (Furman et al., 2003; Guerreiro and Van Gerven, 2011; Guerreiro et al., 2013; but see Guerreiro et al., 2014, 2015), and vibrotactile perception (Poliakoff et al., 2006) tasks. Furthermore, both auditory (Mahboobin et al., 2007) and visual (Redfern et al., 2009) distractors have been shown to impact older adults' postural control. These age-related increases in distractibility are common, but not universal. For example, Campbell et al. (2010) assessed trajectory deviations caused by introducing a visual distractor as participants made saccades towards a multisensory target, and found no effect of age, while Barrett and Newell (2015) similarly showed that a spatially incongruent distractor impaired response times in younger and older adults equally. Townsend et al. (2006) further found no age-related behavioural differences in an fMRI study of modality-specific attention, though the authors do report that older adults displayed significantly increased frontoparietal activations in response to irrelevant stimuli.

TABLE 1 APPROXIMATELY HERE

2.3. Summary and limitations

In summary, there is a diverse collection of existing research into the effects of normal, healthy ageing on multisensory integration. Older adults appear to generally receive at least the same amount of response time benefit from congruent, suprathreshold multisensory stimuli as younger controls. Paradigms that instead assess accuracy benefits for congruent stimuli produce more mixed results, with older adults appearing to benefit less from multisensory stimuli under some situations (particularly as stimuli and task become noisier and more complex). This dissociation may potentially be explained by the fact that the ageing brain is progressively optimised and refined to the statistics of our natural environment, which is beneficial for processing standard suprathreshold stimuli typical for speeded response paradigms. Yet, ageing reduces the brain's complexity, making it harder to adapt to environmental changes, process novel or less likely (e.g. noisy) stimuli, and flexibly interact in more complex contexts (Moran et al., 2014).

When presented with multisensory stimuli that have a small amount of conflict, older adults are often more likely to integrate them, resulting in stronger or more frequent crossmodal biases/perceptual illusions. This somewhat depends on the specifics of the stimuli and task, however. Finally, older adults appear to be substantially more susceptible to distraction from strongly conflicting multisensory stimuli, resulting in impairments to both response time and accuracy.

One of the most striking features of the existing research is the variability in findings. In some cases, older adults seem to have entirely preserved (or even improved) multisensory integration; in others, they perform significantly worse than younger controls. There are several possible explanations for these inconsistencies. It may be that many of the effects seen can be attributed primarily to age differences in unisensory processing, and that these differences are not uniform across sensory modalities and stimulus features. If older adults were especially impaired in auditory temporal perception, for example, this would lead to more age differences in the sound-induced flash illusion (that relies on precise timing perception) than in the ventriloquist illusion (that relies more on spatial perception). Multisensory integration is also closely linked to attentional processes; if older adults are impaired in these, we might expect to see the greatest age differences in complex paradigms that involve processing many stimuli simultaneously. Or it may be that older adults simply differ in their response strategies.

It is also important to acknowledge the likely role individual differences play in the age effects we observe in multisensory integration tasks. Growing evidence suggests that older adults are highly variable in their unisensory abilities, and that correlations in performance *between* ostensibly similar tasks (both unisensory and multisensory) are limited (Bedard & Barnett-Cowan, 2015; Billino et al., 2009; Billino & Pilz, 2019; Grzeczkowski et al., 2017; Shaqiri et al., 2019). This may account for some of the differences in findings between paradigms that use near-threshold versus suprathreshold stimuli, and further brings into question the possibility of finding one or more general mechanisms underlying multisensory ageing.

The above considerations demonstrate that we need to move beyond comparing multisensory integration effects in old and young, towards a framework that enables us to dissociate the various mechanisms by which ageing may impact observers in multisensory contexts. In what follows, we introduce a normative Bayesian framework that provides computational principles against which we can test the effect of ageing on multisensory perception.

3. Part B: A computational perspective on multisensory integration and ageing

3.1. The normative Bayesian framework of perception

In our natural environment, our senses are constantly bombarded with signals. During perception, the observer needs to infer the most likely state of the world from these noisy and uncertain sensory observations. This notion of perception as 'unconscious inference' goes back to Helmholtz in the 19th century (Helmholtz, 1867) and has since been formalised into current Bayesian models of perception**.** The Bayesian framework in neuroscience posits that the brain forms a probabilistic 'generative model' of the sensory inputs, which is inverted during perceptual inference (to create a 'recognition model'). The generative model defines how the sensory observations are generated by the external world. It specifies the a priori probability of different states of the world (e.g. the probable location of light sources, or how likely it is that a street is wet). This is referred to as the ‘prior’, and may be written as *P*(world state). The model also specifies the probability of sensory (e.g. retinal) inputs given that the world is in a particular state. This is referred to as the ‘likelihood’, and may be written as the conditional probability *P*(sensory input | world state). Critically, all sensory inputs are corrupted by various sources of both external (environmental) and internal (neural) noise (Faisal et al., 2008), making them inherently uncertain. For instance, a driver’s view may be obscured by a dirty front screen (external noise), and synaptic transmission is a probabilistic process (internal noise). To constrain the perceptual interpretation of the noisy and ambiguous sensory inputs, the observer is thought to combine likelihood and prior into a ‘posterior probability’: the probability of a particular world state given the sensory inputs, *P*(world state | sensory inputs). According to Bayes’ rule, this posterior probability is proportional to the product of the likelihood and the prior:

$$P(world\ state|sensory\ inputs) = \frac{P(sensory\ inputs|world\ state) * P(world\ state)}{P(sensory\ inputs)}$$

$$\propto P(sensory\ inputs|world\ state) * P(world\ state)$$

Bayes’ rule provides a probability distribution that assigns posterior probabilities to the different possible world states. The width of this posterior distribution thereby quantifies observers’ uncertainty about the state of the world. However, in almost all everyday situations, the observer needs to go a step further and ‘read out’ a single estimate of the state of the world from this distribution. For example, to grasp a cup on a desk, the observer needs a specific location to aim for (not a probability distribution describing where the cup *might* be). This final read out depends on the specific cost or decisional function that the observer employs; common choices in Bayesian inference are the maximum or the mean of the posterior distribution.

In summary, Bayesian probability theory is a normative framework that offers a precise formulation of how observers should combine uncertain information from different senses, together with prior knowledge or expectations, to form a representation of the world. An ideal Bayesian observer sets a benchmark against which human performance can be compared. In the following, we describe two leading Bayesian models that have been used in multisensory perception.

3.2. Multisensory perception: Bayesian models of forced fusion and causal inference

To form a coherent percept when faced with a barrage of complex multisensory signals, an observer must solve two fundamental computational problems. First, they must determine which of the signals belong together—that is, were caused by the same object or event. Those that share the same cause should be processed together ('forced fusion'), while those with different causes should be processed separately ('full segregation'). This 'causal inference' is performed based on several correspondence cues—did the signals appear to occur in the same place (Lewald & Guski, 2003; Slutsky & Recanzone, 2001; Spence, 2013) or at the same time (Lewis & Noppeney, 2010; Maier et al., 2011; Parise & Ernst, 2016), for example—and is computationally challenging because of the huge number of noisy signals entering the system every moment, resulting in many intersensory correspondences that arise dynamically across time. The second problem to be solved is how to weight the relative contributions to the final percept of those signals that share a common source.

