Older adults sacrifice response speed to preserve multisensory integration performance

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Abstract

Ageing has been shown to impact multisensory integration, but the underlying differences in computational mechanisms are poorly understood. An effective observer should integrate those signals that share a common source, weighted by their reliability, and segregate those from separate sources. Observers are thought to accumulate evidence about signals' causal structure over time until a threshold of certainty is reached.

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. A Bayesian Causal Inference model fitted to response choices revealed that ageing did not affect the ability to effectively arbitrate between integration and segregation.

However, an evidence accumulation model, fitted jointly to response times and choices made under speeded conditions, revealed age differences: older observers accumulate noisier auditory representations for longer, set higher decisional thresholds, and have impaired motor speed. Modelling the within-trial dynamics of multisensory evidence accumulation reveals that older observers preserve audiovisual localisation performance by sacrificing response speed.

1. Introduction

Throughout life we are continually exposed to a barrage of sensory signals. Our ability to effectively navigate through and respond to the world requires us to merge information from multiple sensory modalities into a coherent percept. We may, for example, more easily locate a predator in thick foliage by combining the sight of its movement with the sound of footsteps.

Accumulating evidence suggests that ageing affects how observers integrate sensory signals into perceptual decisions. In speeded target detection paradigms older adults show greater multisensory response facilitation (i.e. redundant target effect) that violates the race model predictions of independent sensory processing (Laurienti et al., 2006; Mahoney et al., 2011). Further, older participants have been shown to integrate multisensory stimuli differently in illusionary settings 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). Yet, the computational mechanisms underlying these age differences in multisensory integration remain unclear. Ageing is known to reduce the reliability of auditory and visual representations (Dobreva et al., 2011; Lindenberger & Baltes, 1994; Otte et al., 2013; Salthouse et al., 1996), which may alter the weights that are assigned to the sensory signals during the integration process and thereby the emergence of perceptual illusions. Alternatively, ageing may impact how observers arbitrate between sensory integration and segregation depending on temporal, spatial or higher-order statistical correspondence cues, which again may affect whether observers integrate conflicting sensory signals into perceptual illusions.

In the laboratory, the computational principles of multisensory integration have been studied extensively in spatial ventriloquist paradigms where observers need to report their perceived sound (or visual) location when presented with synchronous, yet spatially disparate, auditory and visual signals. For small spatial disparities observers' perceived sound location is shifted (or biased) towards the location of the visual signal and vice versa depending on the relative auditory and visual reliabilities - a phenomenon known as the spatial ventriloquist effect. Yet, for large audiovisual spatial disparities where it is unlikely that signals come from a common source, audiovisual interactions and crossmodal biases are attenuated. Recent psychophysics and neuroimaging studies have shown that younger observers arbitrate between sensory integration and segregation in a way that is consistent with the predictions of hierarchical Bayesian Causal Inference (BCI; Aller & Noppeney, 2019; Koerding et al., 2007; Rohe, Ehlis, & Noppeney, 2019; Rohe & Noppeney, 2015a, 2015b; Shams & Beierholm, 2010; Wozny et al., 2010). Bayesian Causal Inference enables arbitration between sensory integration and segregation by explicitly modelling the two causal structures (i.e. common or independent events) that could have generated the sensory signals. If signals emanate from a common source they are integrated, weighted in proportion to their relative sensory reliabilities; if they come from different sources they are treated separately. To account for observers' uncertainty about the world's causal structure, a final estimate (e.g. an object's location) is obtained by averaging the estimates under the assumptions of common and independent sources weighted by their respective posterior probabilities, a decision strategy referred to as model averaging (for other decision functions see Wozny et al., 2010). Spatial ventriloquism, together with Bayesian Causal Inference, may thus allow us to tease apart whether ageing affects only sensory reliabilities (i.e. sensory variance) or also observers' binding tendencies (as quantified by the model's causal prior), and to test whether older adults still respond in a way that is consistent with the predictions of BCI.

However, current models of Bayesian Causal Inference do not account for temporal constraints imposed by our natural world and the dynamics of observers' perceptual inference; BCI enables predictions for an observer's response choices (e.g. spatial localisation) but not for his or her response times. In our natural environment we often need to trade off accuracy for speed: a faster, less accurate estimate of the location of a predator may prove far more useful than a highly accurate but slow one. Indeed, recent studies have shown that putatively suboptimal multisensory behaviour can be considered optimal when the dynamics of perceptual decision making, based on both response choices and times, are taken into account (Drugowitsch et al., 2014). Considering response choices and times together is particularly relevant for understanding the impact of ageing on multisensory integration, as older adults have previously been shown to favour accuracy over speed to a greater degree than younger observers (Smith & Brewer, 1995; Starns and Ratcliff, 2010).

Combining psychophysics and computational modelling, the current study was thus designed to investigate how ageing impacts the computational parameters governing multisensory decision making in both unspeeded and speeded contexts (Koerding et al., 2007; Rohe & Noppeney, 2015a, 2015b; Wozny et al., 2010).

First, in an unspeeded spatial ventriloquist paradigm younger and older observers located the source of a sound (which implicitly relies on causal inference; see above) or judged whether the auditory and visual signal originated from the same source (which explicitly requires the observer to infer the causal structure underlying the audiovisual signals). We assessed how ageing affects observers' auditory and visual reliabilities, spatial prior, and prior binding tendency (i.e. causal prior), as key parameters of the Bayesian Causal Inference model.

Second, in a speeded spatial ventriloquist paradigm observers were presented with spatially congruent or incongruent audiovisual signals and rapidly discriminated whether the auditory (or visual) stimulus was presented in their left or right hemifield. We used a modified version of the Bayesian compatibility bias model (Noppeney, Ostwald, & Werner, 2010; Yu et al, 2009) to characterise how observers accumulate evidence concurrently about signal location and audiovisual spatial congruency, and to make predictions jointly for response choices and times. The age groups were compared in terms of auditory and visual reliabilities, prior binding tendency, and final response threshold.

