Older adults sacrifice response speed to preserve multisensory integration performance

Samuel A. Jones[1], Ulrik Beierholm[2], and Uta Noppeney[1]

[1]Computational Neuroscience and Cognitive Robotics Centre, University of Birmingham, UK

[2]Department of Psychology, University of Durham, UK

Corresponding author: Samuel A. Jones, Computational Cognitive Neuroimaging Laboratory, Computational Neuroscience and Cognitive Robotics Centre, School of Psychology, Hills Building, University of Birmingham, B15 2TT, UK. samjones.saj@gmail.com

Acknowledgements: This research was funded by the European Research Council (ERC-2012-StG_20111109 multsens) and the MRC-ARUK Centre for Musculoskeletal Ageing Research (CMAR)

Declarations of interest: none

Abstract

Ageing is thought to impact multisensory integration, but the underlying computational mechanisms are poorly understood. Signals that come from a common source should be integrated, weighted by their reliability; those that do not share a source should be segregated.

Combining psychophysics and Bayesian modelling we investigated how ageing affects audiovisual integration of spatial signals. Under unspeeded conditions, older and younger adults were comparable in their localisation responses and common-source judgements. Likewise, the Bayesian Causal Inference model fitted to observers' response choices indicated that sensory reliabilities and arbitration between integration and segregation were similar across age groups.

However, under speeded conditions, older observers were slower at localising sounds, particularly when they were paired with spatially incongruent visual signals. A Bayesian evidence accumulation model, fitted jointly to response choices and response times, revealed that older observers accumulate noisier auditory representations for longer, set higher decisional thresholds, and have impaired motor speeds. Thus, modelling the within-trial dynamics of multisensory evidence accumulation reveals that older observers preserve audiovisual localisation performance by sacrificing response speed.

1. Introduction

Throughout our lifetime we are continually exposed to a barrage of sensory signals. Our ability to navigate through and interact with the world relies on an accurate interpretation of this multisensory information. To quickly orient towards and identify a threat, for instance, we may rely on both the sound it makes and its appearance: what creature made that growl, where is it, and is it moving towards me? Previous research has demonstrated differences between younger and older adults in their responses to multisensory stimuli. For example, older adults have been shown to respond differently to multisensory perceptual illusions such as the sound-induced flash illusion (DeLoss et al., 2013; McGovern et al., 2014; Setti et al., 2011) and the McGurk-MacDonald effect (Sekiyama et al., 2014; Setti et al., 2013). Further, race-model analyses of reaction times have suggested that older adults may benefit more from congruent, redundant multisensory stimuli (Laurienti et al., 2006; Mahoney et al., 2011). The mechanisms underlying these changes in multisensory perception are unclear; they may be driven in part by age-related changes in sensory reliability (Lindenberger & Baltes, 1994; Salthouse et al., 1996) or higher cognitive functions such as selective attention or executive functions (Turner & Spreng, 2012).

To understand how ageing impacts human behaviour in a multisensory world, we thus need to analyse human behaviour from a computational perspective. Critically, there are two computational problems the brain must solve when integrating sensory signals. First, it must decide whether signals are produced by the same object or event (i.e. share a common source) and should therefore be integrated, or whether they originate from different sources and should be processed separately (segregated). Second, if signals originate from a common source, the brain should integrate them weighted in proportion to their relative reliabilities to obtain the most reliable (i.e. least variable) percept (Alais & Burr, 2004; Ernst & Banks, 2002; Fetsch et al., 2012; Helbig et al., 2012; Rohe & Noppeney, 2018). Thus, statistically optimal integration is dependent on the observer's ability to accurately estimate the reliability of each piece of information.

Hierarchical Bayesian Causal Inference (BCI) is a normative model that describes how the brain should solve these two computational problems. Bayesian Causal Inference explicitly models the potential causal structures that could have generated the sensory signals, i.e. whether

the signals originated from common or separate sources. If signals emanate from a common source they are integrated, weighted in proportion to their relative sensory reliabilities; if they come from independent sources, they are treated independently. To account for observers' uncertainty about the world's causal structure, a final estimate (e.g. object's location) is obtained by combining the estimates under the two causal structures (i.e. common vs. independent sources) according to some decision function (e.g. model averaging or model selection; Wozny et al., 2010). Accumulating evidence from psychophysics suggests that Bayesian Causal Inference accounts well for how human observers integrate and segregate sensory signals in the face of uncertainty about the world's causal structure (Koerding et al., 2007; Rohe & Noppeney, 2015a, 2015b; Shams & Beierholm, 2010; Wozny et al., 2010).

Given this computational framework, ageing may impact multisensory integration at several levels:

First, ageing may reduce the precision of the sensory representations as a result of changes in the peripheral sensory organs (e.g. presbycusis; Gates & Mills, 2005) or central neural processing (Li & Lindenberger, 2002; Salthouse et al., 1996). For instance, older adults have been shown to be less precise when locating sounds, especially in terms of elevation (Dobreva et al., 2011; Otte et al., 2013). Changes in sensory precision or reliability (represented by the variance parameters in the BCI model) will alter the sensory weights during the integration process, leading to changes in crossmodal bias (e.g. the influence of a displaced visual signal on an observer's perceived sound location).

Second, ageing may impair an observer's ability to focus selectively on signals in one sensory modality and ignore signals coming from irrelevant sources in other sensory modalities. Previous research has shown age-related impairments in the ability to focus selectively on task-relevant information in the context of irrelevant distractors, both within (Bugg et al., 2007) and between (Guerreiro & Van Gerven, 2011; Mevorach et al., 2016; Poliakoff et al., 2006) sensory modalities. From the perspective of Bayesian Causal Inference, impairments in selective attention and executive functions may lead to a stronger prior binding tendency (represented by the causal prior parameter in the BCI model), which in turn impacts the arbitration between sensory integration and segregation and the size of the binding window. In the temporal domain,

previous research has indeed shown a larger temporal binding window in older relative to younger adults (Diederich et al., 2008; McGovern et al., 2014).

Third, age-related changes in multisensory integration might also result from how, and for how long, observers of different ages accumulate information before reacting. Current models of hierarchical Bayesian Causal Inference make predictions only for response choices, but not for response times. They thus ignore the temporal dynamics and urgency of making a response. The real world is not so forgiving: one has limited time to react appropriately to a growling animal. To account for these additional temporal constraints we need a dynamic model that allows observers to accumulate multisensory information over time until a decisional threshold is reached and a response elicited. This extra consideration has a significant impact on the definition of optimal multisensory integration: we need to trade off response accuracy against speed and decide when sufficient evidence has been collected for us to respond effectively, a process which may change with age. Previous research in the unisensory domain has demonstrated that older adults use a different speed-accuracy trade-off (Smith & Brewer, 1995; Starns and Ratcliff, 2010), and accumulate evidence less efficiently for longer (Madden & Allen, 1995).

Fourth, ageing may not only influence computational parameters such as the sensory variance or causal prior in Bayesian Causal Inference, but even alter the computational principles that govern multisensory integration. For example, older adults may assign weights to sensory signals that are not in proportion to their reliabilities or perhaps no longer integrate at all, relying exclusively on one signal (see e.g. Gori et al., 2008 for similar results in children). In these cases, ageing would lead to behaviour that is no longer consistent with Bayesian Causal Inference and related models.

Combining psychophysics with Bayesian modelling, this study characterised how ageing affects the computational operations governing audiovisual integration for spatial localisation. First, we assessed i. observers' motor speed, ii. the reliability of their auditory and visual spatial representations, and iii. their executive functions / selective attention.

Second, we investigated how younger and older adults arbitrate between sensory integration and segregation for spatial localisation in an unspeeded spatial ventriloquist paradigm. Observers were presented with audiovisual signals that were synchronous but differed in their

spatial disparity across trials. They either judged whether audiovisual signals came from a common source (explicit causal inference) or located the auditory signals (implicit causal inference; Acerbi et al., 2018; Rohe & Noppeney, 2015).

Third, we investigated how younger and older observers integrate audiovisual signals for spatial localisation under time pressure in a simplified speeded ventriloquist paradigm. In standard analyses based on the general linear model we characterised observers' multisensory integration behaviour in terms of accuracy, crossmodal bias, or spatial integration window. Moreover, we fitted the Bayesian Causal Inference (for the unspeeded task) and compatibility bias (for the speeded task) models to observers' responses to formally assess whether ageing affects the computational principles or model parameters.

2. Methods

2.1. Participants

Twenty-four healthy older and twenty-three younger adults were recruited to the study from a database of participants maintained by the University of Birmingham's School of Psychology. We were unable to contact one older adult following his initial screening session, and a further three were later excluded from analysis: failure to meet inclusion criteria for any one task of the test battery resulted in exclusion from all analyses (see Supplementary Table 1). Three younger adults were also excluded. Therefore, 20 healthy older adults (six male, mean age = 72.4, *SD* = 5.2) and 20 younger controls (eight male, mean age = 19.1, *SD* = 0.9; three exclusions) were included in the study. All reported normal hearing and normal or corrected-to-normal vision. Older participants were also screened using the Montreal Cognitive Assessment; none scored below 25.