Recent research combining psychophysics and computational modelling suggests that human observers solve these two challenges in a way that is consistent with the principles of normative Bayesian inference. In so-called 'forced fusion' situations, where multiple signals are known to come from a common source, observers integrate these signals weighted by their relative reliabilities (i.e. the inverse of variance or noise) as predicted by Bayesian forced fusion models (note that, with a flat prior, this is equivalent to maximum likelihood estimation; Alais & Burr, 2004; Ernst & Banks, 2002; Hillis et al., 2002; Jacobs, 1999; Meijer et al., 2019). They thus give a stronger weight to the more reliable sensory signal. In more complex situations in which observers do not know whether signals share the same source, they arbitrate between integration and segregation in a way that can be predicted by recent Bayesian causal inference models (Körding et al., 2007; Meijer et al., 2019; Rohe & Noppeney, 2015a; Wozny et al., 2010).

Bayesian causal inference models go beyond forced fusion models by accounting for observers' uncertainty about the world's causal structure, i.e. whether signals come from common or independent sources. They account for the causal inference problem by explicitly modelling the possible causal structures (i.e. common or independent sources) that could have generated the sensory signals. In the case of a common source, signals are integrated, weighted by their relative reliability ('forced fusion' model). In the case of separate sources, they are processed independently ('full segregation' model). To account for observers' uncertainty about the world's causal structure, a final estimate is computed by combining the estimates from the forced fusion and full segregation models, weighted by the posterior probability of each causal structure. For instance, according to one decision function ('model averaging'), the final estimate averages the estimates provided by the forced fusion and full segregation models, weighted by their respective posterior probabilities.

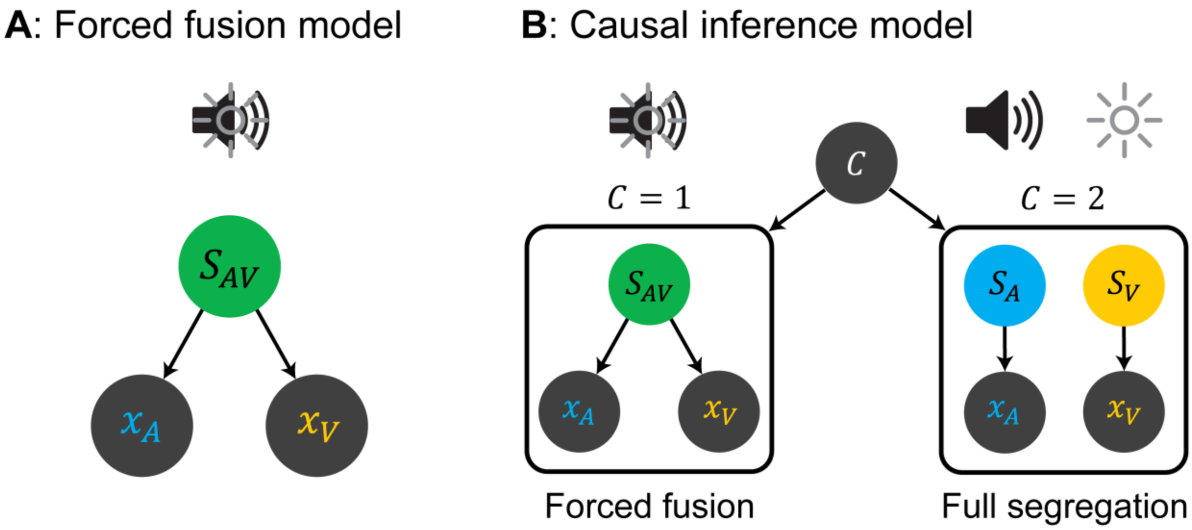

Figure 1. Bayesian models of multisensory integration, using the example of one auditory and one visual spatial cue (x_A and x_V, respectively). A: When two signals are known to share a common cause S_{AV}, they are integrated, weighted by their relative reliabilities, according to the forced fusion model. B: When there is uncertainty about whether signals share a common cause, the Bayesian causal inference model (Körding et al., 2007) instead models the possible causal structures that may have produced the signals. In the case of a common cause (C = 1), one audiovisual source S_{AV} is considered to have produced both sensory signals; these are integrated, weighted by their relative reliabilities (as in the forced fusion model). In the case of separate causes (C = 2), independent auditory S_A and visual S_V sources produced the auditory and visual signals respectively, so these are processed separately (segregated). A final estimate, for example of the sound location, is obtained by combining the estimates from these two possible causal structures according to one of several decision functions: for instance, according to 'model averaging' the two estimates are averaged, weighted by the posterior probabilities of the respective causal structures (i.e. common source vs. separate sources).

Accumulating research has shown that young human observers form perceptual estimates in a way that is consistent with the principles of Bayesian causal inference in a wide range of contexts, including spatial, numerosity, and rate estimation (e.g. Acerbi et al., 2018; Cao et al., 2019; Dokka et al., 2019; Fang et al., 2019; Körding et al., 2007; Magnotti et al., 2018; Magnotti & Beauchamp, 2013; 2017; Mahani et al., 2017; Mohl et al., 2019; Rohe & Noppeney, 2015a; Shams et al., 2005; de Winkel et al., 2018). Most recent fMRI and EEG/MEG research has shown that the human brain accomplishes Bayesian causal inference by dynamically encoding multiple perceptual estimates across the cortical hierarchy (Aller & Noppeney, 2019; Cao et al., 2019; Rohe et al., 2019; Rohe & Noppeney, 2015b; 2016; 2018). For instance, in a spatial ventriloquist paradigm, low-level visual and auditory cortices formed perceptual estimates separately for each sensory modality at around 100 ms post-stimulus ('full segregation'). After around 250 ms, posterior parietal cortices integrated the audiovisual signals under forced fusion assumptions. Critically, only late activity (350-450 ms) at the top of the hierarchy in anterior parietal cortices combined auditory and visual signals into Bayesian causal inference estimates that take into account observers' uncertainty about the world's causal structure. This research suggests that the hierarchical structure of the Bayesian causal inference model is reflected in the dynamic evolution of Bayesian causal inference across the cortical hierarchy.

Collectively, this growing body of psychophysics and neuroimaging research suggests that normative models of Bayesian causal inference provide a useful computational starting point for understanding how human observers combine signals across the senses. However, these standard Bayesian forced fusion and causal inference models are 'atemporal' and do not account for the fact that decision making evolves across time. They can therefore make predictions for response choices, but not for response times. In real life, observers usually accumulate information over time before selecting a response, and often need to make accurate responses under time pressure. If observers try to maximise response speed in addition to accuracy, this alters observers' cost function with significant impact on the definition of Bayesian optimality. Consistent with this conjecture, a recent study has demonstrated (using diffusion models of multisensory decision-making under forced fusion assumptions) that putatively suboptimal visual-vestibular integration for heading discrimination can be considered optimal when decisional dynamics and speed/accuracy trade-off are taken into account (Drugowitsch et al., 2014). Similarly, the current Bayesian causal inference model can be transformed into dynamic models of evidence accumulation. These models assume that the observer concurrently accumulates evidence from multiple senses, both about the world's causal structure (i.e. common vs. independent sources) and about properties of the stimuli (such as spatial location or object size), leading to complex non-linear accumulation processes (Noppeney et al., 2010; Yu et al., 2009).

