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Visual–Vestibular Integration During Self-Motion Perception in Younger and Older Adults

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Younger adults integrate visual and vestibular cues to self-motion in a manner consistent with optimal integration; however, little is currently known about whether this process changes with older age. Our objective was to determine whether older adults, like younger adults, display evidence of optimal visual–vestibular integration, including reductions in bimodal variance (Visual + Vestibular) compared with unimodal variance (visual or vestibular alone), and reliability-based cue weighting. We used a motion simulator and a head-mounted display to introduce a 2-interval forced-choice heading estimation task. Older (65+ years) and younger adults (18–35 years) judged which of two movements was more rightward. Movements consisted of vestibular cues (passive movement in darkness), visual cues (optic flow), or both cues combined. The combined condition contained either congruent cues or incongruent cues (either a subtle 5° or larger 20° conflict). Results demonstrated that older adults had less reliable visual heading estimates than younger adults but comparable vestibular heading estimates. During combined, congruent conditions, both age groups exhibited reductions in combined variance, consistent with predicted optimal integration. During subtle cue conflicts, only younger adults exhibited combined variance consistent with predicted optimal integration, but both age groups displayed reliability-based cue weighting. During larger spatial conflicts, neither group demonstrated optimal reductions in variance. Younger adults displayed reliability-based cue weighting but older adults' heading estimates were biased toward the less reliable visual estimate. Older adults' tendency to incorporate spatially conflicting and unreliable visual cues into their self-motion percept may affect their performance on mobility-related tasks like walking and driving.

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Keywords: multisensory, integration, self-motion, heading, optimal, aging, binding window, heading

Many everyday tasks such as walking and driving involve self-motion through space. To perform these tasks effectively, it is necessary for the observer to maintain reliable estimates of their own movement parameters, including their speed, distance traveled, and heading direction (Campos & Bülthoff, 2012; Cullen, 2014; DeAngelis & Angelaki, 2012; Frenz & Lappe, 2005; Greenlee et al., 2016; Larish & Flach, 1990; Page & Duffy, 2003; Sun, Campos, Young, Chan, & Ellard, 2004; R. Warren & Wertheim, 1990). Multiple sensory systems (e.g., visual, proprioceptive, vestibular) can estimate self-motion parameters, but due to noise within the nervous system and changing behavioral and environmental conditions, the reliability associated with each sensory estimate varies (Ernst & Bülthoff, 2004; Knill & Pouget, 2004; Ma, Beck, Latham, & Pouget, 2006). Research on younger adults and nonhuman primates has shown that observers can reduce the variability of their perceptual estimates of self-motion by integrating redundant sensory estimates (Butler, Campos, Bülthoff, & Smith, 2011; Butler, Smith, Campos, & Bülthoff, 2010; Campos & Bülthoff, 2012; Fetsch, Turner, DeAngelis, & Angelaki, 2009; Gu, Fetsch, Adeyemo, Deangelis, & Angelaki, 2010). This phenomenon has been particularly well characterized at both the behavioral and neurophysiological levels in the context of heading perception (Butler et al., 2011, 2010; Fetsch et al., 2009; Gu et al., 2010).

When presented with visual cues (i.e., optic flow; Gibson, 1950) and vestibular cues (i.e., passive translation; Angelaki & Cullen, 2008), macaque monkeys and young adult humans integrate them such that each estimate is weighted as a function

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of their relative reliabilities and yields a bimodal heading estimate with a lower variance than either unimodal estimate alone (Butler et al., 2011, 2010; Fetsch et al., 2009; Gu et al., 2010). Optimal integration has been observed in numerous behavioral contexts and across different sensory cue combinations but may be uniquely robust for self-motion percepts. Because self-motion simultaneously stimulates the visual and vestibular systems, these causally related cues may be integrated in a more mandatory fashion than, for instance, exteroceptive visual and auditory cues (Blanke, Slater, & Serino, 2015; Campos & Bülthoff, 2012; Frissen, Campos, Souman, & Ernst, 2011; Prsa, Gale, & Blanke, 2012). Optimal visual–vestibular integration is also robust to modest spatial discrepancies (Butler et al., 2011, 2010; Fetsch et al., 2009; Kaliuzhna, Prsa, Gale, Lee, & Blanke, 2015) and to discrepant visual and physical velocity motion profiles (Butler, Campos, & Bülthoff, 2015). However, optimal integration no longer occurs when visual cues to self-motion are not presented stereoscopically (Butler et al., 2011), perhaps because, without depth cues, optic flow may be attributed to object motion rather than self-motion (Butler et al., 2011).

Current knowledge about sensory integration related to self-motion is based primarily on research examining younger adults and nonhuman primates. Little is known about whether age-related changes in sensory reliabilities and/or age-related changes to central sensory integrative mechanisms affect multisensory integration during self-motion. Furthermore, little is known about whether there are age-related differences in the range of spatial and temporal discrepancies that are tolerated before optimal integration no longer occurs. Age-related changes to optimal integration could be consequential to the way that older adults perceive self-motion and how they perform tasks such as standing, walking, and driving.

There is much evidence to suggest that there are broad declines in performance on tasks that require reliable self-motion perception with older age. Older adults are more prone to instability and falls while standing and walking (Hausdorff, Rios, & Edelberg, 2001; Horak, Shupert, & Mirka, 1989; Prince, Corriveau, Hébert, & Winter, 1997; Tinetti, Speechley, & Ginter, 1988) and have greater difficulties with spatial navigation (Adamo, Briceño, Sindone, Alexander, & Moffat, 2012; Allen, Kirasic, Rashotte, & Haun, 2004; Harris & Wolbers, 2012; Setti, Burke, Kenny, & Newell, 2011). In the context of driving, older adults are more likely to be involved in multivehicle collisions than younger adults (Hakamies-Blomqvist, 1993; Langford & Koppel, 2006) and have higher collision rates per kilometer traveled than all but young, novice drivers (Eberhard, 2008). Although much emphasis has been placed on the unimodal, cardiopulmonary, musculoskeletal, neurophysiological, and cognitive factors associated with age-related declines in performance on mobility-related tasks, changes to perceptual and multisensory integrative processes are also likely to contribute to these declines, and yet these contributions are not well understood.

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Older age is characterized by broad changes in sensory functioning and perceptual abilities relevant for self-motion perception. For instance, there are age-related declines in the processing of visual motion cues that cannot be explained by changes in peripheral visual functioning alone (Ball & Sekuler, 1986; Bennett, Sekuler, & Sekuler, 2007; Fernandez, Monacelli, & Duffy, 2013;

Kavcic, Vaughn, & Duffy, 2011; Lich & Bremmer, 2014; Snowden & Kavanagh, 2006; Tetewsky & Duffy, 1999; W. H. Warren, Blackwell, & Morris, 1989), and older adults have higher perceptual thresholds for discerning their heading on the basis of optic flow cues alone (Atchley & Andersen, 1998; Lich & Bremmer, 2014; W. H. Warren et al., 1989). In the vestibular system, a loss of hair cells within the semicircular canals and the otoliths can lead to diminished sensitivity to head rotation and translation (for reviews, see Anson & Jeka, 2016; Zalewski, 2015). Diminished vestibular sensitivity is thought to contribute to higher perceptual thresholds for the detection of passive self-motion in darkness (e.g., Roditi & Crane, 2012). Therefore, older adults may generally be subject to global declines in the reliability with which the individual sensory systems convey self-motion.