Participants gave informed consent prior to the commencement of testing, and were compensated in cash or research credits for their time. The research was approved by the University of Birmingham Ethical Review Committee.

2.2. Experimental Setup

Participants were seated at a chin rest 130 cm from a sound-transparent projector screen. Behind the screen, at the vertical centre, a shelf held an array of nine studio monitors (Fostex PM04n) spaced horizontally by 7° of visual angle, including a speaker in the middle of the screen. Auditory stimuli were presented via these speakers at approximately 75 dB SPL. The locations of the speakers were not known to participants. Images were displayed using a BENQ MP782ST multimedia projector at a total resolution of 1280 x 800. All stimuli were presented using The Psychophysics Toolbox 3 (Kleiner, Brainard, & Pelli, 2007) in MATLAB R2010b running on a Windows 7 PC.

Responses were made using a two-button response pad or optical mouse, and in all cases this was effectively self-speeded; the next trial would not begin until a valid response was made. However, for the cued Eriksen flanker and speeded ventriloquist tasks it was emphasised to participants that they should respond as quickly and as accurately as possible.

2.3. Stimuli

In all but the Eriksen flanker paradigm, visual stimuli consisted of a 50 ms flash of 15 white (88 cd/m²) dots, each 0.44° of visual angle in diameter, against a dark grey (4 cd/m²) background. Dot locations were sampled from a bivariate Gaussian distribution, with a constant vertical standard deviation of 5.4°. The horizontal standard deviation of this dot cloud was varied to manipulate the reliability of spatial information, with a wider cloud (expressed in degrees of visual angle) resulting in less reliable stimuli (Rohe & Noppeney, 2015). We define the horizontal standard deviations below for each experiment.

The auditory stimulus was a burst of white noise (duration: 50 ms) played from one speaker in the array in synchrony with the visual stimulus. Sounds were generated individually for each trial and ramped on/off over 5ms. Across all tasks participants fixated a central cross (0.22° radius) that was constantly presented throughout the entire experiment.

2.4. Experimental design, procedure and analysis

Participants completed a series of seven experiments. First, we assessed motor function (i.e. motor speed), reliability of unisensory spatial representations (i.e. sensory variance), and executive functions/selective attention. Second, using a spatial ventriloquist paradigm we investigated integration of audiovisual spatial signals in explicit (i.e. common source judgement) and implicit (i.e. spatial localisation) causal inference tasks in a non-speeded fashion that emphasised response accuracy. Third, we assessed audiovisual integration for spatial localisation under time pressure in a speeded simplified ventriloquist paradigm. All experiments included a short practice session prior to the first full block of trials.

Dependent variables (response accuracy, time etc.) were entered into general linear model based analyses (*t*-tests and mixed-effects ANOVAs as specified in the results section). For consistency across experiments and analyses, we report all effect sizes as eta-squared (η^2), or partial eta-squared (η^2_p) in the case of ANOVAs. P-values are reported Greenhouse-Geisser corrected for sphericity violations where required, and Welch's *t*-test was used in cases of unequal variances.

2.4.1. Finger tapping – motor speed

This task was used to assess participants' motor speed. Participants were instructed to ball

their hand into a fist, extending their index finger, and to repeatedly tap a key as quickly as possible for 20 seconds. An on-screen progress bar and countdown provided feedback on performance and time remaining. The task was repeated four times (twice per hand, not including a preceding 10-second practice with each hand).

2.4.2. Unisensory auditory and visual left/right discrimination

Participants' spatial hearing performance (i.e. bias and reliability/variance of auditory spatial representations) was measured using a forced left/right spatial discrimination task. Individual bursts of white noise were emitted from one of seven locations (-21°, -14°, -7°, 0°, 7°, 14°, or 21°) in a random order. Participants indicated as accurately as possible via key press whether the sound originated from the left or right half of the screen. This task involved one block of 210 trials (30 per location).

Participants' visual spatial perception (i.e. bias and variance/reliability of visual spatial representations) was measured using a similar left/right spatial discrimination task. Visual stimuli with horizontal *SD* = 2° or 25° were randomly presented centred at one of seven locations (-21°, -14°, -7°, 0°, 7°, 14°, or 21°); participants indicated whether the centre of the dot cloud originated from the left or right side of the screen. This task involved two blocks of 210 trials each (total 30 trials per condition).

2.4.3. Unisensory auditory and visual spatial localisation - continuous responses

Participants' ability to freely localise auditory stimuli was assessed using a unisensory mouse localisation paradigm. On each trial, individual auditory stimuli were presented randomly from one of five locations (-14°, -7°, 0°, 7°, or 14°). After a 500ms post-stimulus delay a mouse-controlled cursor (white, subtending 9° in height and 0.5° wide) whose movement was constrained to the horizontal plane was presented. Participants reported the perceived sound location as accurately as possible in an unspeeded fashion by moving this cursor and clicking with the mouse button. The next trial was started one second after observers had indicated their perceived auditory location.

Localisation of visual stimuli was assessed using a similar paradigm. Visual stimuli were randomly presented at one of five locations (-14°, -7°, 0°, 7°, or 14°) with one of three spatial reliability levels (horizontal *SD* of 2°, 6° or 16°). A fourth level of visual reliability was excluded

from the analysis because the dots were erroneously sampled. After a 500ms post-stimulus delay a mouse-controlled cursor (white, subtending 9° in height and 0.5° wide) whose movement was constrained to the horizontal plane was presented. Participants reported the perceived centre of the visual stimulus as accurately as possible in an unspeeded fashion by moving this cursor and clicking with the mouse button.

2.4.4. Cued Eriksen flanker

A replication of a design conceived by Callejas et al. (2004), based on Fan et al.'s (2002) attentional network task, the cued flanker paradigm assessed three components of attention: alerting, orienting, and executive function. This speeded task conformed to a 2 (cueing sound present/absent) x 3 (orienting stimulus congruent/incongruent/absent) x 2 (flankers congruent/incongruent) design. The cueing sound was a 2000 Hz beep of 50 ms duration, and was present on half of the trials to manipulate alertness. On two thirds of the trials, this was followed (after a 400ms delay) by an orienting stimulus: an asterisk, 1.5° either above or below fixation, presented for 50 ms. The location of the asterisk was uninformative about the location of the subsequent flanker stimulus. On each trial, a standard Eriksen flanker stimulus (Eriksen & Eriksen, 1974) was then presented at 1.5° visual angle either above or below the fixation cross until a response was given. The Eriksen flanker stimulus comprised a target arrow pointing towards the left or right, flanked by distractor arrows (two either side) that were either congruent or incongruent in direction with respect to the target arrow (each of length 1° visual angle, 0.44° separation). The observer decided as quickly and accurately as possible whether the target arrow was directed towards the left or right. This cued flanker task included 192 trials (i.e. 16 trials for each of the 2 x 2 x 3 conditions). Further details of the paradigm can be found in Callejas et al. (2004) and Fan et al. (2002).

2.4.5. Unspeeded ventriloquist paradigm – sound localisation (implicit causal inference)

In a spatial ventriloquist paradigm, auditory and visual stimuli were presented synchronously at either the same or different locations. In an auditory selective attention task, observers reported the location of the sound. On each trial auditory and visual stimuli were independently sampled from five locations (-14°, -7°, 0, 7, or 14°), and could therefore be

spatially congruent or incongruent with varying levels of disparity (0°, 7°, 14° , 21°, or 28°). Visual stimuli had three levels of reliability (horizontal *SD* of 2°, 6° or 16°) (n.b. a fourth level of visual reliability was excluded from the analysis because the dots were erroneously sampled). The paradigm thus conformed to a 5 (A locations) x 5 (V locations) x 3 (V reliabilities) factorial design.

After a 500ms post-stimulus delay participants reported the perceived sound location as accurately as possible in an unspeeded fashion by moving a mouse-controlled cursor (white, subtending 9° in height and 0.5° wide) whose movement was constrained to the horizontal plane. The next trial was started one second after observers clicked the mouse button. Trials were presented pseudorandomly in 200-trial blocks. In total, participants completed 600 trials = 8 (repetitions) x 5 (A locations) x 5 (V locations) x 3 (V reliabilities).

2.4.6. Unspeeded ventriloquist paradigm – common-source judgement (explicit causal inference)

This experimental paradigm conformed again to a 5 (A locations) x 5 (V locations) x 3 (visual reliabilities) factorial design, using the stimulus combinations described above (5). However, in this case participants explicitly judged whether or not auditory and visual signals originated from the same location (i.e. common-source judgement). 500ms after the presentation of the flash and beep, the words “same” and “different” appeared respectively above and below the fixation cross. Participants indicated with a button press whether the sound and flash were generated by a common event. In total, participants completed 600 trials = 8 (repetitions) x 5 (A locations) x 5 (V locations) x 3 (V locations), delivered in three blocks of 200 trials.