In summary, the normative Bayesian framework describes how observers should combine information from multiple sensory channels and prior knowledge into a coherent percept of the world. It thus sets a benchmark of optimal performance to compare with human behaviour. Moreover, accumulating psychophysics and neuroimaging research suggests that young human observers combine signals across the senses, consistent with the principles of Bayesian causal inference. In the following we therefore use it as a starting point to discuss the various ways in which ageing might influence multisensory processing.

3.3. Age-related changes in multisensory perception at the computational level

In this section, we discuss the impact of ageing on the computations necessary for multisensory integration, organised according to the key ingredients of Bayesian inference (as outlined in Section 3.1): the likelihood, the prior, the cost function, and the actual inference process used to compute the posterior.

3.3.1. Likelihood – Sensory representations

The unisensory representations, described within the Bayesian framework as the likelihood, are key elements in multisensory integration. Ageing may lead to degradation of the reliability of these representations in several ways, outlined in the following paragraphs. It may also lead to changed biases. For instance, previous research has suggested that auditory, visual and audiovisual spatial representations are associated differentially with biases towards the centre and the periphery (Odegaard et al., 2015). It is unclear why and how these biases arise, and whether they are stable across the lifespan.

Critically, differences in sensory noise (or reliability) and biases can profoundly alter observers' multisensory perceptual inference. Sensory uncertainty determines how observers weight the sensory signals in the integration process which may, for example, lead to an increase or decrease in the experience of perceptual illusions. Moreover, decreases in sensory reliability make inferring the signals' causal structure more challenging, which can lead to a higher (or lower) probability of integrating conflicting information. It is therefore critical, when investigating multisensory processing, to assess the reliability of the unisensory information as well as the final percept (e.g. perceptual illusion).

As suggested above, it is well established that normal, healthy ageing leads to a decline in the internal reliability of sensory information. On the most basic level, peripheral sensory organs degrade over the lifespan. For example, ageing is associated with a variety of physical changes to the eye, including presbyopia (Glasser & Campbell, 1998), miosis (Sloane et al., 1988), and loss of retinal photoreceptor and ganglion cells (Curcio et al., 1993; Curcio & Drucker, 1993). In terms of hearing, some degree of presbycusis is estimated to be present in at least 90% of humans by age 80 (Cruickshanks et al., 1998; Rodríguez-Valiente, 2020). The deleterious effects of these changes on sensory reliability are compounded by age-related alterations in central processing of sensory stimuli (Elliott et al., 1990; Martin & Jerger, 2005; Simpson et al., 1985; Wang et al., 2006). Visually, this is reflected in impairments to spatial acuity (Klein et al., 1991), temporal acuity, (Eriksen et al., 1970; Kim & Mayer, 1994; Ulbrich, 2009), contrast sensitivity (Ross et al., 1985), and even stereoscopic depth perception (Wright & Wormald, 1992). In the case of hearing, older adults are less able to understand auditory speech embedded in noise (Dubno et al., 1984; Killion et al., 2004; Presacco et al., 2016; Wong et al., 2009) and less precise when locating sounds in both the spatial (Dobreva et al., 2011, 2012; Otte et al., 2013) and temporal (Anderson et al., 2013; Ramamurthy & Recanzone, 2020; Fitzgibbons & Gordon-Salent, 2004; Ng & Recanzone, 2018) domains. The reliability of most other senses, including touch (Wickremaratchi & Llewelyn, 2006), proprioception (Boisgontier et al., 2012; Hurley et al., 1998), balance (i.e. vestibular function; Agrawal et al., 2009; Anson & Jeka, 2016), and smell (Murphy et al., 2002; Welge-Lüssen, 2009) has also been shown to be impacted in some way by ageing.

Changes in unisensory reliability can affect multisensory integration even if all other factors are held equal. For example, older adults' increased susceptibility to the sound-induced flash and stream/bounce illusions could potentially be accounted for by an impaired ability to detect precisely when each of the unisensory stimuli occurred (i.e. the signals' causal structure), leading to more temporally disparate signals being integrated. As noted above, older adults are less able to locate unisensory stimuli in time, and multisensory temporal order judgement studies (that measure the ability to determine relative timings of events perceived by different senses) have found similar age-related impairments (Bedard and Barnett-Cowan, 2015; de Boer-Schellekens and Vroomen, 2013; Setti, Finnigan, et al., 2011;

though see Basharat et al., 2019, and Fiacconi et al., 2013, for whom the age difference was in the same direction but not statistically significant). Another measure of multisensory temporal reliability, explicit simultaneity judgement, has produced more equivocal results: Stevenson et al. (2017) and Chan et al. (2014) report significant age differences, while Basharat et al. (2019), Bedard & Barnett-Cowan (2015), and Degano et al. (2019) do not. However, this most likely reflects the fact that synchrony judgments are prone to numerous biases and are therefore not ideal for assessing observers' temporal precision (Vroomen & Keetels, 2010).

Importantly, associations between unisensory reliability and the sound-induced flash and stream/bounce illusions have been demonstrated in several ways. Setti et al. (2014), for example, showed that training on the temporal-order judgement tasks described above could reduce older adults' susceptibility to the illusion, and Hirst et al. (2019) found that measures of unisensory reliability mediated the relationship between age and SIFI susceptibility in a large sample of 2920 older adults. Sun et al. (2020) further report that older adults' SIFI susceptibility was disproportionately affected by repetition of the auditory stimulus prior to presentation of the flash, which the authors interpret as resulting from a change in auditory sensitivity due to repetition suppression. Finally, Bedard and Barnett-Cowan (2015) showed age differences in both temporal-order judgements and the stream/bounce illusion within the same large sample, suggesting that they may be co-occurring. Taken together, this research indicates that age differences in unisensory temporal reliability play a major, though perhaps not exclusive, role in explaining age differences in the sound-induced flash and stream/bounce illusions.

Looking to other perceptual illusions, unisensory reliability may also help to explain the age differences observed by Chancel et al. (2018) in their illusory motion task. Older adults were far less susceptible to illusions induced by proprioceptive (muscle vibration) cues than those caused by visual or haptic signals, which the authors argue is a result of older adults being more substantially impaired in this sensory modality. This is supported by Riemer et al. (2019), who also found that older adults had disproportionately impaired proprioception (compared with vision and haptics), though this was not found to influence their experience of the rubber hand illusion. However, Higgen et al. (2020) also found age differences in a visual-haptic pattern matching task despite measuring and testing all participants at their individual unisensory perceptual thresholds, suggesting that factors other than sensory reliability must also play a role.