There is also evidence from basic stimulus detection and discrimination tasks indicating that there may be age-related changes in the way that multiple sensory inputs are integrated to form a coherent, unitary percept (e.g., Diederich, Colonius, & Schomburg, 2008; Laurienti, Burdette, Maldjian, & Wallace, 2006; Peiffer, Mozolic, Hugenschmidt, & Laurienti, 2007). This phenomenon has primarily been examined among combinations of Visual + Auditory cues or Visual + Somatosensory cues (for a review, see de Dieuleveult, Siemonsma, van Erp, & Brouwer, 2017). However, in a recent series of experiments, we observed evidence of age-related changes in the effect of multisensory interactions during self-motion perception. We used a simulated driving paradigm to provide visual motion cues alone (via projected display) or in combination with vestibular cues (i.e., moved via a hydraulic motion platform), or auditory cues (i.e., wind, tire, engine sounds). We then measured speed and lane-keeping performance. Results demonstrated that the addition of congruent vestibular and auditory cues to self-motion had a more pronounced effect on older adults' driving performance than it did on younger adults' performance (Ramkhalawansingh, Keshavarz, Haycock, Shahab, & Campos, 2016). Other research examining age-related differences in gait and postural control has demonstrated that older adults are more susceptible to performance declines when presented with incongruent visual or vestibular cues to self-motion (e.g., Allison & Jeka, 2004; Berard, Fung, & Lamontagne, 2012; Deshpande & Patla, 2007). Overall, these observations suggest that older adults may be more reliant on multiple, congruent sensory cues to perform self-motion tasks effectively and are less tolerant to sensory conflicts. But the extent to which these behavioral outcomes reflect age-related differences in underlying cue integration strategies has not been extensively examined.

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Age-related changes in performance on mobility-related tasks has often been attributed to sensory biases either toward visual cues (e.g., Simoneau et al., 1999; Sundermier, Woollacott, Jensen, & Moore, 1996; Wade, Lindquist, Taylor, & Treat-Jacobson, 1995) or vestibular cues (Wiesmeier, Dalin, & Maurer, 2015). However, a systematic bias toward input from one modality or the other does not explain why older adults are more heavily influenced by both visual perturbations (e.g., Berard et al., 2012) and vestibular perturbations (e.g., Deshpande & Patla, 2007) than are younger adults. A more inclusive explanation is that older adults differ in terms of which cues they integrate and how. Specifically, it is possible that when visual cues become uninformative or unreliable (e.g., spatially incongruent or noisy), younger adults may be better able than older adults to strategically assign more

weight to other more reliable or more relevant sensory inputs. However, most studies have examined age-related differences in the use of different sensory cues to guide self-motion by simply adding or removing congruent or incongruent cues and measuring the resulting performance outcomes. To better quantify age differences in multisensory *integration* during self-motion perception, it is necessary to first characterize the unimodal estimates of some parameter of self-motion (e.g., speed, heading, distance) and then determine how these estimates are combined when more than one is available and they are redundant.

To summarize, previous studies involving younger adults have shown that visual and vestibular inputs are combined to yield an optimal reduction in perceptual variance (e.g., Butler et al., 2010; Fetsch et al., 2009), but no previous studies have evaluated whether the same is true for older adults. Likewise, previous studies have demonstrated that younger adults weight visual and vestibular cues as a function of their relative reliabilities (e.g., Butler et al., 2010; Fetsch et al., 2009), but no previous studies have established whether the same is true for older adults. Finally, whereas a few previous studies have explored the types and magnitude of visual and vestibular spatial conflicts that younger adults will tolerate before they no longer integrate (de Winkel, Correia Gracio, Groen, & Werkhoven, 2010; de Winkel, Katliar, & Bülthoff, 2017; Kaliuzhna et al., 2015), the characteristics of the spatial window of integration are unknown for older adults. In fact, age-related changes to the spatial (rather than temporal) window of integration have generally not been well explored, even when considering other types of cue combinations (e.g., visual-auditory) or tasks (e.g., stimulus detection; de Dieuleveult et al., 2017).

The goal of the current investigation was to utilize the well-established heading perception paradigm to investigate whether there are age-related differences in visual–vestibular integration. We employed a heading discrimination task in which visual cues to heading (optic flow) were provided via a head-mounted display (HMD) and vestibular cues to heading (passive translation) were provided via a motion platform. A 2-interval forced-choice (2IFC) task was used in which participants were presented with two movements and reported which movement was more rightward. There were three primary study objectives:

1. Measure performance under each unimodal condition—visual and vestibular alone—(a) as a way of investigating age-related differences in the reliability of each sensory estimate, and (b) to quantify the reliability of unimodal estimates to make predictions about optimal integration during the bimodal conditions.

2. Present congruent visual and vestibular cues simultaneously to determine whether both age groups exhibited optimal integration, defined as a reduction in variance relative to the unimodal estimates.

3. Introduce two levels of intersensory spatial conflict between the visual and vestibular cues: (a) a subtle 5° conflict, and (b) a larger 20° conflict. This allowed us to determine whether reliability-based cue weighting occurred and whether there were age-related differences in the magnitude of spatial conflict that was tolerated.

Method

Participants

Twenty-four older adults (M = 69.6 years, SD = 4.1) and 17 younger adults (M = 22.3, SD = 4.2) were recruited from the community. A prescreening interview screened for self-reported visual, hearing, and/or balance impairments. On-site, older adults were screened for mild cognitive impairment using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005) cutoff score <26, and for medical issues that could affect their performance or compromise their safety (e.g., history of eye disease, stroke, seizures/epilepsy, heart attack). Participants provided informed written consent and were compensated \$10 per hour. This research was approved by the University Health Network's Research Ethics Board (REB 14–8264).

Ten older participants (42%) and two younger participants (12%) were excluded from the analysis because during the experimental task, they selected the comparison as more rightward on roughly 50% of the trials regardless of the magnitude of the comparison heading angle. This signified that participants were guessing whether the comparison heading was more rightward. This resulted in extreme heading discrimination thresholds. Specifically, the two eliminated younger adults and six of the eliminated older adults had extreme thresholds in the visual-only condition, whereas the other four eliminated older adults had extreme thresholds in all sensory conditions. In total, 14 older and 15 younger adults were included in the final analyses (see Table 1). To provide reassurance that the current sample was not biased with respect to factors such as age or basic baseline sensory or cognitive abilities as measured using standardized tests, we compared older adults who were deemed eligible to participate and who were included in the final analysis with the older adults who were deemed eligible to participate but who were excluded from the final analysis due to their extremely poor experimental task performance. Specifically, these two groups of included/excluded older adult participants were compared in terms of their mean age, visual acuity, contrast sensitivity, stereo acuity, and MoCA scores (see below for details regarding these assessments) using a series of independent samples t tests. No comparisons revealed significant group differences, suggesting no biases on the bases of performance on these baseline measures, the implications of which are discussed below.