2.4.7. Speeded ventriloquist paradigm – auditory and visual left/right discrimination (implicit causal inference)

To assess the impact of audiovisual spatial congruence on spatial localisation (i.e. response choices) and reaction times we used a simpler, speeded 2 (auditory location: left vs. right) x 2 (visual location: left vs. right) x 2 (relevant and reported sensory modality: auditory vs. visual) ventriloquist paradigm. On each trial, a visual stimulus with horizontal *SD* = 5.4° was displayed simultaneously with a burst of white noise. The centre of the visual cloud and the white noise were presented at 14° either left or right of a central fixation cross. These audiovisual stimuli

were spatially congruent on half of the trials, and incongruent on the other half. In an auditory or visual selective attention paradigm, participants indicated either the location of the sound (respond-auditory task) or the centre of the cloud (respond-visual task) as quickly and accurately as possible via a two-choice key press, while ignoring the other modality. The tasks were performed in two blocks of 160 trials. The order of these tasks was counterbalanced between participants. In total the experiment included 320 trials: 40 (repetitions) x 2 (visual location) x 2 (auditory location) x 2 (reported sensory modality).

2.5. Computational modelling

In addition to the standard general linear model (GLM) analyses described above, we also analysed participants' behaviour in the unspeeded (sections 2.4.5 and 2.4.6) and speeded (section 2.4.7) ventriloquist paradigms using Bayesian Causal Inference and the compatibility bias model respectively (see supplementary methods for details about model implementation and estimation).

2.5.1. Bayesian Causal Inference model for unspeeded ventriloquist paradigms

The Bayesian Causal Inference model (Figure 1A) explicitly models whether two sensory signals come from common or independent sources. Under the assumption of a common source, the sensory estimates (e.g. location) are combined, weighted according to their reliabilities. Under the hypothesis of independent sources, the signals are treated independently. The brain infers the causal structure (i.e. common or independent sources) from the sensory inputs and computes a final (e.g. spatial) estimate by averaging the estimates from the two causal structures weighted by their posterior probabilities. The Bayesian Causal Inference model included the causal prior p_{common}, the spatial prior standard deviation σ_P, the auditory standard deviation σ_A, and three visual standard deviations σ_{V1}, σ_{V2}, σ_{V3} corresponding to the three visual reliability levels, as free parameters. These were fit jointly to localisation and common source judgments of the non-speeded ventriloquist paradigm, individually for each observer.

2.5.2. Bayesian compatibility bias model for speeded ventriloquist paradigm

In the speeded ventriloquist paradigm observers were asked to make left/right spatial discrimination responses as accurately and *fast* as possible. To account for these temporal constraints, we adapted the "compatibility bias" model that models the within-trial dynamics of audiovisual evidence accumulation leading to predictions for both response choice and response

times (Yu et al., 2009). The compatibility bias model assumes that the visual and auditory sources can either be spatially congruent (both left or both right) or incongruent (e.g. visual source left and auditory source right). During the course of each auditory report trial, observers accumulate evidence concomitantly about (i) the 'true' (i.e. congruent or incongruent) relationship of the auditory and visual signals and (ii) the spatial location of the auditory source. The interference of spatially incongruent visual information should then be particularly pronounced at trial onset. The accumulation process is terminated when the evidence about the auditory spatial location reaches a decisional threshold and a left/right spatial discrimination response is made. In total the model has five free parameters: the compatibility prior (i.e. prior probability of audiovisual signals coming from a common cause) β; the standard deviation of the auditory and visual signals, σ_A and σ_V respectively; the response threshold q; and a non-decision-time parameter t_{nd}. These were fit jointly to response times and final auditory spatial discrimination responses in the speeded ventriloquist paradigm, individually for each observer.

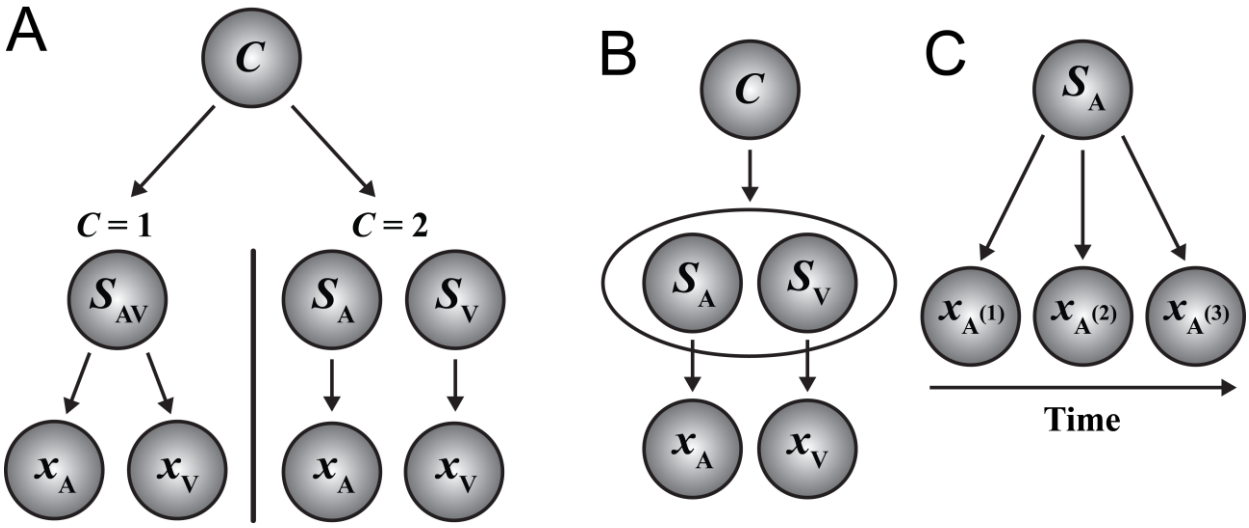

Figure 1. Generative models. (A) Bayesian Causal Inference (BCI) model, based on Koerding et al. (2007). Auditory (x_A) and visual (x_V) signals may be generated by one common ($C = 1$) audiovisual source (S_{AV}), or by separate ($C = 2$) auditory (S_A) and visual (S_V) sources. (B and C) Compatibility bias model, adapted from Yu et al. (2009). B. Auditory (S_A) and visual (S_V) sources can either be congruent ($C = 1$, i.e. in same hemifield) or incongruent ($C = 2$, i.e. in opposite hemifields). Across time, the auditory source generates a series of auditory inputs, and the visual source a series of visual inputs, in an independent and identical fashion (partly shown for the auditory source in C).

2.5.3. Comparison of model parameters between younger and older adults

To investigate whether any of the parameters of these two Bayesian models were significantly different between older and younger adults the fitted parameters were entered into separate non-parametric Mann-Whitney *U* tests. We also calculated Bayes factors using the Bayesian Mann-Whitney test as implemented in JASP (JASP Team, 2018; van Doorn et al., 2018) using the default Cauchy prior (scale = 0.707). In this case, Bayes factors (BF_{10}) represent the probability ratio of the alternative (Hypothesis 1) relative to the null hypothesis (Hypothesis 0). A Bayes factor of > 3 is considered positive evidence for the alternative hypothesis.

3. Results

In the following we focus on the statistically significant results across the different tasks, as well as effects related to aging. The statistics of all significant and non-significant effects are comprehensively summarised in supplementary tables S2-S7.

3.1. Finger tapping – motor speed

The effect of age on motor speed was measured using a speeded finger-tapping task. We analysed the data in terms of the mean time between finger taps in seconds. A two-sample Welch's *t*-test confirmed that younger participants ($M = 0.180$, $SD = 0.014$) were significantly faster than their older counterparts ($M = 0.202$, $SD = 0.027$), $t(28.772) = -3.269$, $p = .003$, $\eta^2 = 0.220$.

3.2. Unisensory auditory and visual left/right discrimination

Participants' auditory and visual spatial reliability (or precision) and left/right bias were assessed using unisensory left/right discrimination tasks. For each participant and stimulus type, we used the Palamedes toolbox for MATLAB (Prins & Kingdom, 2009) to calculate the just-noticeable difference (JND at the at the 84% level; Ernst, 2006) and point of subjective equality (PSE) of cumulative Gaussians fitted to the proportion of "perceived right" responses as a function of true stimulus location. The threshold α and slope β of these functions were allowed to vary freely, while the lapse parameters γ and λ were constrained to fall between 0 and 0.05 (Wichmann & Hill, 2001).

Results are summarised in Figure 2 (top row). In general, older and younger adults were closely matched on these tasks. For auditory spatial discrimination, an independent-samples *t*-test revealed no significant effect of age on JND values, and a Welch's *t*-test showed only a marginally significant effect on PSE values with a stronger bias towards responding "right" for older adults.