The explanatory role of unisensory reliability in age differences is more difficult to assess for multisensory illusions that involve higher phonetic representations such as the McGurk-MacDonald illusion. Studies that have assessed how older adults respond to this illusion have found either no age difference in unisensory responses (Setti et al., 2013) or small differences that occur only under specific conditions (Cienkowsky & Carney, 2002; Sekiyama et al., 2014; Huyse et al., 2014), despite all reporting substantial age differences in the perception of the audiovisual illusion. However, these studies have assessed observers' unisensory representations in simple unisensory phoneme or word recognition tasks. These do not sensitively measure the reliability of observers' sensory representations, as subtle representational changes may be obscured by categorical perception. Future studies are therefore needed that assess unisensory and multisensory reliability in audiovisual speech perception using, for example, psychometric functions. In one such study, Bejjannki et al. (2011) sensitively measured younger adults' visual and auditory reliability for phoneme recognition by estimating psychometric functions based on auditory stimuli that continuously morph from /ba/ to /ga/, and on visual stimuli presented with multiple levels of blur.

Collectively, previous research has demonstrated that unisensory reliability is a key factor in explaining the increases in multisensory illusions in older participants. As shown by Rohe and Noppeney (2015a), sensory reliability shapes the integration of sensory inputs by both altering the relative weights of the sensory inputs and by directly influencing causal inference, as reflected in the binding window. It is therefore important for future studies to directly assess the specific representational reliability that is applicable to the task the observers are executing (e.g. temporal, spatial, speech recognition), separately for all relevant sensory modalities. This would help to better separate age-related changes in unisensory reliability from other effects, and could also go some way towards accounting for the substantial individual differences in older adults' unisensory reliabilities discussed in Section 2.3. However, it is also important to note that the assessment of reliability is particularly challenging for tasks that involve higher-order representations and categorical perception, such as phoneme recognition, where subtle differences in representational reliability may easily evade experimental assessment.

3.3.2. Priors – Expectations and attention

Prior expectations are another crucial ingredient of Bayesian inference, as they usefully constrain the perceptual interpretation of uncertain and ambiguous sensory inputs. Observers form prior expectations about where and when things are likely to happen, about environmental properties (e.g. the most likely colour of an object), and about the world's causal structure (the probability of signals sharing a common source). This latter *causal* prior determines observers' tendency to integrate or segregate sensory signals. For example, when presented with a series of incongruent sensory signals (creating the expectation of more incongruent signals to follow), observers reduce their causal prior and are less likely to integrate sensory signals into one unified percept (Gau & Noppeney, 2016; Nahorna et al., 2015). An age-related change in the causal prior would thus make older adults more, or less, likely to integrate conflicting multisensory signals.

Prior expectations are intimately linked with attentional control, as observers tend to attend to locations where events are likely to occur (Summerfield & Egner, 2009; Zuanazzi & Noppeney, 2018, 2020). Attending to irrelevant stimuli can also reduce the probability of integrating task-relevant stimuli (Alsius et al., 2005; 2007). Furthermore, the causal prior influences how an observer should allocate attention across sensory modalities. If we expect multiple signals to come from a common source, we should distribute our attentional resources across sensory modalities; if we expect signals to come from different sources, we should actively attend to the sensory modality in which signals are task-relevant, and ignore irrelevant sensory signals in other sensory modalities.

Age-dependent declines in attentional control therefore have the potential to impact older adults' multisensory integration in a variety of ways. In particular, we might expect to see less effective suppression of incongruent stimuli, and greater changes in multisensory perception in complex situations that demand more attentional resources (e.g. tasks with many complex stimuli; Talsma et al., 2010). Current models of Bayesian causal inference do not formally accommodate the influence of attention, so changes in attentional control are likely to manifest as changes in priors. For instance, if older observers were less able to selectively attend to one particular sensory modality, this may be reflected in an increased tendency to bind sensory signals (i.e. greater causal prior).

Top-down attentional control processes are, indeed, frequently found to be affected by ageing. For example, it has been well established by multiple large-scale studies that older adults show a greater Stroop effect than their younger counterparts (e.g. Bugg et al., 2007; Van der Elst et al., 2006). This correlates with age-related neural activity changes in a network of attentional control regions including anterior cingulate, dorsolateral prefrontal cortex, inferior frontal gyrus, and anterior insula, suggesting that this system is somehow changed or impaired in older adults (Langenecker et al., 2004; Milham et al., 2002; Mohtasib et al., 2012; Schulte et al., 2011; Zysset et al., 2007). Age differences in this task are also apparent in an auditory equivalent (Sommers & Danielson, 1999), and present even after accounting for response time differences measured in a variety of other tasks (Bugg et al., 2007).

Likewise, in multisensory situations, growing evidence suggests that age-dependent declines in attention may result in a greater degree of cross-sensory distraction. As reviewed in Section 2.2.2, older adults show substantial performance impairments in various selective attention paradigms with large intersensory conflicts. Many of the perceptual illusion paradigms reviewed in Section 2.2.1 also rely on selective attention. In the ventriloquist illusion, for example, observers must report the perceived sound location while attempting to ignore the visual signal; in the sound-induced flash illusion they must report the perceived number of flashes while ignoring the sounds. Declines in attentional control may therefore also account for increases in illusory percepts.

So far we have focused on top-down attentional control, but multisensory integration is also shaped by bottom-up attention, whereby a strong signal in one sensory modality may boost the processing of signals in another modality (Corbetta & Shulman, 2002). For example, Guerreiro et al. (2012) tested younger and older adults on a cross-modal cueing paradigm. A cue (auditory or visual) was presented prior to a target (auditory or visual) at various onset asynchronies, and participants asked to indicate the location of the target as quickly as possible. Various effects of cue type were observed in this task but, crucially, no significant age differences were found. Andrés et al. (2006) also found that simple beep cues benefitted both younger and older adults similarly in a speeded visual decision task, though a more complex natural sound actually impaired the older group's response times. The authors interpret this as an increase in age-related distractibility, in line with the studies discussed earlier in this section. Mahoney et al. (2012) instead measured whether combinations of auditory, visual, and somatosensory pre-stimulus cues improved the speed of responses in an Eriksen flanker task (Eriksen & Eriksen, 1974; Fan et al., 2002). Despite various small age differences (in both directions) between specific conditions, the study generally found that both groups benefitted to some degree from the presentation of cross-sensory cues.

This interesting distinction between multisensory top-down attention (where older adults appear to be substantially impaired) and bottom-up attention (where they do not) may help to account for the age differences seen in complex, multi-source situations such as speech comprehension in noise. In Sections 2.1.2 and 3.3.1, we outlined how older adults are less able to comprehend auditory speech embedded in noise, but benefit substantially from the addition of congruent visual information. It may be that deficits in top-down attentional control impair their ability to separate speech from noise, but that congruent visual stimuli help to boost detection and comprehension via (unimpaired) bottom-up attentional mechanisms.

In general, there appears to be substantial evidence for age differences in cross-sensory attention, which often manifests as differences in the tendency to bind incongruent information (i.e. the causal prior).