2. Methods

2.1. Participants

Twenty-three younger adults (eleven male, mean age = 19.5, *SD* = 1.6, range = 18 – 26 years) and twenty-three older adults (seven male, mean age = 72, *SD* = 5.2, range = 63 – 80 years) were included in the study. One older adult was excluded before testing was completed as she was unable to perform unisensory auditory localisation (approximately the same response was given to all auditory stimuli, regardless of source location). The younger adults were undergraduate psychology students at the University of Birmingham, and were compensated in cash or course credits for their time. Older adults were recruited to the study from a database of local participants maintained by the University of Birmingham's School of Psychology, and were compensated in cash. These community-living older adults had a diverse range of backgrounds; 39% reported education at degree level or above. All participants reported normal hearing and normal or corrected-to-normal vision, and were screened for basic auditory and visual localisation ability using a forced left/right discrimination task (see Supplementary S1). Participants gave informed consent prior to the commencement of testing. 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 speeded ventriloquist task it was emphasised to participants that they should respond as quickly as possible while maintaining accuracy. See Figure 1A for an outline of the setup.

2.3. Stimuli

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 uniquely for each trial 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 specific horizontal standard deviations used for each paradigm below.

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. Unspeeded audiovisual spatial ventriloquist paradigm

2.4.1. Design and procedure

In a spatial ventriloquist paradigm observers were presented with synchronous auditory and visual stimuli at variable audiovisual spatial disparities and performed implicit or explicit causal inference tasks in separate blocks. First, in an auditory selective attention task, observers reported their perceived sound location. As highlighted in the introduction, spatial localisation implicitly relies on solving the causal inference problem. Second, they explicitly inferred and reported the causal structure (i.e. common vs. independent sources) that could have generated the audiovisual signals in common source judgements.

Irrespective of task context, 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 degrees 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.

In the sound localisation task participants reported the perceived sound location as accurately as possible, after a 500ms post-stimulus delay, 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 had indicated their perceived auditory location by clicking the mouse button. Trials were presented randomly in 200-trial blocks. In total, participants completed 600 trials (8 [repetitions] x 5 [A locations] x 5 [V locations] x 3 [V reliabilities)]) of this task.

In the common-source judgment task participants reported whether they perceived the auditory and visual signals to have originated from the same location. 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. Participants again completed 600 trials (8 [repetitions] x 5 [A locations] x 5 [V locations] x 3 [V reliabilities)]) of this task, delivered in three blocks of 200 trials.

Unisensory localisation blocks were also included to improve estimation of sensory reliabilities. In unisensory auditory blocks, observers were presented with sounds randomly at one of the five locations and indicated their perceived sound location with the mouse cursor, as above. 80 trials of this task (16 per location) were completed in one block. In unisensory visual blocks, stimuli from the three reliability levels indicated above (horizontal *SD* of 2°, 6° or 16°) were presented randomly in one of the five locations and participants instructed to locate the centre of the dot cloud with the mouse cursor. 120 trials of this task (8 per location, per reliability level) were completed in one block.

2.4.2. Bayesian Causal Inference model

We investigated whether participants integrate auditory and visual signals into spatial representations that are consistent with Bayesian Causal Inference (BCI). Further, we investigated whether the sensory variances estimated from unisensory auditory or visual blocks can be used to inform estimation of the Bayesian Causal Inference model.

The BCI generative model assumes that common (C = 1) or independent (C = 2) sources are determined by sampling from a binomial distribution with the causal prior $P(C = 1) = p_{\mathrm{common}}$. For a common source, the "true" location S_{AV} is drawn from the spatial prior distribution $N(\mu, \sigma_{\mathrm{P}})$. For two independent causes, the "true" auditory (S_A) and visual (S_V) locations are drawn independently from this spatial prior distribution. For the spatial prior distribution, we assumed a central bias (i.e. $\mu_P = 0$). We introduced sensory noise by drawing x_A and x_V independently from normal distributions centered on the true auditory (respectively visual) locations with parameters σ_A (respectively σ_V for each visual reliability level).

Thus, the generative model included the following free parameters: the causal prior p_{common}, the spatial prior standard deviation σ_P, the auditory standard deviation σ_A, and three visual standard deviations $\sigma_{V1}, \sigma_{V2}, \sigma_{V3}$ corresponding to the three visual reliability levels.

During perceptual inference the observer is assumed to invert this generative model. The probability of the underlying causal structure can be inferred by combining the causal prior with the sensory evidence according to Bayes' rule:

(1) $$p(C = 1|x_A, x_V) = \frac{p(x_A, x_V|C = 1)p_{common}}{p(x_A, x_V)}$$

We assumed that subjects reported 'common source' (i.e. explicit causal inference) when the posterior probability of a common source is greater than the threshold of 0.5:

(2) $$\hat{C} = \begin{cases} 1 & if \;\; p(C = 1|x_A, x_V) > 0.5 \\ 2 & if \;\; p(C = 1|x_A, x_V) \leq 0.5 \end{cases}$$

In the case of a common source (*C* = 1; Figure 1B left), the maximum a posteriori probability estimate of the auditory location is a reliability-weighted average of the auditory and visual estimates and the prior.

(3) $$\hat{S}_{A,C=1} = \frac{\frac{x_A}{\sigma_A^2} + \frac{x_V}{\sigma_V^2} + \frac{\mu_P}{\sigma_P^2}}{\frac{1}{\sigma_A^2} + \frac{1}{\sigma_V^2} + \frac{1}{\sigma_P^2}}$$

In the case of a separate-source inference (*C* = 2; Figure 1B right), the estimate of the auditory signal location is independent from the visual spatial signal.

(4) $$\hat{S}_{A,C=2} = \frac{\frac{x_A}{\sigma_A^2} + \frac{\mu_P}{\sigma_P^2}}{\frac{1}{\sigma_A^2} + \frac{1}{\sigma_P^2}}$$

Given the decisional strategy of model averaging (Wozny et al., 2010) the observer will compute a final auditory localisation estimate by averaging the spatial estimates under common and independent source assumptions, weighted in proportion to their posterior probabilities (i.e. implicit causal inference).