Apparatus

The experiment was conducted at the Toronto Rehabilitation Institute's iDAPT Centre for Rehabilitation Research. It took place in a modular, 8-m³ space (Figure 1A) mounted on a Bosch-Rexroth HyMotion 11,000 6-degrees-of-freedom hydraulic hexa-pod motion platform (Figure 1B). Participants sat in a chair with an adjustable headrest that cradled both the neck and head in order to restrict head movement (Figure 1C). Participants were instructed to keep their head as still as possible. White noise was delivered over a pair of Koss QZ99 passive noise-isolating headphones to mask the sounds of the platform. The experimenter communicated with the participant over the headphones using a Buddy Microphones DesktopMini 7G USB microphone. Visual motion was presented using an Oculus Rift Developer Kit 2 stereoscopic

HMD. The display panel has a 90° horizontal and 100° vertical field of view, with a resolution of 960 × 1080 pixels per eye, a refresh rate of 60 Hz, and a persistence of 2 ms.

Cognitive and Perceptual Performance Assessment Battery

Baseline measures were used to characterize the participant groups and to provide covariates for analyses associated with the heading estimation responses across the different sensory conditions (see Table 1).

Vision. The ETDRS visual acuity test, the Pelli-Robson contrast sensitivity test, and the Randot Stereogram test of stereovision were administered to test visual abilities that could affect visual heading perception. All participants had vision either within the normal range or within the near-normal range (see Colenbrander, 2002, 2010). Older adults and younger adults did not differ significantly in terms of their visual acuity. On the Pelli-Robson contrast sensitivity test, older adults' mean logCS of 1.63 was lower than younger adults' mean of 1.78, indicating poorer contrast sensitivity. On the Randot stereo acuity test, older adults' mean arcsec was 161.4, which was larger than younger adults' mean of 29.4, indicating poorer stereoacuity. Note that the performance on the Pelli-Robson and Randot tests may have been affected by lower than optimal lighting conditions. On the Useful Field of View task, older adults score was 210.5 ms, which was larger than younger adults' score of 56.25 ms, indicating that older adults were slower to process peripheral visual targets (Ball & Owsley, 1993).

Mobility and balance. Participants performed the Timed Up and Go (TUG) test (Podsiadlo & Richardson, 1991) in less than 12 s, which is the cutoff score above which falls risk increases (Bischoff et al., 2003; Shumway-Cook et al., 2000). They also performed posturography, wherein they stood on a forceplate with their feet separated by 17 cm at the heels for 30 s, with their eyes open and closed. The force in Newtons along the x-axis and y-axis over time were used to calculate the length of the center of pressure (CoP) path (cm). This served as an index of postural stability and was used to account for vestibular and/or proprioceptive/somatosensory deficits (Horlings et al., 2008). Older and younger adults were well-matched in terms of their CoP path length.

Cognition. A paper-and-pencil Stroop task (Stroop, 1935) was used to assess participants' speed of information processing and their capacity for response inhibition. Older and younger adults did not differ significantly with respect to Stroop interference.

Stimuli

The vestibular stimulus consisted of physical translations via the motion platform that were 7.8 cm in magnitude and that followed a smooth, sinusoidal acceleration–deceleration profile,

$$s(t) = 0.049\frac{(2\pi t - \sin(2\pi t))}{4\pi^2}, 0 \le t \le 1s, \tag{1}$$

where the maximum rate of acceleration–deceleration was 0.49 m/s², the peak velocity was 0.15 m/s, and the overall duration was 1s (see Figure 1). Note that these motion parameters were based on

Table 1
Summary of Participant Characteristics

...	n	Age (years)	Male: Female	MoCA	ETDRS (logMAR)	Randot graded circles (arcsec)	Pelli-Robson (logCS)	TUG (s)	COP path (cm) Eyes open: eyes closed	Stroop interference (s)	UFOV total (ms)
Older adults	14	69.8 (4.2)	9:5	28.1 (1.5)	.05 (.19)	161.4 (142)	1.63 (.13)	8.66 (.94)	24.67: 32.57	66.28 (22.76)	210.5 (115.05)
Younger adults	15	22.6 (4.5)	9:6	—	-.07 (.17)	29.4 (15.9)	1.78 (.13)	—	29.54: 47.04	49.33 (25.38)	56.25 (11.8)
Older vs. younger (t tests)	—	—	—	—	p = .124	p = .013	p = .007	—	p = .119: p = .211	p = .085	p < .001

Note. Data are means and standard deviations (in parentheses). Columns include sample size, age, ratio of men to women, Montreal Cognitive Assessment (MoCA) scores, Early Treatment Diabetic Retinopathy Study (ETDRS) log minimum angle of resolution (logMAR), Randot graded circles (arcsec), Pelli-Robson log contrast sensitivity, Timed Up and Go (TUG) scores in seconds, Center of Pressure Path Length for eyes open and eyes closed (cm), Stroop task interference score (seconds), and Useful Field of View task total score (ms).
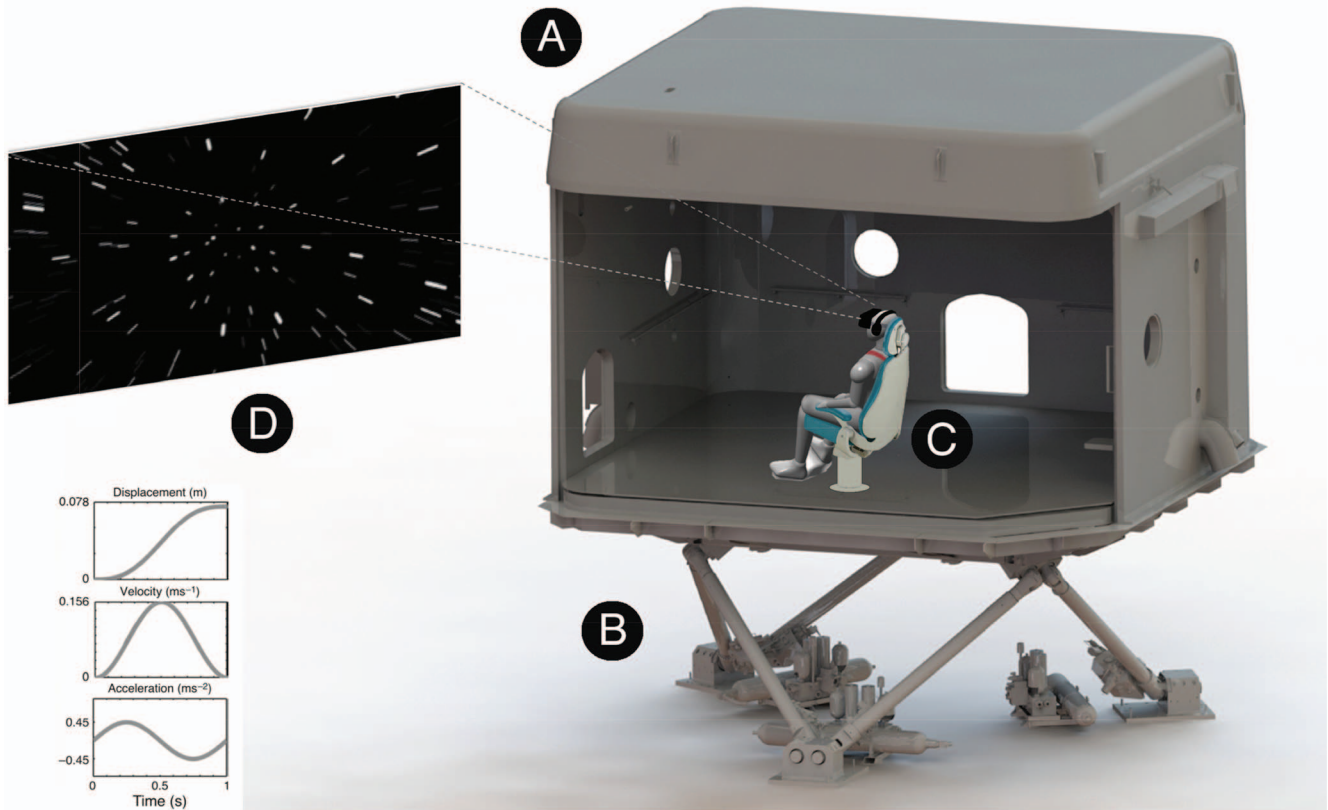
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Figure 1. Depiction of the lab used for this study (A) located at the Toronto Rehabilitation Institute. This lab consists of an 8m³ fiberglass cabin with a steel floor. The lab was mounted to a 6-degree-of-freedom hydraulic motion platform, (B) which provided vestibular cues to heading via passive translation. Participants were seated in a chair that was bolted to the floor (C), and they wore an Oculus Rift stereoscopic head-mounted display (HMD) and noise isolating headphones. The HMD provided optic flow via stereoscopic imagery of an expanding starfield (D). Inset are the characteristics of the visual and vestibular motion profiles. See the online article for the color version of this figure.