3.3.3. Cost function

The final outcomes of perceptual inference and response selection will depend on the cost function for which an observer is optimising. For example, within the Bayesian causal inference framework, observers may implement one of several decisional strategies including model selection, model averaging, and probability matching (Wozny et al., 2010). Cost functions are also important in dynamic models, such as accumulation of evidence or drift diffusion models, in which observers are seen to accumulate evidence over time until a criterion amount of information is obtained and a response made. These dynamic models account for the fact that in our natural environment, observers need to be both fast and accurate, and must find a trade-off between these. This raises the important question of whether some age differences in responses to multisensory stimuli may reflect changes in the speed/accuracy trade-off.

Impaired response times are one of the most consistently replicable behavioural effects of ageing, and are apparent to some degree across most tasks, from simple responses to a tone or visual stimulus (Der & Deary, 2006; Fozard et al., 1994; Gottsdanker, 1982; Verhaegen & Cerella, 2008) to more complex cognitive paradigms such as visual search (Humphrey & Kramer, 1997; Scialfa et al., 1998) and go/no-go tasks (Fozard et al., 1994; Hsieh et al., 2016). Some of this may be attributed to declines in motor speed (Ebaid et al., 2017; Wilson et al., 2004), but substantial differences in the size of the effect between tasks suggest that age-related response time changes also index other central and cognitive factors (Birren & Fisher, 1995; Salthouse, 1996; Sliwinkski & Hall, 1998; Verhaegen & Cerella, 2008). This is complicated, however, by the fact that ageing is associated with a reweighting of speed and accuracy priorities. Even when told to respond as quickly as possible, older adults have been repeatedly shown to prioritise accuracy to a greater degree than younger controls (Rabbitt, 1979; Salthouse, 1979; Smith & Brewer, 1995). Evidence accumulation (or drift-diffusion) models that explicitly model the dynamic process from stimulus to response can help to separate these factors (e.g. Starns & Ratcliffe, 2010).

Recently, we used an accumulation of evidence model (the so-called ‘compatibility bias’ model; Noppeney et al., 2010; Yu et al., 2009) to assess audiovisual interactions in a simplified version of a speeded ventriloquist paradigm (Jones et al., 2019). Unlike standard linear drift-diffusion models (Drugowitsch et al., 2014; Starns & Ratcliffe, 2010), this models the concurrent accumulation of evidence about both the perceptual estimate (e.g. sound location) and the congruence of the sensory signals (e.g. causal structure), leading to a non-linear accumulation process. Our initial model-free analysis of response times revealed an interaction between age and audiovisual spatial congruence, suggesting that older adults had responded disproportionately slower to incongruent stimuli. Fitting the accumulation of evidence model jointly to observers’ response choices and times revealed that older observers accumulate noisier auditory representations for longer, set higher decisional thresholds, and have impaired motor speed. Thus, directly modelling the within-trial dynamics of decision making in response to multisensory stimuli revealed that older adults used a different speed-accuracy trade off, sacrificing speed to preserve response accuracy. These findings are supported by Norman et al. (2006), who found that age differences in a visual-haptic shape perception task were eliminated when the older participants were given an unlimited amount of time to perform it.

These results highlight the possibility that age differences in any paradigm that measures both accuracy and response time, included the speeded discrimination tasks discussed in Section 2.1.1, may be at least partially accounted for by changes in this speed/accuracy trade-off. Future research should therefore aim to dissociate changes in speed-accuracy trade off from more fundamental changes in multisensory processing, for example by explicitly modelling the evidence accumulation process.

3.3.4. Inference and cue weighting

Finally, it may be that ageing affects not only the parameters (sensory variances, priors) or cost functions of multisensory integration, but even the inference process itself. In other words, older observers may no longer comply with the principles of Bayesian causal inference or reliability-weighted integration. In fact, accumulating research suggests that even younger adults do not fully conform to the quantitative predictions of Bayesian inference across a range of perceptual and cognitive tasks (e.g. Bentvelzen et al., 2009; Burr et al., 2009; Rosas et al., 2005; Meijer et al., 2019). Yet, reliability-weighted integration of two sensory signals under forced fusion settings can still be considered a prime example of human Bayesian (near) optimality. In this final section, we review the few recent studies that have formally assessed whether older observers integrate and weight multisensory cues in a way that is consistent with Bayesian principles.

Brooks et al. (2015) assessed relative weighting of auditory and visual signals in a temporal rate perception paradigm. The authors found that both age groups assigned suitable reliability-based weights to the auditory and visual cues, though only the younger group's accuracy benefited from multisensory signals (versus unisensory accuracy). Braem et al. (2014) found similar in a visual-haptic verticality judgement study, though in this case both age groups showed multisensory accuracy benefits. Two studies of visual-haptic size discrimination have found somewhat divergent results: Billino and Drewing (2018) report that older adults weighted the cues near-optimally, and in fact performed better than the younger group (who underweighted the visual signal); conversely, Couth et al. (2019) report no significant age differences, but also found that neither group conformed to the predictions of reliability-weighted integration. Finally, Bates and Wolbers (2014) assessed the use of visual and self-motion cues in a navigation task. They found that, while both younger and older adults benefited from the presence of multisensory information, the older adults underweighted the visual cue.

In general, the available evidence suggests that older adults benefit from, and assign weights to, multisensory cues in a similar way to younger controls under forced-fusion conditions. This is in agreement with the limited research assessing older adults' conformity to Bayesian causal inference under conditions of perceptible conflict, which has also found that the age groups perform similarly (Jones et al., 2019; Park et al., 2020).

4. Conclusions

We began this review by summarising existing research into the effects of normal, healthy ageing on multisensory integration, finding results that are extremely diverse across stimulus types and paradigms. We then outlined and applied a Bayesian framework for distinguishing the level(s) at which these age-related changes may occur. Based on this framework, some general themes have emerged. It is clear, for example, that reduced unisensory reliability (i.e. likelihood) plays a substantial role in many of the age differences that are observed. Ageing also appears to be associated with significant changes in attentional control, which often lead to an increased tendency to bind incongruent information (i.e. greater causal prior) and impairments such as increased response times. Furthermore, it is possible that some of the effects observed result from older adults using different response strategies (cost functions), rather that perceptual differences per se; we consider evidence for changes in speed/accuracy trade-off, but it may be that there are similar age differences in the application of decision functions in other contexts.

That these three appear to be the main driving factors behind age differences in multisensory integration also accounts for the fact that we do not see impairments in the simple, congruent reaction time tasks described in the first part of Section 2.1.1. These tasks:

are generally strongly suprathreshold, so are not influenced by sensory reliability; are always congruent, so do not place high demands on selective attention; and do not require complex decisional strategies, so are less susceptible to differences in speed/accuracy trade-off.

We have not, however, found much evidence for age differences in the integration process itself. That is, the specific computational operations the sensory system uses to infer whether signals share a cause, and to integrate those that do. Based on the existing literature, older and younger adults appear to conform similarly to the predictions of Bayesian causal inference and reliability-weighted integration. The age differences discussed above simply adjust the parameters of these models.