(5) $$\hat{S}_A = p(C = 1|x_A, x_V)\hat{S}_{AV,C=1} + \left(1 - p(C = 1|x_A, x_V)\right)\hat{S}_{A,C=2}$$

The predicted distributions of the auditory spatial estimates, $p(\hat{S}_A|S_A, S_V)$, and the common source estimates, $p(\hat{C}|S_A, S_V)$, were obtained by marginalising over the internal variables x_A and x_V. For the unisensory auditory and visual localisation tasks, we used the predicted distributions $p(\hat{S}_{A,C=2}|S_A)$ for auditory blocks and $p(\hat{S}_{V,C=2}|S_V)$ respectively.

These distributions were generated by simulating x_A and x_V 10000 times for each of the conditions and inferring $\hat{S}_A$, $\hat{S}_{A,C=2}$, $\hat{S}_{V,C=2}$, and $\hat{C}$ from the equations above. Based on these predicted distributions (given an additional noise kernel with $\sigma_{motor} = 1$), we computed the log-likelihood of participants' auditory localisation and common-source judgement responses. Assuming independence of conditions and task responses, we summed the log-likelihoods across conditions and across auditory localisation and common-source judgement responses to obtain a single log-likelihood for each subject. To obtain maximum likelihood estimates for each subject's model parameters (p_{common}, σ_P, σ_A, σ_{V1} - σ_{V3} for each of the three levels of visual reliability) we used a Bayesian adaptive search algorithm (BADS; Acerbi & Ma, 2017) with the parameters for initialisation determined by a prior grid search.

2.4.3. Model selection and group comparison of parameters

It is unclear whether the visual and auditory reliabilities depend only on the external sensory signals and the noise imposed by the peripheral sensory processing, or also on task and stimulus (i.e. unisensory vs. bisensory) context. In the former case, estimation of the auditory and visual reliabilities based on data from the audiovisual and unisensory experiments together would provide more precise parameter estimates. In the latter case, it would lead to biased estimation. Likewise, the spatial priors may potentially depend on stimulus blocks and task context. To formally address these questions we compared the following three models, which differed by whether the sensory variances, spatial and causal priors were allowed to vary across task-context.

Model A assumed that sensory variances and spatial prior parameters differed between unisensory and audiovisual contexts. Hence, this model included 11 parameters: p_{common}, $\sigma_{P\ uni}$, $\sigma_{A\ uni}$, $\sigma_{V1\ uni}$, $\sigma_{V2\ uni}$, $\sigma_{V3\ uni}$, $\sigma_{P\ bi}$, $\sigma_{A\ bi}$, $\sigma_{V1\ bi}$, $\sigma_{V2\ bi}$, $\sigma_{V3\ bi}$.

Model B assumed that sensory variances and priors were equal for unisensory and bisensory blocks. This model thus included six parameters: p_{common}, σ_P, σ_A, σ_{V1}, σ_{V2}, σ_{V3}.

Model C constrained the spatial prior to be equal for unisensory and audiovisual blocks, but allowed the sensory noise parameters to differ between unisensory and audiovisual contexts, yielding ten parameters: p_{common}, σ_P, $\sigma_{A\ uni}$, $\sigma_{V1\ uni}$, $\sigma_{V2\ uni}$, $\sigma_{V3\ uni}$, $\sigma_{A\ bi}$, $\sigma_{V1\ bi}$, $\sigma_{V2\ bi}$, $\sigma_{V3\ bi}$.

We arbitrated between these three models using the Bayesian information criterion

(BIC) as an approximation to the model evidence, and Bayesian model comparison at the group (random effects) level, pooled across age groups (Rigoux et al., 2014).

The parameters (causal prior, spatial prior[s], and sensory variances) obtained from the winning model were compared between age groups using 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). A similar group comparison was also conducted for a measure of model fit, R^2, to assess whether the ability of the BCI model to predict responses differed between age groups.

2.5. Speeded ventriloquist paradigm

2.5.1 Design and procedure

To assess participants' audiovisual integration of spatial cues under speeded conditions, taking into account both final responses and reaction times, we used a simpler 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 cloud (respond-visual task) as quickly and accurately as possible via a two-choice key press, while ignoring the other modality. The task was self-speeded in this way (i.e. no response deadline) as any imposed incentives or timing criteria may have affected the groups differently; we rely on the compatibility bias model (described below) to separate age differences in motor speed and speed/accuracy trade-off from potential differences in sensory reliability/evidence accumulation. 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).

2.5.2 Compatibility bias model

To assess age differences in responses to multisensory stimuli under temporal constraints, we analysed the respond-auditory data by adapting the “compatibility bias” model to an audiovisual context (Noppeney, Ostwald, & Werner, 2010; Yu et al., 2009). This models the within-trial dynamics of audiovisual evidence accumulation, leading to predictions for both response choice and response times.

The 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 response is made.

See Yu et al. (2009) for full details about the compatibility bias model. Briefly, this generative model assumes that congruent (C = 1) or incongruent (C = 2) sources are determined by sampling from a binomial distribution with the compatibility or congruency prior $P(C = 1) = p_{congruency}$. The visual S_V and auditory S_A sources can either be left (–1) or right (+1). For a congruent trial, the auditory and visual locations are identical, i.e. $S_A = S_V$ (S_A and S_V are either both left or both right). For an incongruent trial, the auditory and visual locations are in opposite hemifields, i.e. $S_A = –S_V$ (two possibilities: $S_A = –1$ and $S_V = 1$, or $S_A = 1$ and $S_V = –1$). Hence we obtain a total of four possible stimulus combinations. We then sample noisy sensory inputs successively for each time point within a trial by drawing $\boldsymbol{x_t} = [x_A(t) \quad x_V(t)]$ independently from normal distributions centred on S_A (or S_V) with parameters σ_A (or σ_V respectively). This thereby models that the brain receives progressively more information about the location of the auditory and visual sources and thus, indirectly, about whether or not they are congruent (n.b. though in our experiment auditory and visual inputs are brief, we model the accumulation in areas via feedback loops as a series of sensory inputs). Based on a stream of audiovisual inputs $\boldsymbol{X}_t = [\boldsymbol{x}_1, \boldsymbol{x}_2, \boldsymbol{x}_3 \ldots \boldsymbol{x}_t]$ the observer is then assumed to compute the posterior probability over congruency C

and auditory (or visual) source location iteratively according to Bayes' rule (initialised with the prior $P(C) = \beta$):