those previously utilized by Butler, Smith, Beykirch, and Bülthoff (2006; Butler et al., 2010) and were well above human detection thresholds (see Benson, Spencer, & Stott, 1986) to ensure that older adults would be able to detect the vestibular heading cues. Note that these passive translations also innervate the proprioceptive system (e.g., the neck) but are assumed to be discriminated primarily using vestibular cues. This is supported by the fact that labyrinthectomized macaques undergoing passive translation in the dark display heading perception thresholds 10 times higher than when their labyrinths are intact (Gu, DeAngelis, & Angelaki, 2007).

The visual stimuli were generated using Unity Version 5.2.0 (Unity Technologies, 2015). Unity is a video game and VR development platform. A 1,000 m × 1,000 m × 1,000 m virtual space was populated with 200 white Gaussian blobs that were spawned at random locations to create a starfield (see Figure 6.1D). Each blob was the same size, but their visual angle could vary depending on their depth within virtual space. At the maximum depth, a blob could be as small as a single pixel or 0.2° horizontal visual angle. At the minimum depth, a blob could occupy nearly the entire field of view. A virtual camera was placed at the face of the starfield and then traveled toward the stars. The camera followed the same

acceleration–deceleration profile as the motion platform. This perspective was then displayed on the HMD in stereo, giving the observer the visual impression that they were translating through the starfield and creating optic flow. We used a small sample of pilot younger adult participants to match heading discrimination thresholds between the visual only and vestibular only conditions.

Procedure

The experiment was divided into two sessions, each lasting approximately 2 hr. In the first session, we obtained informed consent; performed the cognitive, sensory, and balance/mobility assessments; and administered the personal and medical history questionnaire. The second session consisted of the heading perception task, which was comprised of a 2IFC task in which participants were asked to judge "in which of the two intervals did you move more to the right?" Each trial consisted of a standard heading interval (0°, 5°, or 20°) and a comparison heading interval (±2°, 5°, 10°, 20°; Figure 2). The order in which the standard and comparison intervals were presented was counterbalanced across trials. All participants performed the task under three sensory
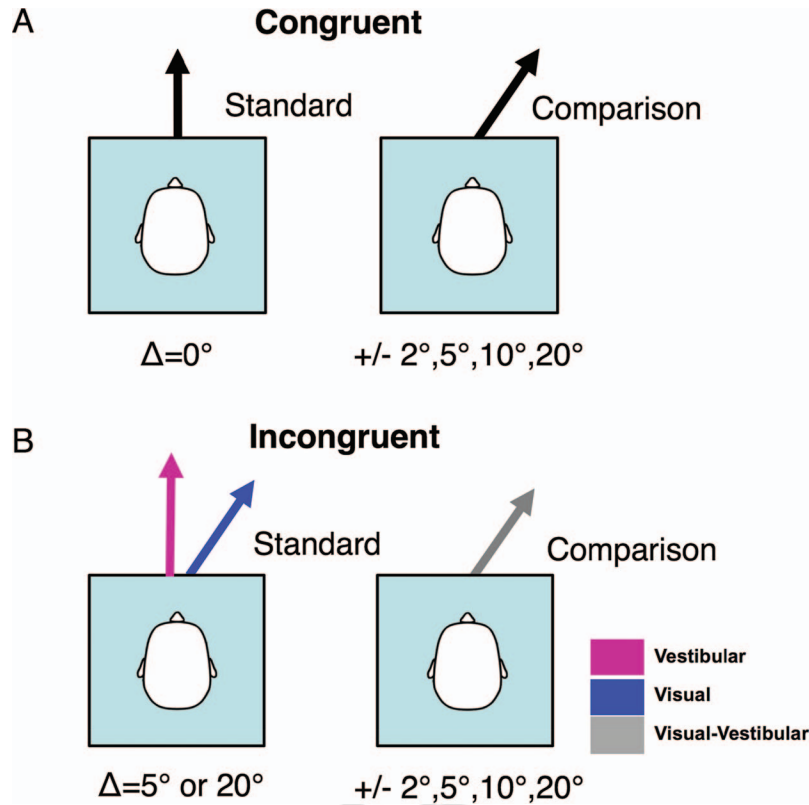
Figure 2. Depiction of 2-interval forced-choice task in which participants were asked to judge which of two headings was more to the right. Panel A depicts the congruent condition where the standard heading was always 0°. Panel B depicts the incongruent condition where the standard contained a 0° vestibular heading and visual heading that was either 5° rightward or 20° rightward. The comparison heading angles were centered around 2.5° and 10°, respectively. See the online article for the color version of this figure.

conditions: visual, vestibular, and visual and vestibular combined (bimodal).

Two levels of intersensory incongruencies were also introduced, wherein the vestibular cues were straight ahead (0°), but the visual cues were simultaneously present but offset to the right by either $\Delta = 5°$ (subtle conflict) or $\Delta = 20°$ (larger conflict).

Unimodal and congruent conditions. To establish the unimodal reliability of visual and vestibular heading estimates, participants completed a block of visual-only and vestibular-only trials. Participants also completed a block of congruent bimodal trials. For each of these conditions, the standard heading angle was $\Theta = 0°$ and the comparison heading angles varied around the standard in increments of $\pm 2°$, 5°, 10°, and 20°.