However, these conclusions are largely based on paradigms that were not designed to address this question, and future studies may benefit from applying this framework in their designs and analysis. We can make several suggestions. First, when assessing age differences in multisensory integration, it is important to also measure unisensory performance for the specific representational reliability of interest (e.g. temporal, spatial). Considering the evidence that there is limited correlation in performance between seemingly similar tasks (Bedard & Barnett-Cowan, 2015; Billino et al., 2009; Billino & Pilz, 2019; Grzeczkowski et al., 2017; Shaqiri et al., 2019), this should be done in a way that is as close as possible to the multisensory task. Second, further attempts should be made to evaluate specifically whether/how ageing influences the complex relationship between prior expectations, attentional context, and multisensory integration. There is a wealth of recent literature probing these effects in young adults (see e.g. Beierholm et al., 2020; Gau & Noppeney, 2016; Nahorna et al., 2015; Noppeney, In press; Odegaard et al., 2016; Zuanazzi & Noppeney, 2020) that could, in many cases, be easily applied to an older population. Third, the role of cost functions in paradigms that involve decision making should be more widely acknowledged and accounted for, as cost functions that differ systematically between groups can make results different to interpret: were older participants simply optimising their responses for a different goal (Wozny et al., 2010)? Fourth, research should continue to assess whether older adults do indeed perform Bayesian causal inference and reliability-weighted cue integration in the same way as younger groups in a variety of contexts; our tentative conclusion that these processes do not appear to change with age is based on a limited range of studies. Even where the goal of future studies is not directly to address the above outstanding questions, we hope that this computational framework may aid researchers in designing paradigms and analyses that can better discern the levels at which age differences in multisensory perception arise.

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Table 1.

Study	Age of participants (years) Younger	Older	Sensory modalities	Measure/task	Key result(s)
Speeded paradigms (response time enhancement)					
Couth et al., 2018	*M* = 21.3, *SD* = 5.2	*M* = 73.2, *SD* = 6.1	Auditory, visual, haptic	Speeded detection	Older adults showed greater multisensory RT enhancement under some conditions; size of race model violation correlated with unisensory response times
Diaconescu et al., 2013	20-29, *M* = 23.5, *SD* = 3.1	66-78, *M* = 69.9, *SD* = 4.8	Auditory, visual	Speeded detection; semantic classification; MEG	Both age groups showed multisensory RT enhancement in speeded detection task, neither in semantic classification; significant age differences in cortical responses to multisensory stimuli
Diederich et al., 2008	20-22	65-75, *M* = 69.6	Auditory, visual	Speeded saccadic localisation	Older adults showed greater multisensory RT enhancement
Laurienti et al., 2006	*M* = 28, *SD* = 5.6	*M* = 71, *SD* = 5.0	Auditory, visual	Speeded colour discrimination	Older adults showed greater multisensory RT enhancement
Mahoney et al., 2011	*M* = 19.2, *SD* = 2.7	*M* = 76.4, *SD* = 7.91	Auditory, visual, haptic	Speeded detection	Older adults showed greater multisensory RT enhancement from visual/haptic stimuli; age groups performed similarly for other pairings
Mahoney et al., 2015	N/A	66-92, *M* = 77.2, *SD* = 6.75	Visual, haptic	Speeded detection	Size of multisensory RT enhancement associated with amount of physical activity
Mahoney et al., 2019	N/A	*M* = 76.7, *SD* = 6.37	Visual, haptic	Speeded detection	Size of multisensory RT enhancement related to participants' history of falls
Mahoney, Holtzer, & Verghese, 2014	N/A	*M* = 75.1, *SD* = 6.29	Visual, haptic	Speeded detection	Size of multisensory RT enhancement related to participants' history of falls and static balance scores
Mahoney, Wang, et al., 2014	N/A	*M* = 74	Visual, haptic	Speeded detection	Stimulus location had no effect on size of multisensory RT enhancement

Study	Age of participants (years)		Sensory modalities	Measure/task	Key result(s)
	Younger	Older			
Mahoney & Verghese, 2018	N/A	*M* = 76.53, *SD* = 6.22	Visual, haptic	Speeded detection	Size of multisensory RT enhancement associated with some aspects of gait performance
Mahoney & Verghese, 2020	N/A	*M* = 76.9, *SD* = 6.5	Visual, haptic	Speeded detection	Cognitive impairment mediates a relationship between size of multisensory RT enhancement and unipedal balance scores
Murray et al., 2018	*M* = 22.0, *SD* = 3.9	Healthy: *M* = 72.7, *SD* = 6.2; MCI: *M* = 76.9, *SD* = 8.4	Auditory, visual	Speeded detection	Subset of healthy older adults showed greater multisensory RT enhancement; multisensory integration and sensory dominance metrics associated with mild cognitive impairment (MCI)
Peiffer et al., 2007	18-38	65-80	Auditory, visual	Speeded detection	Older adults showed greater multisensory RT enhancement
Stephen et al., 2010	20-33	65-78	Auditory, visual	Speeded spatial discrimination; MEG	Only younger adults showed multisensory RT enhancement; significant age differences in cortical responses to multisensory stimuli
Wu et al., 2012	22-28, *M* = 23.9	60-78, *M* = 68.6	Auditory, visual	Speeded spatial discrimination	Younger adults showed greater multisensory RT enhancement
Zou et al., 2017	*M* = 24.9	*M* = 67.7	Auditory, visual	Speeded spatial discrimination; EEG	Older adults showed greater multisensory RT enhancement; significant age differences in ERP responses to multisensory stimuli
Unspeeded paradigms (accuracy enhancement)					
Anderson Gosselin & Gagné, 2011	Experiment 1: 18-33, *M* = 23.5, *SD* = 3.6; Experiment 2: 20-43, *M* = 24.9, *SD* = 5.6	Experiment 1: 64-76, *M* = 69.0, *SD* = 4.0; Experiment 2: 65-77, *M* = 69.4, *SD* = 3.5	Auditory, visual	Comprehension of speech in noise	Addition of visual stimuli led to similar improvement in comprehension in both age groups; older adults expended more listening effort under all conditions