(6)
$$P(S_A, C|\boldsymbol{X}_t) = \frac{p(\boldsymbol{x}_t|S_A, C)P(S_A, C|\boldsymbol{X}_{t-1})}{\sum_{C'S'_A} p(\boldsymbol{x}_t|S'_A, C')P(S'_A, C'|\boldsymbol{X}_{t-1})}$$

A left/right decision is then made when the evolving trajectory of the marginal

(7)
$$\mathrm{P}(\mathrm{S_A} = 1|\mathbf{X}_\mathrm{t}) = \mathrm{P}(\mathrm{S_A} = 1, \mathrm{C} = 1|\mathbf{X}_\mathrm{t}) + \mathrm{P}(\mathrm{S_A} = 1, C = 2|\mathbf{X}_\mathrm{t})$$

reaches a threshold q.

Thus, incongruent visual information should be most influential on perceived auditory location at the onset of the trial, when the initial compatibility prior dominates, but this influence decreases as information about the location of each stimulus is accumulated. The process is terminated when sufficient evidence is accumulated about the location of the auditory stimulus for a decisional threshold to be reached, after which a left/right spatial response is made. To accommodate that older adults have slower motor speed than younger adults (as confirmed by a separate finger tapping task reported in Supplementary S2), we included an additional non-decision-time parameter t_{nd} to account for motor delays.

The model therefore has five free parameters in total: 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} that allows for a variable motor delay between the threshold being reached and a response being given.

As in the Bayesian Causal Inference model we obtained the predicted distributions of the auditory spatial estimates, $P\left(\hat{S}_A\middle|S_A, S_V\right)$, and response times, $P\left(\widehat{RT}_A\middle|S_A, S_V\right)$, by marginalising over the internal variables x_A and x_V. These distributions were generated by simulating x_A and x_V for 300 time steps (of 10 ms length) 10000 times for each of the conditions. For each simulated trial with a series of 300 x_A and x_V, we then computed the response time and choice when $P(S_A = -1|\boldsymbol{X}_t)$ first crossed the decisional threshold q using Equations 5 and 6 above. Based on these predicted response choice and response time distributions, we computed the log-likelihood of participants' auditory (or visual) localisation responses and the response times (after adding the non-decision time t_{nd}). Assuming independence of conditions as well as independence of the log-likelihoods for response times and choices, we summed the log-likelihoods across conditions and across response times and choices for a particular subject. To obtain maximum likelihood estimates for the model parameters for each subject (β, σ_A, σ_V, q, t_{nd}), we used a Bayesian Adaptive Search optimisation algorithm (BADS; Acerbi & Ma, 2017) with parameters initialised based on a grid search.

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).