For visual discrimination, a 2 (age) x 2 (reliability) mixed ANOVA of JND values revealed a strong main effect of spatial reliability, as expected, but no main effect of age or age x reliability interaction. A similar mixed ANOVA of PSE values revealed no significant main effects of age or reliability, nor any interaction. See Supplementary Table S2 for full details.

3.3. Unisensory auditory and visual spatial localisation - continuous responses

Unisensory spatial localisation was assessed using mouse-cursor localisation tasks. We derived three performance indices by fitting a linear regression model (with true stimulus location as the predictor variable) to each participant's localisation responses. The slope (i.e. non-dimensional units) of this line provides an approximate measure for observers' central bias in responses, while the intercept represents biases to the left or right of space (in degrees of visual angle). Finally, the root mean squared error (RMSE) between the response data and the fitted line is a measure of reliability.

The age groups also performed similarly at these tasks (Figure 1, bottom row). For auditory localisation, *t*-tests on RMSE values (as an index for response reliability) and intercept values (as a measure of left/right bias) revealed no significant differences between age groups. However, older adults did show significantly smaller slope parameters, indicating a stronger central bias.

Younger and older adults were similarly matched at visual localisation: 2 (age) x 2 (reliability) mixed ANOVAs of RMSE, intercept, and slope values showed no significant effects of age. We only observed a significant main effect of spatial reliability for all three parameters: participants' responses were less reliable (RMSE), had a stronger rightward bias (intercept), and showed a weaker central bias (slope) as the visual stimulus decreased in reliability (larger horizontal *SD*). None of these were found to interact with age. See Supplementary Table S3 for further details.

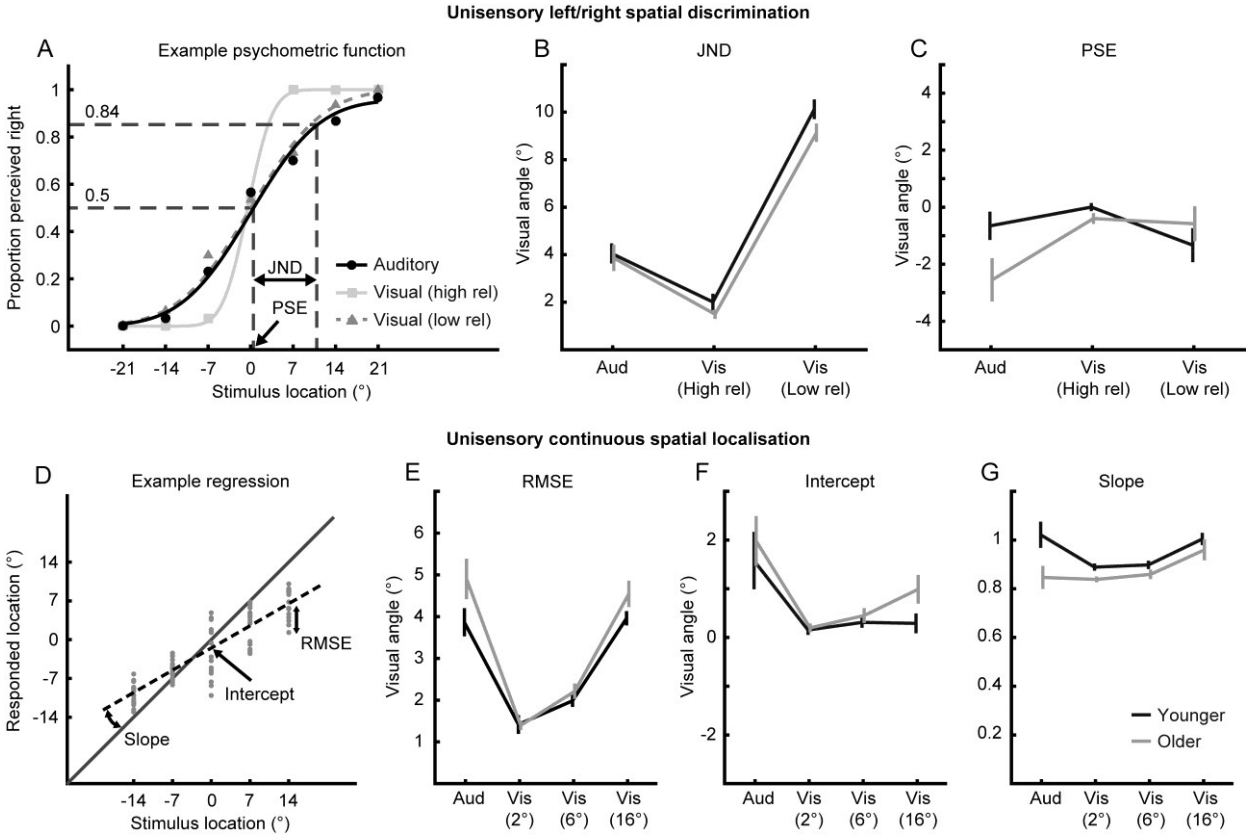

Figure 2. Unisensory auditory and visual spatial discrimination (top row) and localisation (bottom row) in younger and older adults. Top row: Left/right spatial discrimination. (A) Example psychometric function fit to left/right response data for one participant in three conditions, showing calculation of reliability (JND) and bias (PSE). (B and C) Mean (± *SEM*) JND and PSE values for younger and older participants. Bottom row: Continuous spatial localisation. (D) Example continuous-response data for one participant in one condition, with the fitted regression line and derivation of reliability (RMSE), left/right bias (intercept), and central bias (slope) measures. (E, F, and G) Group mean (± *SEM*) of RMSE, intercept, and slope values for younger and older adults in the continuous-response localisation tasks.

3.4. Cued Eriksen flanker

The cued Eriksen flanker task aimed to assess age differences in three attentional networks: alerting, orienting, and executive function. Results are summarised in Figure 3. A 2 (age) x 2 (cueing sound present/absent) x 3 (orienting stimulus congruent/incongruent/absent) x 2 (flankers congruent/incongruent) mixed ANOVA of median response times revealed a main effect of age: older participants were significantly slower than the younger age group. We also observed significant main effects of beep cue (alerting), spatial cue (orienting), and flanker congruence (executive function) on RTs, but these did not interact with age or with each other.

Accuracy in this task was defined as the proportion of left/right responses that were consistent with the direction of the target arrow. Main effects of age and flanker congruence in a mixed ANOVA of accuracy scores revealed that older adults were significantly more accurate overall, and that accuracy was lower in trials with incongruent flankers. We also observed a significant interaction between age and congruency: older adults showed a stronger effect of congruency than younger adults. No other main effects or interactions were significant. See Supplementary Table S4 for further details.

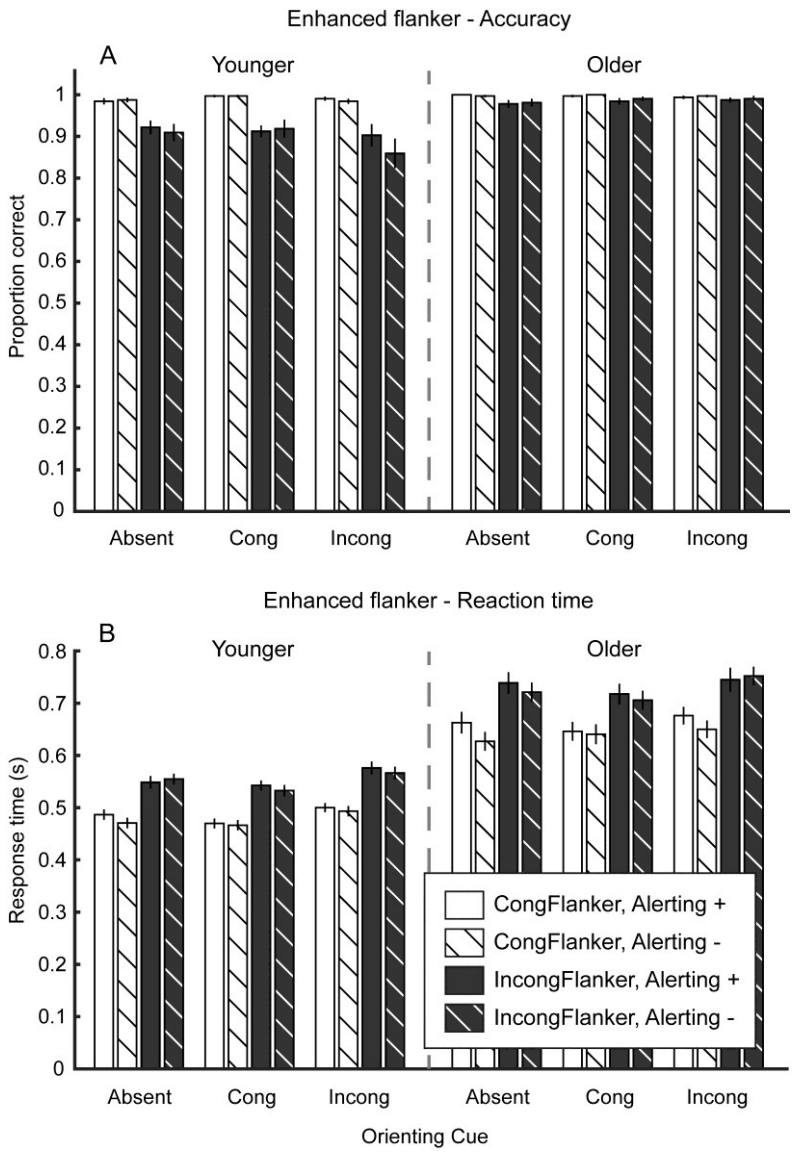

Figure 3. Performance accuracy and response times on the cued Eriksen flanker task. (A) Performance accuracy (across-participants mean ± 1 *SEM*) in each condition: alerting cue present/absent, orienting cue present/absent, flanker arrows congruent/incongruent. (B) Median response times (across-participants mean ± 1 *SEM*).