Incongruent conditions. To quantify the relative weights of the visual and vestibular heading estimates, we introduced a block of bimodal trials in which the standard heading contained a 5° intersensory conflict. Specifically, the standard consisted of a vestibular heading angle of 0° and a visual heading angle 5° to the right ($\Delta = 5°$). The comparison heading angle centered around $\Delta/2$ (2.5°) and varied in increments of $\pm 2°$, 5°, 10°, and 20°. This level of intersensory conflict is comparable with that previously used to introduce slight, presumably unnoticeable spatial disparities as a strategy for quantifying sensory cue weighting (Butler et al., 2010; Fetsch et al., 2009). To determine whether the weighting was

optimal, the observed bimodal estimates were compared with those predicted by the observed unimodal estimates. In order to establish an estimate of reliability for unimodal visual estimates when the standard was 5°, participants completed a visual only block with a $\Theta = 5°$ rightward standard as a benchmark for comparison. The comparison heading angle centered around 5° rightward and varied in increments of $\pm 2°$, 5°, 10°, and 20°.

Participants also completed a block of bimodal trials for which a larger intersensory conflict of 20° was introduced. Here the aim was to determine whether there are age-related differences in the level of spatial conflict for which optimal integration no longer occurs. This allowed us to gain novel insight into possible age-related differences with respect to the spatial window of integration. For these trials, the standard consisted of a vestibular heading angle of 0° and a visual heading angle 20° to the right ($\Delta = 20°$). The comparison heading angle centered around $\Delta/2$ (10°) and varied in increments of $\pm 2°$, 5°, 10°, and 20°. To determine whether the weights were optimal, the observed bimodal estimates were compared with those predicted by the observed unimodal estimates. Participants also completed a visual only block where the standard was $\Theta = 20°$ rightward as a benchmark for comparison. The comparison heading angle centered around $\Delta/2$ (10°) and varied in increments of $\pm 2°$, 5°, 10°, and 20° around the standard.

All participants completed seven experimental blocks in total: one vestibular block, three visual blocks (0°, 5°, 20° standards), and three bimodal blocks (0°, 5°, 20° visual offset). Figure 3 provides a depiction of the counterbalancing scheme. The presentation of each trial was triggered when the experimenter entered the response to the previous trial on the tablet computer. Within each trial, the two movements were separated by a 2-s pause. Once both movements were complete, the participant stated which of the two headings was more to the right ("first" or "second"). Once the response was entered, there was a 750-ms pause before the next trial. In the vestibular alone and bimodal conditions, a longer intertrial delay was necessary because the motion platform required 5 s to return to its starting position subthreshold. Prior to each block, participants were told which condition they would be performing, but they were not informed at any time that a spatial conflict between visual and vestibular cues would be present.

Before the experiment, each participant completed 12 practice trials, four for each sensory condition apart from the incongruent conditions. If participants responded incorrectly for two or more of the practice trials, the practice session was repeated to ensure that they grasped the task. To reduce fatigue, boredom, and acquiescence, one mandatory break was introduced in the middle of the experiment, but breaks between each block were provided as requested.

Data Analysis

The portion of rightward responses that the participant made was plotted for each comparison heading angle within each block and the data were fitted with a cumulative Gaussian function using the psignifit toolbox (Wichmann & Hill, 2001). The cumulative Gaussian functions were used to derive the point of subjective equality (PSE), the point at which the heading was selected as more rightward 50% of the time, and the just noticeable difference (JND),

$$JND = \sqrt{2}\sigma. \tag{2}$$

The JND was defined as the difference in heading angle between the PSE and the point at which heading was selected as more rightward 84% of the time, or a threshold of one standard deviation above the mean (Ernst, 2005; Rohde, van Dam, & Ernst, 2016; Wichmann & Hill, 2001). The JND is inversely related to the variance, and thus the larger the JND, the less reliable the estimate.

Maximum likelihood estimation. The JND and PSE were used to estimate the likelihood distribution for visual cues, $\hat{S}_{Vis}$, vestibular cues $\hat{S}_{Vest}$, and visual–vestibular cues combined (bimodal). If visual and vestibular cues to heading are integrated in a statically optimal fashion, the bimodal likelihood, $\hat{S}_{Bimodal}$, can be predicted by the linear weighted sum of the unimodal estimates,

$$\hat{S}_{Bimodal} = w_{Vis}\hat{S}_{Vis} + w_{Vest}\hat{S}_{Vest}, \tag{3}$$

where the weights w_{vis} and w_{vest} are derived from the reliability (inverse variance) of the unimodal cues,

$$w_{Vis} = \frac{1/JND_{Vis}^2}{1/JND_{Vis}^2 + 1/JND_{Vest}^2}, \tag{4}$$

$$w_{Vest} = 1 - w_{Vis}, \tag{5}$$

and where JND_{vis} and JND_{vest} represent the JND of the unimodal visual cues and vestibular cues, respectively, and serve as estimates of unimodal variance. The observed weights are calculated by determining the proportional proximity of the bimodal PSE to each unimodal PSE,

$$w_{Vis} = \frac{PSE_{Bimodal} - PSE_{Vest}}{PSE_{Vis} - PSE_{Vest}}, \tag{6}$$

and

$$w_{Vest} = \frac{PSE_{Bimodal} - PSE_{Vis}}{PSE_{Vest} - PSE_{Vis}}. \tag{7}$$

The observed weights, Equations 4 and 5, can then be compared with the predicted weights, Equations 6 and 7. We can also predict the JND of the bimodal condition using the sum of the unimodal reliabilities,

$$\frac{1}{JND_{Bimodal}^2} = \frac{1}{JND_{Vis}^2} + \frac{1}{JND_{Vest}^2}, \text{ or}$$
$$JND_{Bimodal}^2 = \frac{JND_{Vis}^2 JND_{Vest}^2}{JND_{Vis}^2 + JND_{Vest}^2}. \tag{8}$$

Thus, the bimodal JND should be less than or equal to the lowest unimodal JND,

$$JND_{Vis-Vest} \le \min(JND_{Vis}, JND_{Vest}). \tag{9}$$
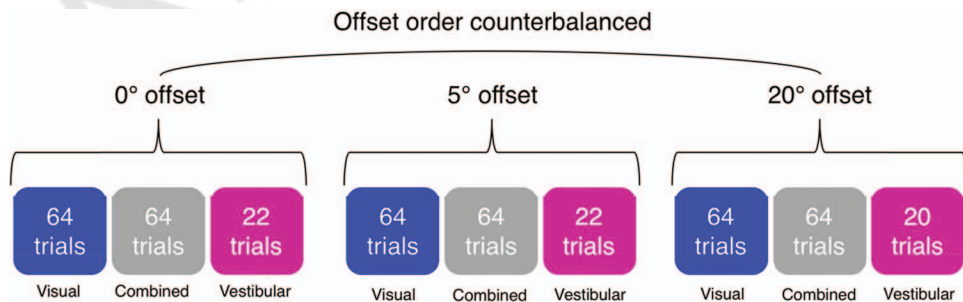
(Formulae adapted from Butler et al., 2010)

Figure 3. Depiction of counterbalancing scheme. The order in which participants experienced each angular offset (0°, 5°, 20°) was counterbalanced. The order in which participants experienced each sensory condition was the same. See the online article for the color version of this figure.