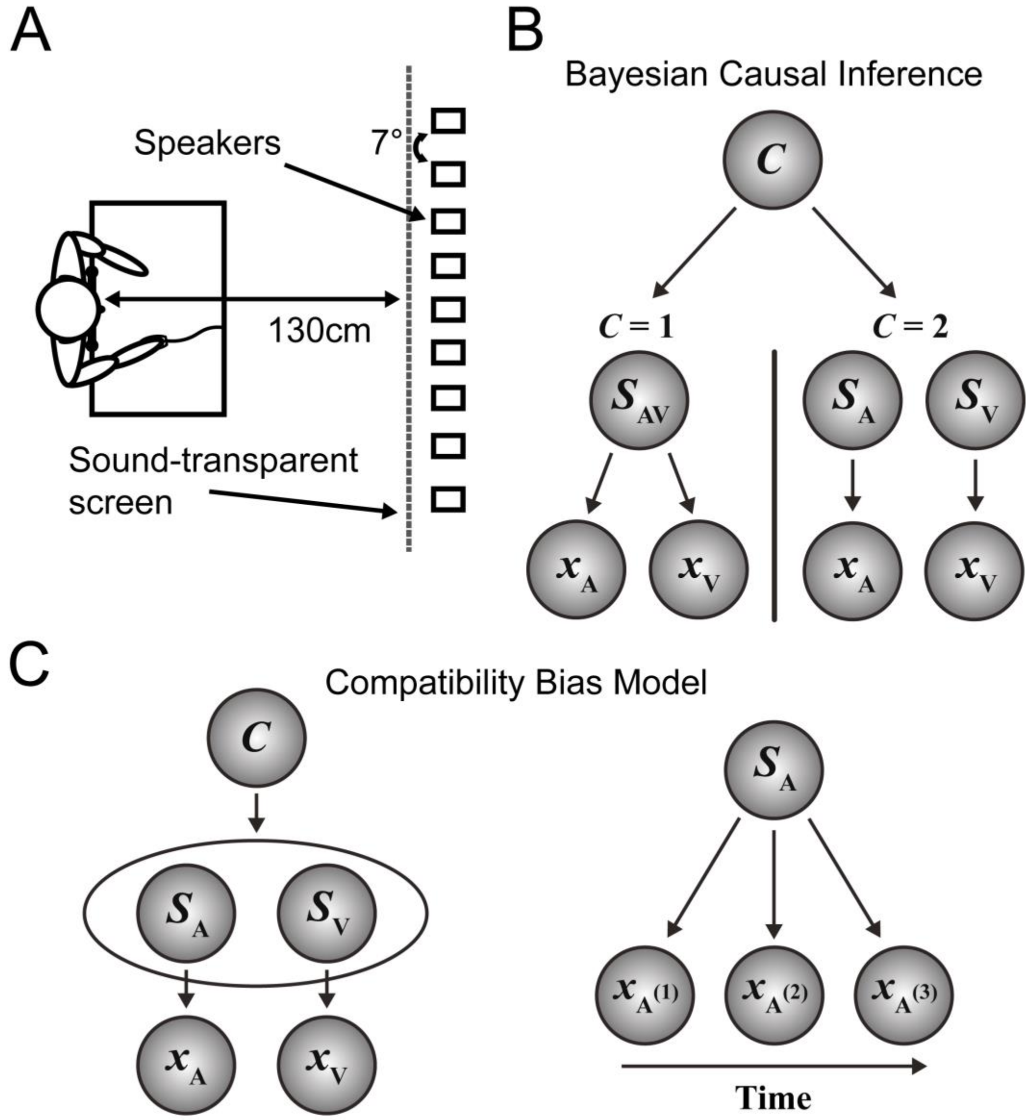

Figure 1. Experimental setup and generative models. (A) Participants were presented with visual stimuli on a sound-transparent projector screen. Sounds were produced by individual speakers concealed behind this screen, which were separated by 7° of visual angle. Responses were given via a mouse or a two-button response pad. (B) 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. (C) Compatibility bias model, adapted from Yu et al. (2009). Left: 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). Right: Across time, the auditory source generates a series of auditory inputs, and the visual source (not shown) a series of visual inputs, in an independent and identical fashion.

3. Results

3.1 Unisensory screening tests and the Montreal Cognitive Assessment

All observers were screened for basic auditory and visual localisation ability with a left/right forced-choice spatial task. Individuals were characterised in terms of the slope and threshold of psychometric functions fitted to these responses. Older and younger adults were closely matched: no significant age differences were apparent for either auditory or visual stimuli, suggesting that sensory spatial reliability was approximately similar between age groups. No participants were excluded as a result of poor performance on this task. See Supplementary S1 for full details.

Older participants were also screened using the Montreal Cognitive Assessment with a cut-off score of 23 (Coen et al., 2011; Roalf et al., 2013; Luis et al., 2009); none scored below 25.

3.2 Unspeeded ventriloquist paradigm

An unspeeded spatial ventriloquist paradigm was used to compare younger and older adults' responses to audiovisual spatial stimuli in the absence of temporal constraints. Figure 2 shows participants' auditory localisation (presented in terms of the magnitude of ventriloquist effect, $VE = [A_{resp} - A_{loc}] / [V_{loc} - A_{loc}]$) and common-source judgement responses (characterised as the probability of responding "same-source") as a function of visual reliability level and audiovisual disparity. As predicted by Bayesian Causal Inference, the ventriloquist effect was strongest when visual reliability was high and the audiovisual disparity small. The age groups performed remarkably similarly on both measures, with standard GLM analyses revealing no significant effects of age on final response choices. However, common-source judgement reaction times (Figure 2D) did reveal age differences, including significant interactions between age, visual reliability, and audiovisual disparity. See Supplementary S3 for full GLM analyses of these results.

3.2.1 Bayesian modelling

Three models, based on Bayesian Causal Inference, were fitted to localisation and common-source response data for each participant. The model that fitted sensory variance and spatial prior parameters separately for unisensory and bisensory contexts (described earlier as Model A) outperformed the others at the group level, with a protected exceedance probability of 0.58 (compared with values of 0.18 for Model B, and 0.24 for Model C). This suggests that the task and stimulus context influenced the estimates of sensory variances and spatial priors to some degree. We therefore report, and compare between groups, the parameters obtained from Model A.

Table 1 summarises the parameters of these fits and their R^2 (goodness of fit) values, including nonparametric significance tests of group differences and corresponding Bayes factors. Small but significant group differences in sensory variances were apparent for parameters estimated based on unisensory localisation tasks alone, suggesting that older adults were slightly less able to accurately localise both auditory and unreliable visual stimuli.

Bayesian Causal Inference: These group differences were not apparent in the sensory variance parameters estimated based on bimodal responses, possibly because this approach is less sensitive to such small differences (in the bimodal case, auditory stimuli are always presented in the presence of a visual distractor, while visual variance estimates are based only on auditory localisation and common-source responses). Crucially, however, no significant group differences were apparent for the P_{common} or σ_P parameters, or for R^2 values. This suggests that the two age groups had similar causal priors and central spatial priors, and that older and younger adults' multisensory integration behaviour (in an unspeeded context) was consistent with Bayesian Causal Inference to a similar degree.

To verify that these results were not confounded by possible age differences in response reliability (i.e. noisier mouse responses), we also fitted a version of the winning model that allowed the parameter σ_{motor} to vary freely (this was fixed at 1° for all participants in the main analysis). The pattern of results remained similar and there were no significant group differences in the σ_{motor} parameter ($p > .05$, $BF_{01} = 3.15$). See Supplementary S5 for details.

In summary, age did not influence observer's implicit (auditory localisation) or explicit (common-source judgement) causal inference in terms of response choices. Taken together with the results of the BCI model fitting, this suggests that despite some small differences in sensory reliability, older adults integrate audiovisual spatial information in a way that is very similar to younger adults and consistent with Bayesian Causal Inference. Ageing was, however, associated with complex changes in reaction times to multisensory stimuli. The profile of these age differences suggests that older adults took more time to respond when the causal structure of the stimuli was more ambiguous and the task therefore more challenging, such as when the visual stimulus was less reliable and/or the audiovisual disparity small. Interpreting this finding is difficult for the present task, however, as participants were not under speed instructions. The following section describes the results of the speeded ventriloquist task, for which differences in reaction times can be more readily characterised and understood.