3.5. Unspeeded ventriloquist paradigm – sound localisation (implicit causal inference)

In order to quantify the effect of a simultaneous visual stimulus on the perceived location of a sound (Figure 4A), we analysed the reported sound location in terms of the relative crossmodal bias (*CMB*). This is defined as the distance between the actual and the responded location, scaled by the size of the audiovisual spatial disparity, $CMB = (A_{resp} - A_{loc})/(V_{loc} - A_{loc})$. A 2 (age) x 4 (conflict size [pooled over direction]) x 3 (visual reliability) mixed ANOVA showed that age had no main effect on crossmodal bias, nor did it interact with any other factors. As anticipated, we observed a significant main effect of conflict size and visual reliability: the crossmodal bias was greater at smaller audiovisual conflict sizes and for more reliable visual stimuli. These factors also significantly interacted. In sum, the crossmodal bias or ventriloquist effect followed an expected pattern, but did not differ between age groups.

Aside from a main effect of age, response times did not differ significantly between conditions. This is unsurprising, as mouse movements are far more variable (and take much longer) than button presses, so any small effects of condition are likely to be lost. See Supplementary Table S5 for full details.

3.6. Unspeeded ventriloquist paradigm – common-source judgement (explicit causal inference)

Common-source judgements provide an explicit measure of participants' tendency to integrate or segregate audiovisual stimuli under various conditions. Responses are analysed in terms of the proportion of "same source" responses in each condition (Figure 4C). The 2 (age) x 5 (conflict size) x 3 (reliability) mixed ANOVA on these values revealed no main effect of, or interaction with, age. As expected, the proportion of same-source responses was significantly higher when the auditory and visual stimuli were closer together and when visual stimuli were more reliable. These factors also interacted, suggesting audiovisual disparity was a more informative cue to integration when stimulus reliability was higher.

Age had no significant effect on any parameter of the Gaussians fitted to the above responses. The height parameter was significantly affected by the reliability of the stimuli, but the mean and width were not.

Reaction times in this common-source judgement task do reveal several age-related effects. A main effect of age in the mixed ANOVA of reaction times confirmed that older adults were slower overall. Furthermore, age interacted significantly with visual reliability and audiovisual disparity, and the three-way interaction was also significant. Main effects of reliability and disparity were also apparent, as was the interaction between these.

In summary, ageing did not influence observer's explicit causal inference in terms of response choices (i.e. "same source" responses). However, ageing influenced observers' response times interactively with visual reliability and audiovisual disparity. See Supplementary Table S6 for further details.

3.7. Bayesian Causal Inference model – Unspeeded ventriloquist paradigms

The Bayesian Causal Inference model was fitted jointly to auditory localisation and common-source judgement responses individually for each participant. Table 1 summarises the parameters of these fits, including nonparametric significance tests of group differences and corresponding Bayes factors. In agreement with the GLM-based analyses above, there was no evidence of a between-group difference for any of the fitted parameters. In particular, we observed no significant differences across groups for the causal prior as an index for observer's integration and segregation tendency, or their auditory or visual variances (σ_A, $\sigma_{V1\text{-}V3}$). Collectively, these results suggest that older and younger observers arbitrate between integration and segregation similarly and weight signals in proportion to their relative uncertainties. Moreover, ageing does not significantly affect the sensory reliability of auditory or visual representations in our older group.

Table 1. Bayesian Causal Inference parameters (across-participants mean), Mann-Whitney *U* tests, and Bayes factors

		P_{common}	σ_P	σ_A	σ_{V1}	σ_{V2}	σ_{V3}
Younger (n = 20)	*Mean*	0.389	41.455	8.464	2.247	4.659	15.408
	SD	0.128	29.117	3.740	5.529	5.907	10.588
Older (n = 20)	*Mean*	0.403	35.711	9.174	0.996	4.300	17.780
	SD	0.118	25.991	4.241	2.894	7.866	16.662
Mann-Whitney	*U*	188	172	172	158	154	200
	p	.745	.449	.449	.256	.213	> .999
	η^2	.003	.014	.014	.032	.039	0
Bayes factors	BF_{10}	0.342	0.441	0.378	0.530	0.475	0.321
	BF_{01}	2.924	2.694	2.266	1.887	2.106	3.120

Note. Bayesian Causal Inference parameters (across-participants mean, *SD*) for younger and older participants. Mann-Whitney *U* tests with Bayes factors comparing the BCI parameters between older and younger adults: the causal prior p_{common}, standard deviation of the spatial prior σ_P, standard deviation of the auditory noise σ_A, and standard deviation of visual noise for each of the three visual reliability levels σ_{V1}, σ_{V2}, and σ_{V3}. BF_{01} quantifies evidence for the null hypothesis that there is no difference between groups relative to the alternative hypothesis; BF_{10} quantifies the evidence for the alternative hypothesis that the groups differ relative to the null-hypothesis. A Bayes factor > 3 is considered positive evidence.