Statistical analyses. To compare precision between age groups, the visual and the vestibular unimodal JNDs were submitted to a 2 age (older vs. younger) $\times$ 4 unimodal condition (vestibular; visual 0°, 5°, 20°) mixed factorial ANOVA. To determine whether younger and older adults were matched with respect to the PSE of the unimodal heading estimates, the differences between the objective heading angle of the unimodal stimuli (i.e., offset angle) and participants' estimates of heading angle (i.e., PSEs) were calculated and submitted to a 2 (older vs. younger) $\times$ 4 (vestibular; visual 0°, 5°, 20°) mixed factorial ANOVA. To determine whether participants' individual characteristics as determined by baseline sensory, cognitive, and motor tasks influenced the precision with which they estimated their heading, bivariate correlations were used to examine the relationship between each baseline measure for each unimodal condition and heading estimates for each standard heading angle. To test for increases in precision observed in the bimodal condition relative to the unimodal conditions, a series of 2 age (older vs. younger) $\times$ 3 sensory condition (visual, vestibular, bimodal) mixed factorial ANOVAs were conducted for each visual offset (0°, 5°, and 20°). To determine whether the gains in precision associated with bimodal cues were consistent with optimal integration, paired-samples t tests comparing the observed JNDs with the predicted optimal JNDs were conducted for the 0°, 5°, and 20° offsets within each age group. Likewise, to test whether the available cues were weighted in manner consistent with optimal integration, paired-samples t tests were used to compare the predicted optimal PSEs with the observed PSEs for the 5° and 20° offsets within each age group. The 0° offset was omitted because the PSEs associated with the

visual and vestibular cues were the same, and thus there can be no observable differences in terms of their relative weighting. When Mauchly's test of sphericity indicated that the assumption of sphericity had been violated, degrees of freedom were corrected using Greenhouse-Geisser estimates. The critical p value for all analyses reported was $\alpha = .05$.

Results

Unimodal JNDs

Reliability (JND). JNDs for the two age groups, the vestibular condition, and each of the three visual conditions (i.e., $\Theta = 0°$, 5°, and 20°) were submitted to a 2 (older vs. younger) $\times$ 4 (unimodal conditions) mixed factorial ANOVA. There was a main effect of age group, $F(1, 27) = 7.16$, $p = .013$, $\eta_p^2 = .210$, in which older adults had higher JNDs overall (see Figure 4). There was also **F4** a main effect of sensory condition, $F(3, 81) = 15.52$, $p < .001$, $\eta_p^2 = .365$. Post hoc t tests using Bonferroni correction revealed that vestibular JNDs ($M = 4.37$, $SE = .46$) were lower than visual JNDs at $\Theta = 0°$ ($M = 7.34$, $SE = .65$; $p = .002$) and $\Theta = 20°$ ($M = 9.46$, $SE = .95$; $p < .001$), and that visual $\Theta = 20°$ JNDs were higher than visual $\Theta = 0°$ ($p = .044$) and $\Theta = 5°$ ($M = 6.08$, $SE = .63$; $p = .002$) JNDs. There was also a significant Age $\times$ Sensory Condition interaction, $F(3, 81) = 3.06$, $p = .033$, $\eta_p^2 = .102$. Post hoc Bonferroni tests comparing age groups within each sensory condition demonstrated that vestibular only JNDs did not differ significantly ($p = .559$) between older ($M = 4.65$, $SE = .661$) and younger ($M = 4.11$, $SE = .639$) adults. Likewise, visual
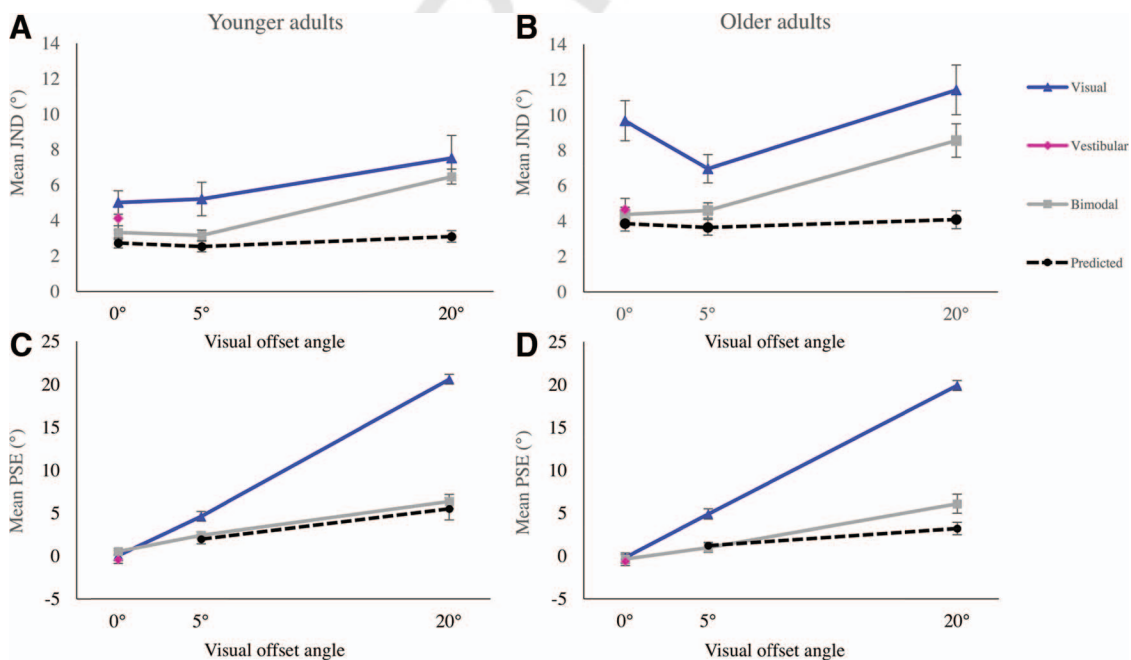
Figure 4. The top row depicts the unimodal, bimodal, and predicted optimal heading discrimination thresholds (y-axis), for (A) younger adults and (B) older adults, each plotted as a function of visual offset angle (x-axis). The bottom row depicts the unimodal, bimodal, and predicted optimal PSEs (y-axis) for (C) younger adults and (D) older adults, each plotted as a function of visual offset angle (x-axis). Error bars are +1 *SE*. PSE = point of subjective equality. See the online article for the color version of this figure.