	Younger		Older		Mann-Whitney *U*			Bayes factors	
	Mean	*SD*	Mean	*SD*	*W*	*p*	η^2	BF_{10}	BF_{01}
Unisensory									
σ_P	37.20	35.69	24.79	28.63	299	.305	.02	0.46	2.16
σ_A	5.27	1.96	6.79	2.76	155	**.026**	.11	2.19	0.46
σ_{V1}	1.76	1.22	2.10	1.06	174	.075	.07	1.10	0.91
σ_{V2}	2.32	0.76	2.89	1.52	198	.218	.04	0.54	1.84
σ_{V3}	4.22	1.00	5.38	1.67	132	**.005**	.17	4.95	0.20
Bisensory									
P_{common}	0.42	0.13	0.43	0.13	245	.866	< .01	0.30	3.28
σ_P	38.71	25.88	32.20	27.37	303	.264	.03	0.40	2.49
σ_A	8.59	4.40	9.37	5.78	234	.677	< .01	0.35	2.84
σ_{V1}	3.19	4.08	3.08	3.13	241	.796	< .01	0.30	3.31
σ_{V2}	5.12	4.32	6.07	5.47	204	.274	.03	0.44	2.25
σ_{V3}	12.79	9.72	20.61	26.13	209	.327	.02	0.48	2.09
R^2	0.78	0.10	0.78	0.10	255	.973	< .01	0.31	3.25

Table 1. Bayesian Causal Inference parameters (across-participants mean, *SD*) for younger (n = 23) and older (n = 22) participants. Mann-Whitney *U* tests with Bayes factors comparing the BCI parameters between older and younger adults. To unisensory responses we fitted the standard deviation of the spatial prior σ_P, the standard deviation of the auditory noise σ_A, and standard deviations of the visual noise for each of the three visual reliability levels σ_{V1}, σ_{V2}, and σ_{V3}. Separately, to multisensory responses (auditory localisation and common-source judgement) we fitted the causal prior p_{common} as well as σ_P, σ_A, and $\sigma_{V1\text{-}V3}$. R^2, a measure of model fit, is calculated according to Nagelkerke (1991) compared to a null model consisting of random responses. BF_{10} quantifies degree of support for the alternative hypothesis that the groups differ, relative to the null hypothesis; BF_{01} shows degree of support for the null hypothesis that there is no difference between groups, relative to the alternative hypothesis.

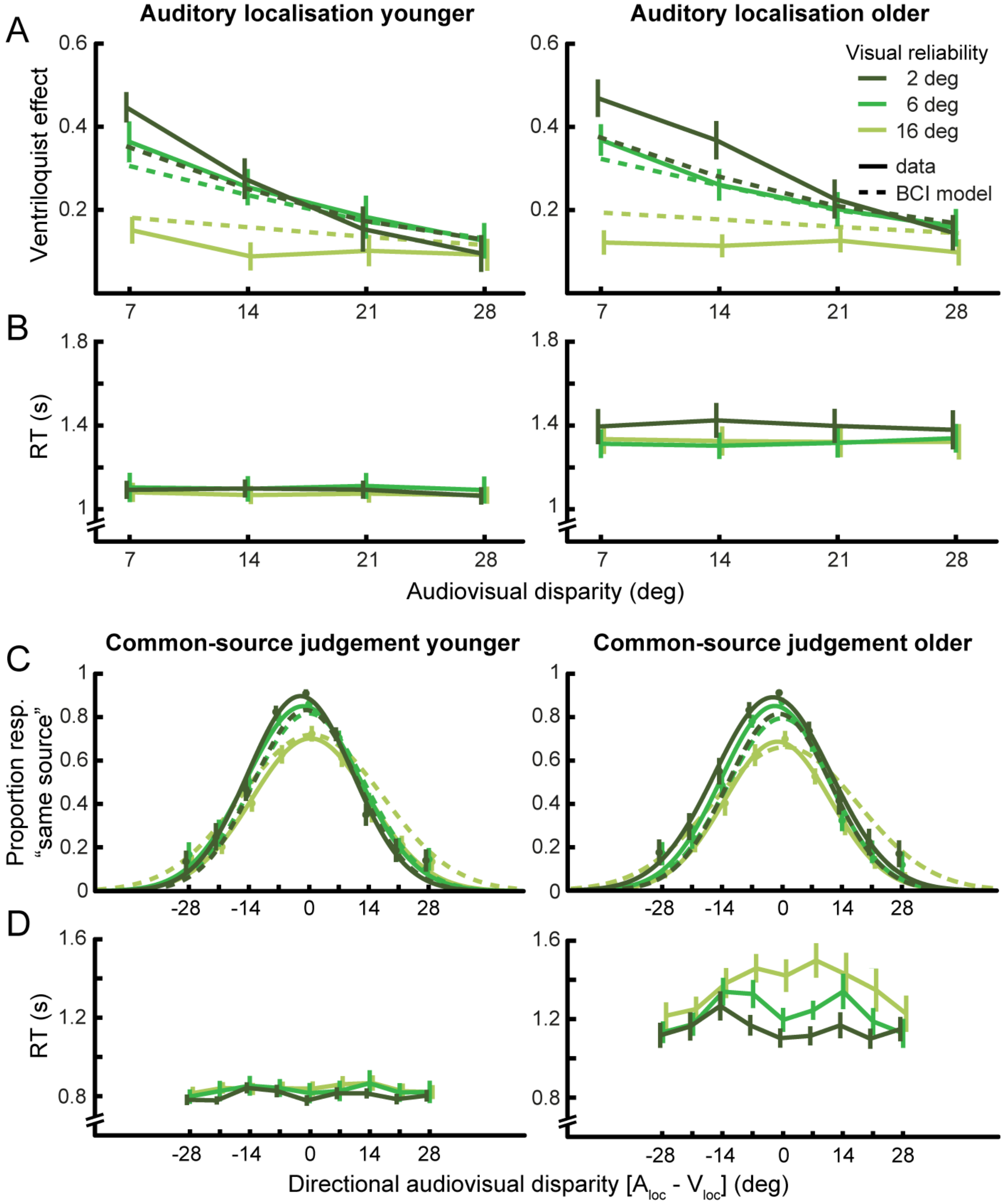

Figure 2. Behavioural responses, reaction times and BCI model predictions for younger and older adults. (A) Relative ventriloquist effect ($VE = [A_{resp} - A_{loc}] / [V_{loc} - A_{loc}]$) for auditory localisation, shown as a function of audiovisual disparity (*x*-axis, pooled over direction) and visual reliability (colour coded). Behavioural data (mean across subjects, solid lines) and the predictions of the Bayesian Causal Inference model (dashed lines) are shown. (B) Reaction times in auditory localisation task. (C) Proportion reported "same 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 (mean across subjects, solid lines) and the predictions of the Bayesian Causal Inference model (dashed lines). (D) Reaction times (pooled over response; mean across subjects) in common-source judgement task. Error bars show ±1 *SEM*.