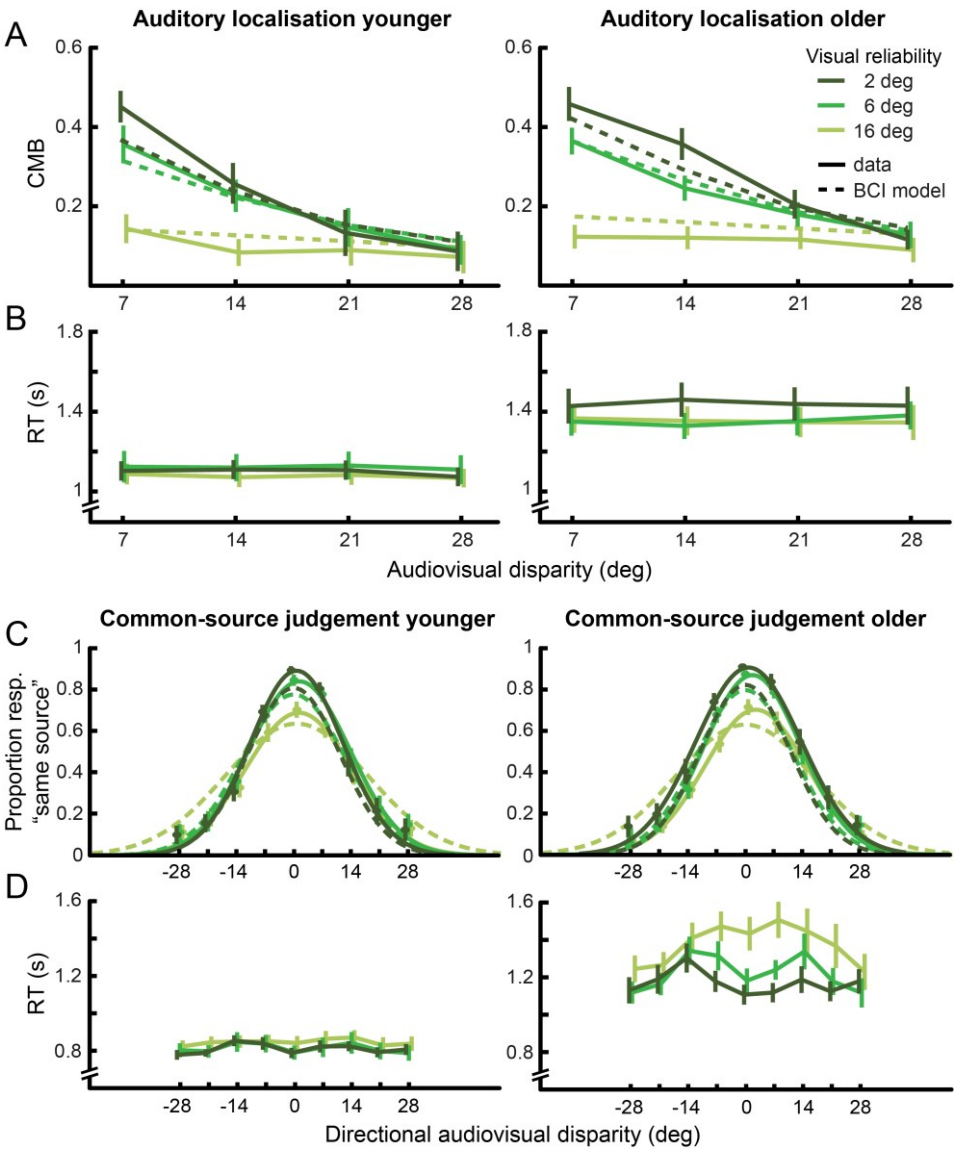

Figure 4. Behavioural responses, reaction times and BCI model predictions for younger and older adults. (A) Relative crossmodal bias (CMB = $[A_{resp} - A_{loc}] / [V_{resp} - [V_{loc}])$ for auditory localisation, shown as a function of audiovisual disparity (*x*-axis, pooled over direction) and visual reliability (colour coded). The panels show the behavioural data (across subjects' mean ± *SEM*, solid lines) and the predictions of the Bayesian Causal Inference model (BCI, dashed lines) (B) Reaction times in auditory localisation task. (C) Proportion reported "common source" in common-source judgement task, as a function of audiovisual disparity and visual reliability. The panels show the Gaussians fitted to the behavioural response (across subjects' mean ± SEM, solid lines) and the predictions of the Bayesian Causal Inference model (BCI, dashed lines) (D) Reaction times (across subjects' mean ± *SEM*, solid lines) (pooled over response) in common-source judgement task.

3.8. Speeded ventriloquist paradigm – auditory and visual left/right discrimination (implicit causal inference)

The speeded ventriloquist paradigm assessed how older and younger adults integrate AV signals into spatial responses under time pressure. For GLM-based (ANOVA) analysis, trials were pooled over left and right locations (instead characterised as spatially congruent or incongruent). Accuracy was quantified as the proportion of correct localisation responses per condition. See Figure 4 for a summary.

For auditory responses, a 2 (age) x 2 (congruence) mixed ANOVA on performance accuracy showed that participants were significantly less accurate when locating incongruent than congruent audiovisual stimuli (i.e. main effect of congruency). However, we did not observe any main effect of age or any interaction between age and congruency.

A 2 (age) x 2 (AV congruence) mixed ANOVA revealed a main effect of age, confirming that older participants reacted more slowly overall. Importantly, we also found an interaction between the effects of age and congruence, indicating that older participants' response times were more affected by audiovisual spatial (in)congruence than younger adults. Further, we observed a main effect of congruence: participants were generally faster when the visual distractor was spatially congruent with the auditory target.

For visual responses, 2 (age) x 2 (AV congruence) mixed ANOVAs on performance accuracy and response times showed that participants were again significantly more accurate and faster on congruent than incongruent trials. Further, older participants were more accurate overall. See Supplementary Table S7 for more details.

3.9. Compatibility bias model – Speeded ventriloquist paradigm

A compatibility bias model was fitted to participants' auditory spatial discrimination responses and reaction times; this allowed us to characterise how younger and older observers accumulate audiovisual evidence about spatial location and audiovisual congruency until a decisional threshold is reached. Fitted parameters were compared using separate Mann-Whitney *U* tests and a Bayesian equivalent. See Supplementary Table 2 for a summary of results. Corroborating the findings of the BCI model of unspeeded spatial localisation, the age groups did not differ in their prior tendency to integrate multisensory stimuli, characterised in this case by the

parameter β. The groups did not differ either in the reliability of visual input σ_V. However, the remaining three parameters were significantly different between the groups. First the non-decision time t_{nd}, which captures the time between a decision is made and the response given, was significantly higher for the older age group. This is unsurprising, and consistent with the reduced motor speed seen for older adults in the finger tapping task. Second, older adults also set their decision threshold q significantly higher, requiring more evidence before deciding on a response. This is consistent with the increase in performance accuracy for older adults in the cued Eriksen flanker task. Third, and crucially, the auditory signal (σ_A) was significantly noisier in older than younger adults, leading to a slower accumulation of evidence and thus slower response times (in combination with the motor slowing and higher decision threshold). This indicates that it takes older participants longer than their younger counterparts to reach any given level of evidence about the location of an auditory stimulus. See Figure 5A for an illustration of the model.

Table 2. Compatibility bias model parameters (across-participants mean), Mann-Whitney *U* tests, and Bayes factors

		σ_{auditory}	σ_{visual}	β	q	t_{nd}
Younger (n = 20)	*M*	0.887	0.681	0.804	0.918	0.234
	SD	0.397	0.999	0.103	0.046	0.058
Older (n = 20)	*M*	1.424	0.500	0.772	0.943	0.358
	SD	0.857	0.387	0.140	0.072	0.068
Mann-Whitney *U*	*W*	291.0	218.0	195.5	291.0	355.0
	p	**0.013**	0.640	0.914	**0.013**	**< .001**
	η^2	0.151	0.006	0	0.151	0.439
Bayes factors	BF_{10}	6.172	0.313	0.329	2.531	162.239
	BF_{01}	0.162	3.196	3.038	0.395	0.006

Note. Compatibility bias parameters (across-participants mean, *SD*) for younger and older participants. Mann-Whitney *U* tests with Bayes factors comparing the compatibility bias parameters between older and younger adults: standard deviation of the auditory signal σ_A, standard deviation of the visual signals σ_V, compatibility prior β, response threshold q, and non-decision-time t_{nd}. BF_{01} quantifies degree of support for the null hypothesis that there is no difference between groups; BF_{10} shows degree of support for the alternative hypothesis that the groups differ.