$\Theta = 5°$ JNDs did not differ ($p = .171$) between older ($M = 6.96$, $SE = .89$) and younger ($M = 5.20$, $SE = .86$) adults. However, visual $\Theta = 0°$ JNDs differed ($p < .001$) between older ($M = 9.67$, $SE = .93$) and younger ($M = 5.02$, $SE = .89$) adults, and visual $\Theta = 20°$ JNDs differed ($p = .049$) between older ($M = 11.42$, $SE = 1.36$) and younger ($M = 7.51$, $SE = 1.32$) adults. Post hoc Bonferroni tests comparing sensory conditions within each age group revealed that older adults were driving the effect of sensory condition such that younger adults' JNDs did not differ significantly across any of the unimodal conditions ($p > .104$). Conversely, older adults had lower JNDs in the vestibular condition ($M = 4.65$, $SE = .66$) than in the visual $\Theta = 0°$ ($M = 9.67$, $SE = .93$, $p < .001$) and $\Theta = 20°$ ($M = 11.42$, $SE = 1.36$; $p < .001$) conditions but not the $\Theta = 5°$ ($M = 6.96$, $SE = .89$; $p = .173$) condition. Also, older adults had lower JNDs in the visual $\Theta = 5°$ condition than in the visual $\Theta = 0°$ ($p = .032$) and $\Theta = 20°$ ($p = .005$) conditions.

Weighting (PSE). The mean difference between the objective heading angle of the unimodal motion stimuli (i.e., actual heading angle) and participants' estimates of heading angle (i.e., PSEs) was calculated (see Figure 4C and 4D). The mean differences were submitted to a 2 (older vs. younger) $\times$ 4 (unimodal conditions) mixed factorial ANOVA. As expected, there was no effect of age group, $F(1, 27) = 1.31$, $p = .262$, or unimodal condition, $F(3, 81) = .462$, $p = .710$, and no interaction, $F(3, 81) = 1.59$, $p = .198$.

Correlations between unimodal JNDs and baseline measures. Bivariate correlations were used to examine the relationship between age, visual acuity, contrast sensitivity, stereo acuity, TUG, COP path length, and JND at each visual offset and for each unimodal condition and each standard heading angle to determine whether age-related declines in baseline sensory/motor functioning predicted unimodal heading perception. No correlations were significant ($r \leq -.283$, $p \geq .077$), and thus these particular participant characteristics were not predictive of unimodal precision in this sample.

Unimodal Versus Bimodal JND

Congruent conditions. Unimodal and bimodal JNDs for $\Delta = 0°$ were submitted to a 2 (age) $\times$ 3 (sensory condition: visual, vestibular, bimodal) mixed factorial ANOVA. There was a main effect of age group, $F(1, 27) = 9.25$, $p = .005$, $\eta_p^2 = .255$, a main effect of sensory condition, $F(1.42, 38.43) = 19.87$, $p < .001$, $\eta_p^2 = .424$, and a significant Age $\times$ Sensory Condition interaction, $F(1.42, 38.43) = 7.02$, $p = .006$, $\eta_p^2 = .206$. Post hoc Bonferroni tests revealed that for older adults, bimodal cues ($M = 4.38$, $SE = .41$) yielded a significantly lower ($p < .001$) JND than visual cues ($M = 9.67$, $SE = .93$; see Figure 4). No other comparisons were significant.

Incongruent conditions. Unimodal and bimodal JNDs for $\Delta = 5°$ were submitted to a 2 (age) $\times$ 3 (sensory condition: visual, vestibular, bimodal) mixed factorial ANOVA. There was a main effect of sensory condition, $F(1.62, 43.70) = 7.99$, $p < .001$, $\eta_p^2 = .228$, but no effect of age group, $F(1, 27) = 3.48$, $p = .073$, $\eta_p^2 = .114$, and no interaction, $F(1.62, 43.70) = .597$, $p = .554$, $\eta_p^2 = .022$. Post hoc Bonferroni tests revealed that bimodal JNDs ($M = 3.88$, $SE = .26$) were significantly lower ($p = .002$) than

visual JNDs ($M = 6.08$, $SE = .625$; see Figure 4). No other comparisons were significant.

Unimodal and bimodal JNDs for $\Delta = 20°$ were submitted to a 2 (age) $\times$ 3 (sensory condition: visual, vestibular, bimodal) mixed factorial ANOVA. There was a main effect of sensory condition, $F(1.38, 37.16) = 17.00$, $p < .001$, $\eta_p^2 = .386$, a main effect of age group, $F(1, 27) = 6.01$, $p = .021$, $\eta_p^2 = .182$, but no interaction, $F(1.38, 37.16) = 1.83$, $p = .182$, $\eta_p^2 = .064$. Post hoc Bonferroni tests revealed that bimodal JNDs ($M = 7.52$, $SE = .51$) were significantly greater ($p < .001$) than vestibular JNDs ($M = 4.38$, $SE = .46$) and that older adults had greater JNDs ($M = 8.21$, $SE = .640$; $p < .001$) than younger adults ($M = 6.03$, $SE = .618$; see Figure 4).

Observed Versus Predicted Optimal JNDs

Predicted optimal JNDs were calculated from the unimodal JNDs using Equation 8. The observed and predicted bimodal JNDs were submitted to paired-samples t tests for each heading angle and for each age group.

Congruent conditions. Consistent with previous research, younger adults' observed and predicted JNDs did not differ significantly at $\Delta = 0°$, $t(14) = -1.58$, $p = .136$. Likewise, older adults' observed and predicted JNDs did not differ significantly at $\Delta = 0°$, $t(13) = -1.10$, $p = .291$.

Incongruent conditions. For younger adults, observed and predicted JNDs did not differ significantly at $\Delta = 5°$, $t(14) = 2.10$, $p = .055$, but they were significantly different at $\Delta = 20°$, $t(14) = -6.69$, $p < .001$. For older adults, observed and predicted JNDs differed significantly at both $\Delta = 5°$, $t(13) = 2.41$, $p = .031$, and $\Delta = 20°$, $t(13) = 5.22$, $p < .001$.

Observed Versus Predicted Optimal PSEs

For the incongruent conditions, $\Delta = 5°$ and $\Delta = 20°$, predicted PSEs were calculated by using Equations 4 and 5 to derive estimates of the relative weights associated with the unimodal heading estimates (see Figure 4). No predictions were made for $\Delta = 0°$, as a spatial conflict is necessary to estimate relative weights. The predicted combined PSE was calculated by taking the linear weighted sum of the visual and vestibular PSEs (Equation 3). Two-tailed t tests were used to compare the observed bimodal PSE with the optimal PSE. At $\Delta = 5°$, younger adults' observed bimodal PSEs ($M = 2.41$, $SE = .40$) were not significantly different from predicted PSEs ($M = 1.97$, $SE = 0.55$), $t(14) = -.82$, $p = .426$. At $\Delta = 5°$, older adults observed bimodal PSEs ($M = .99$, $SE = .58$) were not significantly different from predicted PSEs ($M = 1.22$, $SE = 0.37$), $t(13) = .301$, $p = .768$. At $\Delta = 20°$, younger adults' observed PSEs did not differ from their predicted PSEs, $t(14) = .652$, $p = .525$. At $\Delta = 20°$, but older adults' observed PSEs ($M = 6.09$, $SE = 1.11$) were significantly greater (i.e., closer to the observed visual only PSE) than their predicted PSEs ($M = 3.20$, $SE = .70$), $t(13) = 2.27$, $p = .041$.

Discussion

The purpose of the current investigation was to determine whether older adults differ from younger adults in terms of how they integrate multisensory information during self-motion percep-

tion. Specifically, the objectives were to assess whether older adults integrate visual–vestibular cues optimally such that (a) congruent bimodal cues yield a reduction in variance relative to unimodal cues, and (b) these cues are weighted according to their respective reliabilities. We also considered whether older adults demonstrate differences in visual–vestibular integration under varying levels of spatial conflict compared with younger adults.