3.2. Speeded ventriloquist paradigm

A simplified, speeded ventriloquist paradigm was used to assess younger and older adults' responses to audiovisual spatial stimuli under speed instructions. Figure 3 summarises response accuracy (panel B) and speed (panel C) for younger and older adults; trials are pooled over left and right and instead characterised in terms of spatial (in)congruence. Standard GLM analysis of these results shows that older adults were significantly more accurate that younger adults in the respond-visual task. Older adults were also significantly slower overall and, importantly, age interacted with congruence in the respond-auditory tasks: mirroring the profile of the common-source judgement responses, older adults took disproportionately longer to respond under the most challenging conditions (locating the auditory signal in the presence of an incongruent visual distractor). See Supplementary S4 for full GLM analysis.

3.2.1 Compatibility bias model

A compatibility bias model was fitted to participants' auditory spatial 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 and a response given. Fitted parameters were compared using separate Mann-Whitney *U* tests and a Bayesian equivalent. See Table 2 for a summary of results. Corroborating the findings of the BCI model, 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_{visual}. 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; our older adults' impaired motor speed is confirmed by a separate finger-tapping task reported in Supplementary S2. Second, older adults also set their decision threshold q significantly higher, requiring more evidence before deciding on a response. Third, and crucially, the auditory signal (σ_{auditory}) was significantly noisier in older than younger adults, leading to a slower accumulation of evidence and thus (in combination with the motor slowing and higher decision threshold) slower response times. 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 3A for an illustration of the model.

	Younger		Older		Mann-Whitney *U*			Bayes factors	
	Mean	*SD*	Mean	*SD*	*W*	*p*	η^2	BF_{10}	BF_{01}
σ_A	1.53	0.54	2.93	4.01	164	**.044**	.09	3.11	0.32
σ_V	1.85	3.50	0.87	0.97	283	.507	.01	0.44	2.27
β	0.75	0.12	0.78	0.13	192	.169	.04	0.56	1.79
q	0.93	0.05	0.95	0.07	141	**.010**	.14	2.68	0.37
t_{nd}	0.22	0.05	0.33	0.07	54	< **.001**	.45	5101.52	< 0.01

Table 2. Compatibility bias parameters (across-participants mean, *SD*) for younger (n = 23) and older (n = 22) 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 signal σ_V, compatibility prior β, response threshold q, and non-decision-time t_{nd}. BF_{10} quantifies degree of support for the alternative hypothesis that the groups differ, relative to the null hypothesis; BF_{01} shows degree of support for the null hypothesis that there is no difference between groups, relative to the alternative hypothesis.