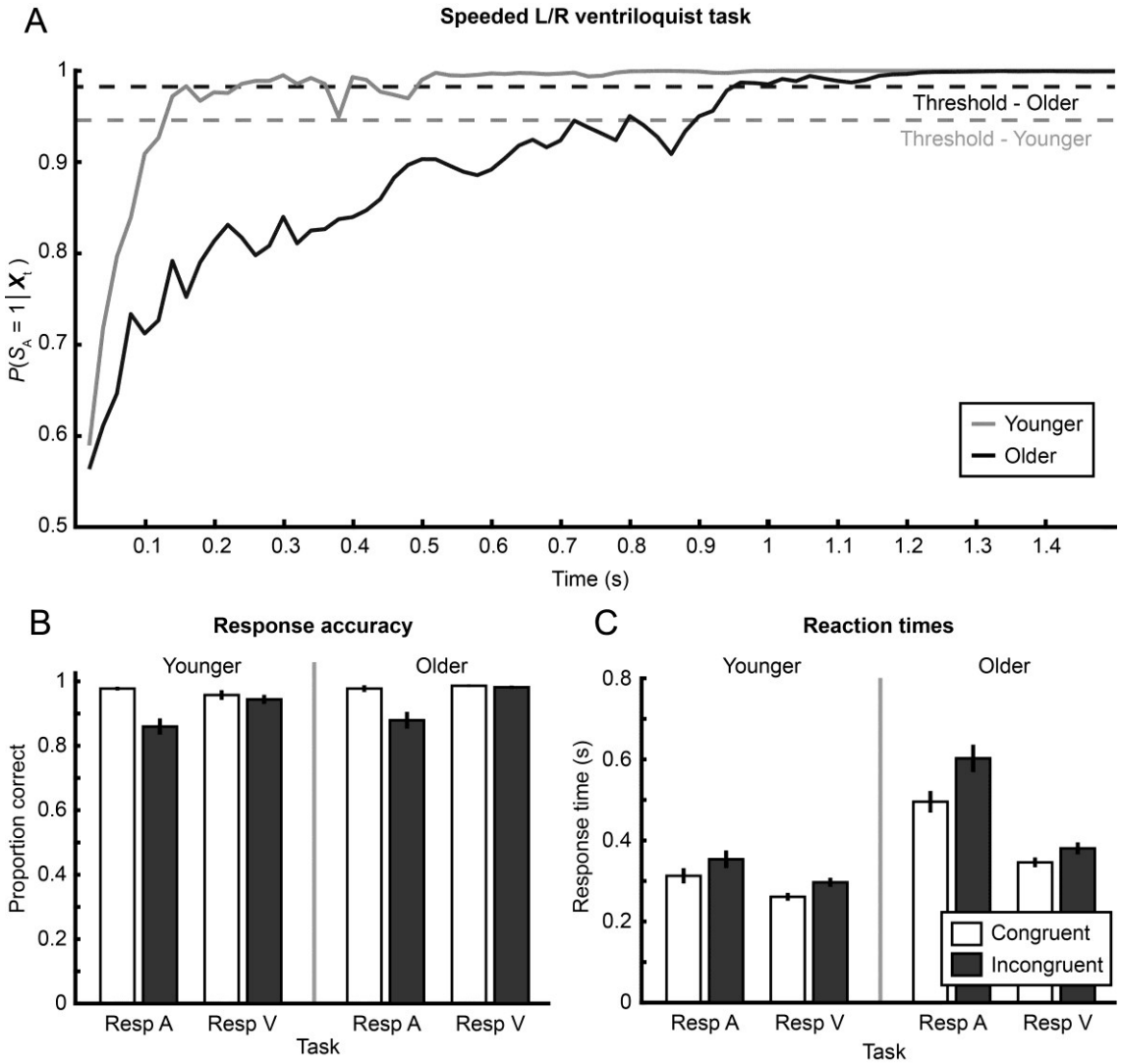

Figure 5. Speeded left/right ventriloquist paradigm and compatibility bias model. (A) Accumulation of evidence traces for the compatibility bias model: for 'respond auditory' trials the observer is thought to accumulate audiovisual evidence about whether the auditory source is left = -1 or right = 1 within a trial until a decisional threshold is reached and a response elicited. Solid lines show the posterior probability $P(S_A = 1|\boldsymbol{X}_t)$ as a function of within-trial time with auditory and visual inputs arriving every 10 ms. Each trace represents the mean across ten (incongruent, auditory right) simulated trials for a representative participant in each group (dark grey = older, light grey = younger participants), using each participant's maximum likelihood parameters. Dashed lines indicate these participants' fitted decisional thresholds. Older observers accumulate noisier evidence until a higher decisional threshold is reached. (B and C) Response accuracy and reaction times (across-participants mean ± 1 *SEM*) for respond-auditory and respond-visual tasks, separated by spatial congruence (i.e. pooled over left and right).

4. Discussion

This study investigated how older and younger adults solve the two computational challenges facing the brain in an uncertain multisensory world: i. causal inference and ii. reliability-weighted integration. To determine the role of sensory acuity and selective attention or executive functions (Tsvetanov et al., 2013) in these multisensory computations, we assessed participants' auditory and visual reliability and biases in spatial localisation, as well as their attentional/executive functions (as measured by a cued Eriksen flanker task).

Surprisingly, the GLM analyses of common-source judgement and crossmodal bias responses, as an index of visual influence on observers' perceived sound location, suggested that older and younger adults are comparable in both their explicit (i.e. common source judgement) and implicit (i.e. spatial localisation) causal inference. As expected, greater spatial disparities and lower visual reliability levels led to decreases in crossmodal bias and the proportion of common-source judgements, but this pattern was similar between age groups. These findings were confirmed by our Bayesian Causal Inference analysis, which formally computed visual and auditory reliability and causal prior as parameters of the BCI model. Auditory and visual variance parameters were comparable across groups in the Bayesian inference model, a finding which dovetails closely with the results of our unisensory discrimination and localisation paradigms: the JND of the psychometric functions (i.e. spatial discrimination) and the RMSE of the linear regression (i.e. spatial localisation), as measures for sensory reliability, were similar between groups. Likewise, the causal prior parameter, which indexes a participant's prior tendency to bind signals and may be related to selective attention and executive functioning, was not affected by ageing. Again this converges with the results in our cued Eriksen flanker task, where older adults were actually more accurate than younger controls (for response times see below). Previous research on executive functions in Stroop or flanker tasks has shown age-related decline only inconsistently (e.g. Bugg et al., 2007; but see Dey & Sommers, 2015; Jennings et al., 2007). Potentially, these inconsistencies across the literature can be explained by sampling biases. For instance, our sample may be biased towards including higher-performing older adults who were able to maintain performance throughout a demanding multi-session study.

Our results so far therefore suggest that healthy ageing has negligible effects on how

human observers integrate and segregate signals from audition and vision for spatial localisation, at least when considering only response choices (i.e. not reaction times) in older adults that have preserved executive functioning and normal auditory and visual spatial reliabilities. These results may be initially surprising in light of accumulating research showing that ageing alters multisensory integration. For example, older adults have consistently been shown to have greater susceptibility to the sound-induced flash illusion (DeLoss et al., 2013; McGovern et al., 2014; Setti et al., 2011) and to respond differently to McGurk-MacDonald stimuli (Sekiyama et al., 2014; Setti et al., 2013).

Potentially, susceptibility to the sound-induced flash illusion is changed with age because it relies on precise representations of stimulus timing that have been shown to be impaired by ageing (Mazelová et al., 2003). Ng and Recanzone (2017) provide a possible mechanism for this decline: a study of neural responses to simple stimuli in macaque primary auditory cortex found that aged monkeys showed firing patterns that were noisier (i.e. less temporally precise) and less selective than those seen in younger animals. Age-related differences in perception of McGurk-MacDonald stimuli may also be due in part to impaired temporal perception, as the fine temporal structure of speech signals is an important cue for comprehension (especially in the context of competing noise; Moore, 2008). However, in this case the effect is likely to be compounded by reductions in speech comprehension that result from presbycusis that particularly affects higher sound frequencies (Pichora-Fuller & Souza, 2003).

In contrast, the estimation and integration of spatial information along the azimuth does not rely to the same degree on fine temporal features of the stimuli, so impaired perception of these features may not have a strong impact on an observer's ability to determine the location of a signal. Indeed, the results of our unisensory spatial discrimination and localisation tasks demonstrate that older and younger adults obtain equally reliable spatial estimates, in both auditory and visual modalities. This is in agreement with previous work that showed limited age differences in localisation of transient broadband sounds and visual flashes along the azimuth (e.g. Dobreva et al., 2011; Otte et al., 2013).

Our discussion of age differences in multisensory integration has thus far addressed only final response choices, ignoring reaction times, but our natural environment does not afford us

infinite time to react to multisensory stimuli. When we define and evaluate multisensory integration performance, it is therefore also important to consider the time taken to respond.

In fact, older adults were significantly slower to give both spatial localisation and common-source judgement responses in the unspeeded ventriloquist paradigm. While an overall response time increase in these tasks may be attributed to older observers' reduced motor speed (as measured in the finger-tapping task), the interactions between age, disparity, and stimulus reliability on common-source response times are less easily explained, as any impact of motor speed should be mainly additive. The profile of these interactions suggests that older adults responded disproportionately slower to more challenging multisensory stimuli (i.e. those with an ambiguous causal structure caused by small spatial disparity and/or unreliable stimuli), an interpretation that is reinforced by the presence of an interaction between age and stimulus congruence in the speeded simplified ventriloquist paradigm.

Critically, the classical Bayesian Causal Inference model cannot account for these reaction time interactions, as it only makes predictions about final response choices. We therefore adapted the compatibility bias model (Yu et al., 2009) to the speeded ventriloquist paradigm, where observers make binary left/right responses about auditory location as accurately and fast as possible. The compatibility bias model assumes that the observer accumulates auditory and visual evidence about the location of the reported stimulus, and about the causal structure of the signals, until a decisional threshold is reached and a response given. Predictions can thus be made jointly for observers' spatial choices and response times (in terms of the time until the decisional threshold has been reached, which can be dissociated from aging-related effects on motor speed that were explicitly modelled separately as non-decision time). The compatibility bias model thereby provides an important perspective on the dynamics of decision making within a trial. In contrast to the BCI model results, the compatibility bias analyses revealed that multisensory decision making is affected by ageing and slower in older relative to younger adults for three reasons. First, older adults have impaired motor speed, as indexed by the non-decision time variable and confirmed by the finger tapping task. Second, they use a higher response threshold, requiring a greater degree of certainty before a response is given. This is consistent with our findings of age-related accuracy increases in the cued Eriksen flanker task, and with previous

studies of age differences in speed/accuracy trade-off (Smith & Brewer, 1995; Starns and Ratcliff, 2010). Third, the compatibility bias model analysis suggests that the auditory representations are less reliable (i.e. greater auditory variance) in older participants, such that evidence accumulates more slowly (see Figure 5). In other words, the initial auditory representation may be noisier and less reliable for older adults, but they can achieve equal performance levels (in terms of final response) to younger participants by accumulating this noisy evidence for longer via internal feedback loops. It is important to note that neither classical non-dynamic models that rely on psychometric functions, nor the Bayesian causal inference model, revealed these differences in internal sensory noise because they only consider the final spatial representation that is mapped onto an observer's response. This illustrates how dynamic models that accommodate both reaction time and final response choices can provide critical new insights into evidence accumulation and perceptual decision making.

In conclusion, our results demonstrate that multisensory spatial localisation and causal inference is preserved in older adults. However, older observers only maintain this performance by accumulating noisier auditory information over a longer period of time. When combined with well-established changes in motor speed and speed/accuracy trade-off, this leads to significant and nonlinear age differences in reaction times to complex multisensory stimuli during spatial localisation.

References

Acerbi, L., Dokka, K., Angelaki, D.E., Ma, W.J., 2018. Bayesian comparison of explicit and implicit causal inference strategies in multisensory heading perception. PLOS Computational Biology 14, e1006110.