Study	Age of participants (years)		Sensory modalities	Measure/task	Key result(s)
	Younger	Older			
Dey & Sommers, 2015	*M* = 20.4, *SD* = 1.5	*M* = 71.98, *SD* = 7.2	Auditory, visual	Comprehension of speech in noise	For lexically easy task, addition of visual information improved comprehension similarly in both age groups; for lexically hard task, addition of visual information benefitted older adults less
Dobreva et al., 2012	18-30	65-81	Auditory, visual	Spatial localisation	Addition of visual stimuli improved localisation accuracy to a greater extent in older adults
Gordon & Allen, 2009	*M* = 20.0, *SD* = 1.8	*M* = 73.1, *SD* = 5.8	Auditory, visual	Comprehension of speech in noise	Addition of intact visual stimuli led to similar improvement in comprehension in both age groups; older adults benefitted less from degraded visual stimuli
Helfer, 1998	N/A	61-88, *M* = 72, *SD* = 7.68	Auditory, visual	Comprehension of speech in noise	Addition of visual information improved comprehension in older adults; accuracy of audiovisual speech recognition was inversely correlated with age
Huyse et al., 2014	*M* = 20.9, *SD* = 0.7	*M* = 68.3, *SD* = 0.9	Auditory, visual	Comprehension of speech in noise	Addition of intact visual stimuli led to similar improvement in comprehension in both age groups; older adults benefitted less from degraded visual stimuli
Legault et al., 2010	*M* = 23.5, *SD* = 2.6	*M* = 67.6, *SD* = 3.1	Auditory, visual	Comprehension of speech in noise	Addition of visual stimli, at various levels of degradation (blurring), improved comprehension to a similar degree in both age groups
Maguinness et al., 2011	18-30, *M* = 21.1, *SD* = 2.4	61-76, *M* = 68.6, *SD* = 1.1	Auditory, visual	Speech comprehension	Degraded visual signal led to impaired comprehension in older adults only
Roudaia et al., 2018	19-31, *M* = 26.0	61-76, *M* = 67.5	Auditory, visual	Detection of a moving stimulus among distractors	Presence of auditory stimuli improved detection in younger, but not older, adults
Sommers et al., 2005	*M* = 20.1, *SD* = 2.1	*M* = 70.2, *SD* = 6.8	Auditory, visual	Comprehension of speech in noise	Improvement in comprehension resulting from addition of visual stimuli was smaller in older adults; difference was accounted for by impaired lipreading ability
Stevenson et al., 2015	19-38, *M* = 22.8, *SD* = 4.7	45-67, *M* = 57.3, *SD* = 6.9	Auditory, visual	Comprehension of speech in noise	For whole-word recognition, younger adults benefitted more from the addition of visual stimuli; for phoneme recognition, the age groups performed similarly

Study	Age of participants (years) Younger	Older	Sensory modalities	Measure/task	Key result(s)
Tye-Murray et al., 2010	18-27, *M* = 23.0, *SD* = 2.1	65-85, *M* = 73.7, *SD* = 5.9	Auditory, visual	Comprehension of speech in noise	Addition of intact visual stimuli led to similar improvement in comprehension in both age groups; older adults benefitted less from degraded visual stimuli
Tye-Murray et al., 2016	22-30, *M* = 25.2 31-50, *M* = 43.6 51-65, *M* = 58.9 66-80, *M* = 74.8 81-92, *M* = 85.5		Auditory, visual	Comprehension of speech in noise	Addition of intact visual stimuli led to similar improvement in comprehension in all age groups
Winneke & Phillips, 2011	*M* = 24.5, *SD* = 3.4	*M* = 68.5, *SD* = 5.0	Auditory, visual	Comprehension of speech in noise; EEG	Addition of intact visual stimuli led to similar improvement in comprehension in both age groups; significant age differences in ERP responses to multisensory stimuli
Small conflicts – Crossmodal biases and perceptual illusions					
Bedard & Barnett-Cowan, 2015	18-28, *M* = 22, *SD* = 2.1	58-80, *M* = 69, *SD* = 6.3	Auditory, visual	Simultaneity judgement; temporal order judgement; stream/bounce illusion	Older adults susceptible to stream/bounce illusion across a wider range of SOAs; older adults less able to discern audiovisual temporal order; no age differences in synchrony judgement
Berard et al., 2012	*M* = 23.5, *SD* = 4.7	*M* = 76.2, *SD* = 3.1	Visual, proprioceptive, haptic, vestibular	Virtual reality navigation	Older adults less able to inhibit perturbed visual signals that conflict with other cues
Chancel et al., 2018	*M* = 29, *SD* = 10	*M* = 71, *SD* = 7	Visual, proprioceptive, haptic	Hand movement illusion	Older adults reported more salient visuohaptic illusions
Cienkowski & Carney, 2002	Normal group: *M* = 22.3, *SD* = 6.9; Threshold-shifted group: *M* = 21.7, *SD* = 2.9	*M* = 70.1, *SD* = 3.5	Auditory, visual	McGurk-MacDonald illusion	Age groups similarly susceptible to illusion; older adults' percepts biased towards visual

Study	Age of participants (years) Younger	Older	Sensory modalities	Measure/task	Key result(s)
DeLoss et al., 2013	*M* = 20.8, *SD* = 0.6	*M* = 75.7, *SD* = 5.1	Auditory, visual	Sound-induced flash illusion	Older adults more susceptible to illusion
DeLoss & Andersen, 2015	*M* = 23.2, *SD* = 4.3	*M* = 71.5, *SD* = 3.1	Auditory, visual	Sound-induced flash illusion	Age groups similarly susceptible to illusion
Deshpande & Patla, 2007	20-35	65-85	Visual, proprioceptive, haptic, vestibular	Locomotion with vestibular perturbation	Older adults less able to inhibit perturbed vestibular signals that conflict with other cues
Higgen et al., 2020	*M* = 24.1, *SD* = 2.5	*M* = 72.1, *SD* = 4.5	Visual, haptic	Crossmodal pattern matching	Older adults less able to determine congruence of visual and haptic patterns presented near perceptual threshold
Hirst et al., 2019	50-64, *M* = 58.4, *SD* = 3.5 65-74, *M* = 68.7, *SD* = 78.4 ≥75, *M* = 78.4, *SD* = 3.4		Auditory, visual	Sound-induced flash illusion	Susceptibility to illusion increased with age
Huyse et al., 2014	*M* = 20.9, *SD* = 0.7	*M* = 68.3, *SD* = 0.85	Auditory, visual	McGurk-MacDonald illusion	Older adults more susceptible to illusion, particularly under conditions of degraded stimuli
Jones et al., 2019	*M* = 19.5, *SD* = 1.6	*M* = 72.0, *SD* = 5.2	Auditory, visual	Ventriloquist illusion	Age groups similarly susceptible to illusion
McGovern et al., 2014	18-30, *M* = 24	65-88, *M* = 71	Auditory, visual	Sound-induced flash illusion	Older adults more susceptible to fission illusion; age groups similarly susceptible to fusion illusion
Park et al., 2020	18-35, *M* = 23.5	62-82, *M* = 69.0	Auditory, visual	Ventriloquist illusion	Age groups similarly susceptible to illusion
Parker & Robinson, 2018	5-12, *M* = 8.9, *SD* = 2.2 18-20, *M* = 19.3, *SD* = 0.7 62-89, *M* = 74.9, *SD* = 9.5		Auditory, visual	Sound-induced flash illusion	Limited age differences in susceptibility to illusion