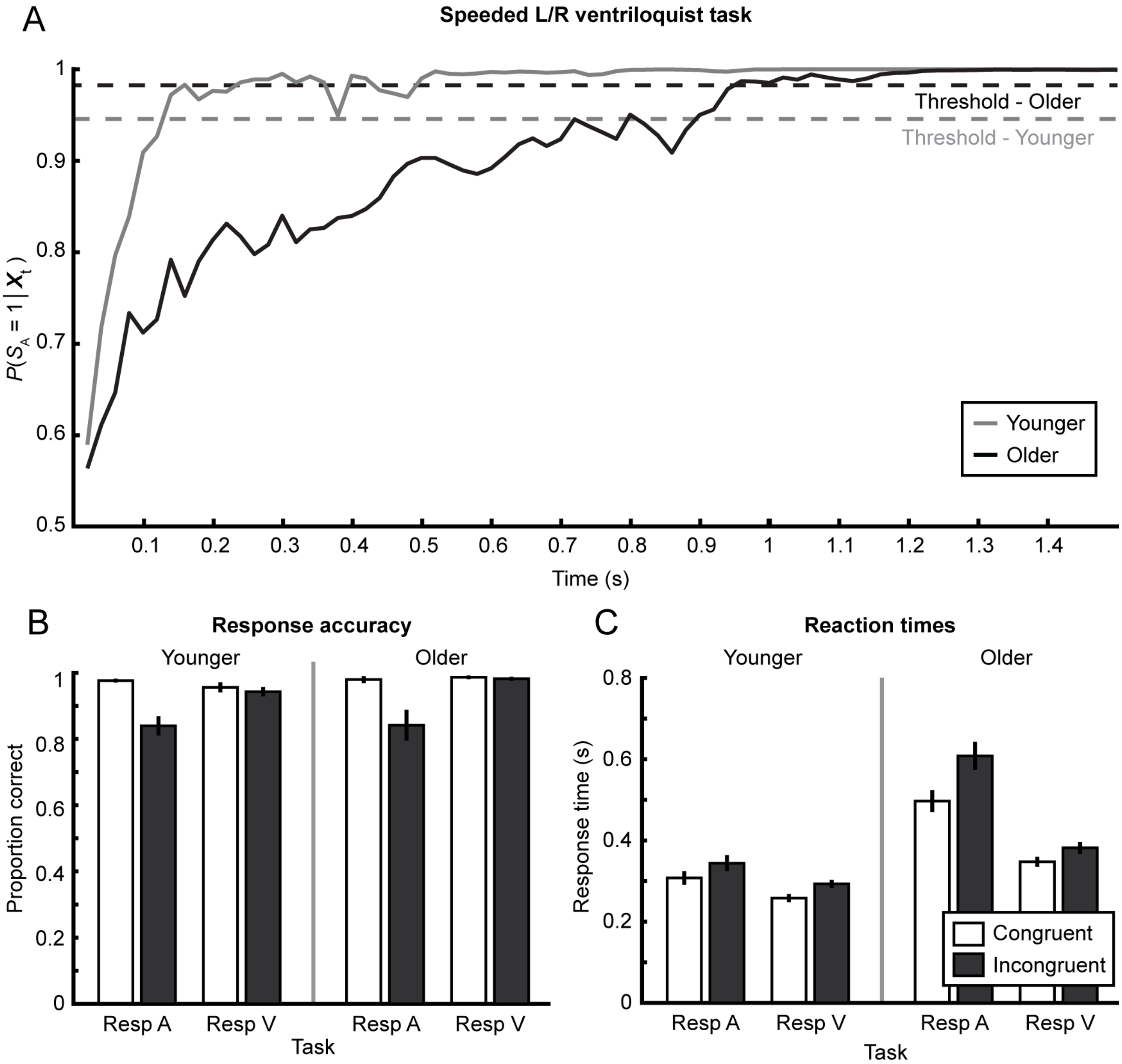

Figure 3. Speeded left/right ventriloquist paradigm and compatibility bias model. (A) Accumulation of evidence traces for the compatibility bias model: for 'respond auditory' trials the observer is thought to accumulate audiovisual evidence about whether the auditory source is left = -1 or right = 1 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, 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 applied audiovisual spatial tasks to investigate the effects of ageing on multisensory integration under both speeded and unspeeded conditions. Based on screening tests involving straightforward left/right judgements, younger and older adults appeared similar in their ability to locate unisensory auditory and visual stimuli. The sensory variance parameters of a Bayesian Causal Inference model fitted to multisensory localisation and common-source judgement responses also did not differ between age groups. However, the same parameters fitted using unisensory free-localisation responses did reveal small but significant age differences in sensory variances: older adults were less reliable in their localisation of both auditory and (low-reliability) visual stimuli.

A possible reason for this disagreement between task contexts is that they vary in their sensitivity to detect small differences in sensory variances. In the multisensory context, auditory variances are estimated based on sounds that are always presented alongside a visual distractor, while visual variances are estimated based only on the interaction between the auditory and visual signals. The full multisensory BCI model is complex, and any small group differences may be lost in the estimation of multiple related parameters, while in the unisensory context the sensory variance parameters are measured more directly. It is also possible that sensory parameters estimated in a multisensory context reflect not only signal and peripheral sensory noise, but also central sensory noise, making the comparison between groups more complex. This is supported by the results of our formal model comparison, which showed that estimates of sensory variances cannot be transferred between unisensory and bisensory contexts.

Existing literature is similarly ambiguous about age-related declines in (especially) auditory localisation. Dobreva et al. (2011) report limited but significant age differences in observers’ ability to freely localise transient broadband stimuli along the azimuth, while Otte et al. (2013) found no such effects. It therefore seems that the effects of normal, healthy ageing on auditory localisation ability may be subtle and difficult to detect. In terms of visual localisation, we note that our older adults are likely to have had impaired accommodation responses compared to the younger age group (Glasser & Campbell, 1997). Depending on the corrective lenses worn (participants were instructed to wear their normal spectacles for testing), this may have led to the older group expending more effort to keep the visual stimuli in focus and/or the stimuli appearing less focused. The small but significant age differences we observed in unisensory visual localisation may be, in part, a reflection of this reduced accommodation ability.

Crucially, however, the fitted spatial and coupling prior parameters of the normative BCI model did not differ between age groups. Older and younger adults also gave comparable localisation and common-source judgement responses, and the BCI model was found (based on R^2 values, a measure of model fit) to account equally well for the groups' behaviour. This suggests that, in an unspeeded context, our younger and older adults processed complex audiovisual spatial stimuli in a remarkably similar way; the fundamental computations underlying multisensory integration appear unchanged with age.

These results may initially seem surprising in light of accumulating research showing that ageing alters multisensory integration. For example, older adults have been shown to be more susceptible 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 (Chan et al., 2014; 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). In this case the effect is likely to be further compounded by reductions in speech comprehension, resulting from presbycusis that particularly affects higher sound frequencies (Pichora-Fuller & Souza, 2003).

In contrast, the estimation and integration of spatial information 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, our results (and those of others; Dobreva et al., 2011; Otte et al., 2013) demonstrate only limited age differences in localisation of transient broadband sounds and visual flashes along the azimuth.

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, GLM-based analyses of common-source judgement reaction times suggested that older adults took disproportionately longer to respond to more challenging or ambiguous stimuli. Such findings imply the presence of differences in the groups' evidence accumulation and decision-making process, and/or in their speed/accuracy criteria, even in an unspeeded context.

We thus applied a simplified, speeded ventriloquist paradigm to directly address the question of age differences in response times to multisensory spatial stimuli. GLM analyses again showed that older adults were disproportionately slower in the most challenging condition (in this case locating a sound in the presence of an incongruent visual distractor). To characterise the computational processes underlying these differences, it is necessary to move beyond the static BCI model to a dynamical approach that can make predictions jointly about observers' spatial choices and response times. We thus applied the compatibility bias model (Noppeney, Ostwald, & Werner, 2010; Yu et al, 2009) to participants' auditory judgement responses in this paradigm.

This 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. It 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 a supplementary finger-tapping task; see Supplementary S2). Second, they use a higher response threshold, requiring a greater degree of certainty before a response is given. This is consistent 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 3). 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 the Bayesian causal inference model, and other approaches that consider only the observer's final response, are insensitive to these age-related changes in internal sensory noise (though the unisensory localisation data do provide some evidence of small reliability differences). This illustrates how dynamical models that accommodate both reaction times 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.

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