Acerbi, L., Ma, W.J., 2017. Practical Bayesian Optimization for Model Fitting with Bayesian Adaptive Direct Search. arXiv:1705.04405 [q-bio, stat].

Alais, D., Burr, D., 2004. The Ventriloquist Effect Results from Near-Optimal Bimodal Integration. Current Biology 14, 257–262.

Bugg, J.M., DeLosh, E.L., Davalos, D.B., Davis, H.P., 2007. Age Differences in Stroop Interference: Contributions of General Slowing and Task-Specific Deficits. Aging, Neuropsychology, and Cognition 14, 155–167.

Callejas, A., Lupiáñez, J., Tudela, P., 2004. The three attentional networks: On their independence and interactions. Brain and Cognition 54, 225–227.

DeLoss, D.J., Pierce, R.S., Andersen, G.J., 2013. Multisensory Integration, Aging, and the Sound-Induced Flash Illusion. Psychol Aging 28, 802–812.

Dey, A., Sommers, M.S., 2015. Age-related Differences in Inhibitory Control Predict Audiovisual Speech Perception. Psychol Aging 30, 634–646.

Diederich, A., Colonius, H., Schomburg, A., 2008. Assessing age-related multisensory enhancement with the time-window-of-integration model. Neuropsychologia 46, 2556–2562.

Dobreva, M.S., O'Neill, W.E., Paige, G.D., 2011. Influence of aging on human sound localization. Journal of Neurophysiology 105, 2471–2486.

Ernst, M.O., Banks, M.S., 2002. Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415, 429–433.

Fan, J., McCandliss, B.D., Sommer, T., Raz, A., Posner, M.I., 2002. Testing the Efficiency and Independence of Attentional Networks. Journal of Cognitive Neuroscience 14, 340–347.

Fetsch, C.R., Pouget, A., DeAngelis, G.C., Angelaki, D.E., 2012. Neural correlates of reliability-based cue weighting during multisensory integration. Nature Neuroscience 15, 146–154.

Gates, G.A., Mills, J.H., 2005. Presbycusis. The Lancet 366, 1111–1120.

Gori, M., Del Viva, M., Sandini, G., Burr, D.C., 2008. Young Children Do Not Integrate Visual and Haptic Form Information. Current Biology 18, 694–698.

Guerreiro, M.J.S., Van Gerven, P.W.M., 2011. Now you see it, now you don't: Evidence for age-dependent and age-independent cross-modal distraction. Psychology and Aging 26, 415–426.

Helbig, H.B., Ernst, M.O., Ricciardi, E., Pietrini, P., Thielscher, A., Mayer, K.M., Schultz, J., Noppeney, U., 2012. The neural mechanisms of reliability weighted integration of shape information from vision and touch. NeuroImage 60, 1063–1072.

Jennings, J.M., Dagenbach, D., Engle, C.M., Funke, L.J., 2007. Age-Related Changes and the Attention Network Task: An Examination of Alerting, Orienting, and Executive Function. Aging, Neuropsychology, and Cognition 14, 353–369.

Körding, K.P., Beierholm, U., Ma, W.J., Quartz, S., Tenenbaum, J.B., Shams, L., 2007. Causal Inference in Multisensory Perception. PLoS ONE 2, e943.

Laurienti, P.J., Burdette, J.H., Maldjian, J.A., Wallace, M.T., 2006. Enhanced multisensory integration in older adults. Neurobiology of Aging 27, 1155–1163.

Li, K.Z.H., Lindenberger, U., 2002. Relations between aging sensory/sensorimotor and cognitive functions. Neuroscience & Biobehavioral Reviews 26, 777–783.

Lindenberger, U., Baltes, P.B., 1994. Sensory functioning and intelligence in old age: A strong connection. Psychology and Aging 9, 339–355.

Madden, D.J., Allen, P.A., 1995. Aging and the Speed/Accuracy Relation in Visual Search: Evidence for an Accumulator Model. Optometry and Vision Science 72, 210.

Mahoney, J.R., Li, P.C.C., Oh-Park, M., Verghese, J., Holtzer, R., 2011. Multisensory integration across the senses in young and old adults. Brain Res 1426, 43–53.

Mazelová, J., Popelar, J., Syka, J., 2003. Auditory function in presbycusis: peripheral vs. central changes. Experimental Gerontology, Proceedings of the 6th International Symposium on the Neurobiology and Neuroendocrinology of Aging 38, 87–94.

McGovern, D.P., Roudaia, E., Stapleton, J., McGinnity, T.M., Newell, F.N., 2014. The sound-induced flash illusion reveals dissociable age-related effects in multisensory

integration. Front Aging Neurosci 6.

Mevorach, C., Spaniol, M.M., Soden, M., Galea, J.M., 2016. Age-dependent distractor suppression across the vision and motor domain. Journal of Vision 16, 27.

Ng, C.-W., Recanzone, G.H., 2018. Age-Related Changes in Temporal Processing of Rapidly-Presented Sound Sequences in the Macaque Auditory Cortex. Cereb Cortex 28, 3775–3796.

Otte, R.J., Agterberg, M.J.H., Van Wanrooij, M.M., Snik, A.F.M., Van Opstal, A.J., 2013. Age-related Hearing Loss and Ear Morphology Affect Vertical but not Horizontal Sound-Localization Performance. J Assoc Res Otolaryngol 14, 261–273.

Pichora-Fuller, M.K., 2003. Processing speed and timing in aging adults: psychoacoustics, speech perception, and comprehension. International Journal of Audiology 42, 59–67.

Poliakoff, E., Ashworth, S., Lowe, C., Spence, C., 2006. Vision and touch in ageing: Crossmodal selective attention and visuotactile spatial interactions. Neuropsychologia 44, 507–517.

Prins, N., Kingdom, F.A.A., 2018. Applying the Model-Comparison Approach to Test Specific Research Hypotheses in Psychophysical Research Using the Palamedes Toolbox. Front. Psychol. 9.

Rohe, T., Noppeney, U., 2018. Reliability-Weighted Integration of Audiovisual Signals Can Be Modulated by Top-down Control. eNeuro ENEURO.0315-17.2018.

Rohe, T., Noppeney, U., 2015. Sensory reliability shapes perceptual inference via two mechanisms. Journal of Vision 15, 22.

Rohe, Tim, Noppeney, U., 2015. Cortical Hierarchies Perform Bayesian Causal Inference in Multisensory Perception. PLOS Biology 13, e1002073.

Salthouse, T.A., Hancock, H.E., Meinz, E.J., Hambrick, D.Z., 1996. Interrelations of Age, Visual Acuity, and Cognitive Functioning. J Gerontol B Psychol Sci Soc Sci 51B, P317-330.

Sekiyama, K., Soshi, T., Sakamoto, S., 2014. Enhanced audiovisual integration with aging in speech perception: a heightened McGurk effect in older adults. Front Psychol 5.

Setti, A., Burke, K.E., Kenny, R., Newell, F.N., 2013. Susceptibility to a multisensory speech illusion in older persons is driven by perceptual processes. Front Psychol 4.

Setti, A., Burke, K.E., Kenny, R.A., Newell, F.N., 2011. Is inefficient multisensory processing

associated with falls in older people? Exp Brain Res 209, 375–384.

Shams, L., Beierholm, U.R., 2010. Causal inference in perception. Trends in Cognitive Sciences 14, 425–432

Smith, G.A., Brewer, N., 1995. Slowness and age: Speed-accuracy mechanisms. Psychology and Aging 10, 238–247.

Starns, J.J., Ratcliff, R., 2010. The effects of aging on the speed-accuracy compromise: Boundary optimality in the diffusion model. Psychol Aging 25, 377–390.

Tsvetanov, K.A., Mevorach, C., Allen, H., Humphreys, G.W., 2013. Age-related differences in selection by visual saliency. Attention, Perception, & Psychophysics 75, 1382–1394.

Turner, G.R., Spreng, R.N., 2012. Executive functions and neurocognitive aging: dissociable patterns of brain activity. Neurobiology of Aging 33, 826.e1-826.e13.

van Doorn, J., Ly, A., Marsman, M., Wagenmakers, E.-J., 2017. Bayesian Latent-Normal Inference for the Rank Sum Test, the Signed Rank Test, and Spearman's Rho. arXiv:1712.06941 [stat].

Wichmann, F.A., Hill, N.J., 2001. The psychometric function: I. Fitting, sampling, and goodness of fit. Perception & Psychophysics 63, 1293–1313.

Wozny, D.R., Beierholm, U.R., Shams, L., 2010. Probability Matching as a Computational Strategy Used in Perception. PLoS Computational Biology 6, e1000871.

Yu, A.J., Dayan, P., Cohen, J.D., 2009. Dynamics of Attentional Selection Under Conflict: Toward a Rational Bayesian Account. Journal of Experimental Psychology 35, 700–717.