Study	Age of participants (years)		Sensory modalities	Measure/task	Key result(s)
	Younger	Older			
Riemer et al., 2019	18-30, *M* = 23.3	65-79, *M* = 70.8	Visual, haptic, proprioceptive	Rubber hand illusion	Age groups similarly susceptible to illusion
Roudaia et al., 2013	*M* = 20.0, *SD* = 1.8	*M* = 67.7, *SD* = 6.3	Auditory, visual	Stream/bounce illusion	Age differences in illusion perception only present when point of coincidence was visually occluded
Scurry et al., 2019	Experiment 1: 18-28, *M* = 21.9, *SD* = 2.8; Experiment 2: 19-28, *M* = 22.6, *SD* = 2.9	Experiment 1: 65-73, *M* = 68.6, *SD* = 2.2; Experiment 2: 65-74, *M* = 69.0, *SD* = 2.3	Auditory, visual	Crossmodal duration perception	Age groups similarly susceptible to auditory-induced compression of visual stimulus duration, but older adults more susceptible to auditory-induced expansion of visual stimulus duration
Sekiyama et al., 2014	*M* = 20.4, *SD* = 0.9	*M* = 62.3, *SD* = 0.9	Auditory, visual	McGurk-MacDonald illusion	Older adults less able to inhibit incongruent visual signals
Setti et al., 2013	*M* = 22.0, *SD* = 4	*M* = 65.5, *SD* = 4	Auditory, visual	McGurk-MacDonald illusion	Older adults more susceptible to illusion
Setti et al., 2014	N/A	Training group: 61-86, *M* = 72.8, *SD* = 6.3; Control group: 70-83, *M* = 75.8, *SD* = 4.4	Auditory, visual	Temporal order judgement; sound-induced flash illusion	Training on a temporal order judgement task reduced older adults' susceptibility to the sound-induced flash illusion
Sun et al., 2020	18-26, *M* = 22	60-76, *M* = 64	Auditory, visual	Sound-induced flash illusion	Older adults less susceptible to illusion when presented in the context of preceding auditory stimulation

Large conflicts – Cross-sensory distraction and interference

Study	**Age of participants (years)**		**Sensory modalities**	**Measure/task**	**Key result(s)**
	Younger	**Older**			
Barrett & Newell, 2015	8-9, *M* = 8.8, *SD* = 0.4 12-14, *M* = 12.8, *SD* = 0.9 18-27, *M* = 20.9, *SD* = 2.2 60-79, *M* = 66.7, *SD* = 5.6		Auditory, visual	Spatial and object categorisation	Older adults' responses more impaired by presence of incongruent cross-sensory distractors
Campbell et al., 2010	18-29, *M* = 20.9, *SD* = 2.9	61-73, *M* = 67.1, *SD* = 4.2	Auditory, visual	Saccadic localisation	Age groups showed similar trajectory deviations in response to cross-sensory (and bisensory) distractors
Furman et al., 2003	20-30, *M* = 23.5, *SD* = 2.9	65-76, *M* = 69.3, *SD* = 3.2	Auditory, visual, vestibular	Various auditory reaction time tasks	Older adults' response times more impaired by presence of visual distractors
Guerreiro et al., 2013	20-27, *M* = 21.7, *SD* = 2.3	60-73, *M* = 65.4, *SD* = 3.7	Auditory, visual	Memory task with distraction	Only older adults' accuracy scores impaired by cross-sensory visual distraction
Guerreiro et al., 2014	19-29, *M* = 24.1, *SD* = 3.0	62-80, *M* = 68.7, *SD* = 5.1	Auditory, visual	Selective facial/voice recognition; EEG	Accuracy and RT scores similarly affected by cross-sensory distractors in both age groups; no relevant age differences observed in EEG data
Guerreiro et al., 2015	20-29, *M* = 23.4, *SD* = 2.9	60-71, *M* = 64.8, *SD* = 3.6	Auditory, visual	Memory task with distraction	Accuracy scores similarly affected by cross-sensory distractors in both age groups; no relevant age differences observed in EEG data
Guerreiro & Van Gerven, 2011	20-29, *M* = 22.3, *SD* = 2.2	61-77, *M* = 67.7, *SD* = 5.5	Auditory, visual	Memory task with distraction	Older adults' response times more impaired by presence of visual distractors
Mahboobin et al., 2007	22-33, *M* = 25, *SD* = 3	61-85, *M* = 73, *SD* = 8	Auditory, visual, proprioceptive, vestibular	Postural control with auditory distraction	Only older adults' postural control was impaired by auditory distraction
Mevorach et al., 2016	18-36, *M* = 23	63-85, *M* = 71	Visual, proprioceptive, haptic	Global/local visual attention task; reaching task with visual distraction	Older adults' response time and accuracy scores more impaired by visual distractors

Study	Age of participants (years)		Sensory modalities	Measure/task	Key result(s)
	Younger	Older			
Pitts & Sarter, 2018	19-27, *M* = 22.7, *SD* = 2.7	Working: 65-78, *M* = 68.2, *SD* = 3.8; Retired: 65-72, *M* = 68.3, *SD* = 2.2	Auditory, visual, haptic	Detection task during simulated driving	Older adults less accurate in most conditions, and more likely to miss unisensory components of simultaneous multisensory presentations
Poliakoff et al., 2006	19-25, *M* = 21.7 65-72, *M* = 69.4 76-92, *M* = 80.8		Visual, haptic	Location discrimination	Older adults' accuracy scores more impaired by cross-sensory visual distraction
Puschmann et al., 2014	20-30, *M* = 25, *SD* = 3	Normal hearing: 52-72, *M* = 63, *SD* = 7; Impaired hearing: 54-74, *M* = 65, *SD* = 5	Auditory, visual	Motion discrimination	Older adults' accuracy scores more impaired by cross-sensory distraction (both visual and auditory); degree of age-related hearing loss associated with susceptibility to visual distractors during auditory task
Redfern et al., 2009	21-34, *M* = 25.7, *SD* = 3.8	70-82, *M* = 74.2, *SD* = 4.4	Visual, proprioceptive, vestibular	Visual discrimination	In older adults, greater cross-sensory distractibility associated with increased postural sway
Townsend et al., 2006	18-41, *M* = 27.9, *SD* = 8	65-89, *M* = 70.7, *SD* = 7	Auditory, visual	Auditory and visual discrimination tasks; fMRI	Age groups affected similarly by presence of cross-sensory distractors; older adults show greater frontoparietal activation in response to incongruent stimuli
Cue weighting					
Bates & Wolbers, 2014	19-23, *M* = 21.6, *SD* = 1.2	60-82, *M* = 69.9, *SD* = 5.0	Visual, proprioceptive, vestibular	Spatial navigation with degraded/conflicting cues	Accuracy in both age groups improved by multisensory cues, but older adults underweighted visual information

Study	**Age of participants (years)**		**Sensory modalities**	**Measure/task**	**Key result(s)**
	Younger	**Older**			
Billino & Drewing, 2018	20-25, *M* = 22.5, *SD* = 1.6	69-77, *M* = 72.6, *SD* = 2.7	Visual, haptic	Length discrimination	Accuracy in both age groups improved by multisensory cues; cue weighting was approximately optimal only in older adults
Braem et al., 2014	*M* = 23.9, *SD* = 2.3	*M* = 53.5, *SD* = 6.9	Visual, haptic	Verticality judgement	Accuracy in both age groups improved by multisensory cues; cue weighting was approximately optimal in both age groups
Brooks et al., 2015	22-32, *M* = 26	60-74, *M* = 68	Auditory, visual	Flutter/flicker rate discrimination	Only younger adults' accuracy improved by multisensory cues; cue weighting was approximately optimal in both age groups
Couth et al., 2019	*M* = 21.8, *SD* = 6.0	*M* = 73.2, *SD* = 6.1	Visual, haptic	Length discrimination	Multisensory cues did not improve accuracy in either age group; cue weighting was sub-optimal in both age groups

Please note that studies are listed under the section in which they are first mentioned (i.e. no duplicates)