Age-Related Differences in Unimodal Reliability

Vestibular JNDs. In the current investigation, older and younger adults did not differ with respect to their heading discrimination thresholds when they were passively moved in the dark. There is a large body of work indicating that age-related declines in the vestibular system (e.g., hair cell loss, nerve cell loss) changes one's capacity to detect inertial cues to self-motion (Anson & Jeka, 2016), but the nature of these perceptual declines likely depends on the characteristics of the movements. Roditi and Crane (2012) presented older adults (50+ years) and younger adults (21–50 years) with passive anterior or posterior sinusoidal translations that ranged in magnitude from 0.12 cm to 15 cm at either 1 Hz or a 0.5 Hz and asked them report the direction of self-motion. At 0.5 Hz, older adults had greater thresholds for detecting passive translations than younger adults, but at 1 Hz, older adults and younger adults did not differ significantly (Roditi & Crane, 2012). Therefore, in the current study, age-related differences in vestibular precision may not have been observed because the rate of acceleration may have exceeded both younger and older adults' perceptual thresholds. More systematic investigations using varied motion profiles are required to disentangle age-related differences in vestibular function as it relates to self-motion perception.

Visual JNDs. At $\Theta = 0°$, older adults were significantly more variable than younger adults when using visual cues alone to discriminate heading. Older adults' mean visual JND at $\Theta = 0°$ was 9.67°, which was nearly twice as high as younger adults' mean visual JND. Previous work has shown that even when controlling for specific visual declines (e.g., diminished visual acuity, diminished contrast sensitivity), older adults display higher perceptual thresholds, such that they require faster optic flow rates and a higher level of coherence to derive reliable estimates of speed and heading (Atchley & Andersen, 1998; Bennett et al., 2007; Snowden & Kavanagh, 2006; Tetewsky & Duffy, 1999; W. H. Warren et al., 1989). Neurons within ●●● (MST) become less selective to visual heading with age (Liang et al., 2010), and neural network models have shown that age-related cortical cell loss within area MST predicts the increased heading perception thresholds observed in older adults (Lich & Bremmer, 2014). There is also evidence that in MST, there is a neural overrepresentation for angular headings, which biases heading perceptions away from 0° (i.e., straightforward; Cuturi & MacNeilage, 2013; Gu et al., 2010). Many behaviors involve maintaining straightforward movement, and therefore this systematic bias in heading perception may enable observers to more readily categorize headings as left or right of center, making them more sensitive to deviations from their intended path (Cuturi & MacNeilage, 2013). However, this heading bias may also lead to the overestimation of headings that are close to 0° (Cuturi & MacNeilage, 2013). For older adults, the confluence of heading overestimation and broad changes in head-

ing selectivity may lead to increased heading discrimination thresholds at 0°, although this has not been empirically tested.

The observation that older adults' visual JNDs were lower at $\Theta = 5°$ than at $\Theta = 0°$ may reflect the different properties of visual motion present during each respective standard (e.g., the retinal eccentricity of the focus of expansion, the prevalence or salience of dynamic occlusion). It is also possible that because standard headings of $\Theta = 5°$ conveyed directionality, these headings were more easily categorized as rightward and were less susceptible to perceptual biases than standard headings of $\Theta = 0°$. That said, for standard headings of $\Theta = 20°$, older adults had significantly greater visual JNDs than at $\Theta = 5°$ (whereas younger adults did not). Previous studies have shown that heading discrimination thresholds increase with a more eccentric point of reference and are thereby much higher at standard headings of 20° than they are at standard headings of 5° (Crowell & Banks, 1993; Gu et al., 2010). This may be because many MST neurons are tuned such that their peak heading discriminability is for headings near 0° (forward) and 180° (backward; Gu et al., 2010). The higher eccentricity of the $\Theta = 20°$ standard in concert with decreased heading selectivity may have increased older adults' heading discrimination thresholds relative to the $\Theta = 5°$ standard (Gu et al., 2010).

Congruent sensory cues. To assess whether younger and older adults integrate visual and vestibular cues to heading optimally, we compared observed bimodal JNDs with predicted optimal JNDs derived from the unimodal JNDs. Consistent with previous findings (Butler et al., 2010; Fetsch et al., 2009), younger adults integrated congruent visual and vestibular cues in a manner consistent with optimal integration, and for the first time, this pattern was also evidenced in older adults. That said, although the observed JNDs did not differ from the predicted optimal JNDs, younger adults also did not display a significant reduction in variance over visual or vestibular cues alone when comparing the average JND values across conditions. For older adults, bimodal cues yielded a significant reduction in variance over visual cues alone but not vestibular cues alone. Participants may have performed close to ceiling within one or both of the unimodal conditions, and therefore there was not enough room for a statistically significant improvement in averaged precision values. Basic principles of multisensory integration indicate that bimodal performance gains are the largest when the two cue reliabilities are equal and near threshold, and thus the most sensitive approach would be to map the threshold values for each unimodal cue and try to equate unimodal estimates (within and between age groups) a priori. Future investigations could seek to implement this approach when investigating the integration of visual and vestibular cues in order to maximize sensitivity to age-related differences in optimal integration (although see also the Future Directions section).

Incongruent Sensory Cues

Subtle cue conflict. For the subtle conflict ($\Delta = 5°$), younger adults exhibited optimal integration as indicated by no significant differences between the observed and optimal predicted estimates. This observation is consistent with previous work demonstrating that younger adults integrate optimally in the presence of spatial conflicts of 4°, 6°, and 10° (Butler et al., 2010; Fetsch et al., 2009). However, the bimodal JNDs were not significantly different from

the vestibular JNDs, suggesting that vestibular inputs were used more heavily. On the other hand, at the 5° conflict, older adults' observed bimodal JNDs were significantly greater than their predicted optimal JNDs. This suggests that even at relatively small spatial conflicts, there may be a lower bimodal benefit afforded by redundant sensory inputs compared with that observed in younger adults in terms of increased reliability. Note that for the 5° trials specifically, there was no significant difference in the unimodal visual and unimodal vestibular JNDs between older and younger adults or within older adults. Again, because the greatest gains in precision occur when unimodal reliabilities are matched, this condition would be the most sensitive to evidence of age-related differences in optimal integration, and indeed, age-related differences were observed. Notably, the PSE values demonstrated that neither age group demonstrated biases in their absolute thresholds during the 5° conflict condition, and both groups showed evidence of reliability-based cue weighting at this subtle cue conflict level.

Large cue conflict. For the larger conflict ($\Delta = 20°$), both age groups had bimodal JNDs that were significantly greater than the predicted JNDs. Although younger adults did not demonstrate greater precision for bimodal relative to unimodal estimates, their PSEs did match the predicted PSE, suggesting they utilized reliability-based cue weighting. Older adults, however, had bimodal PSEs that were not consistent with the predicted optimal PSEs based on reliability-based weighting. Because the vestibular estimates were far more reliable than the visual estimates, optimal integration would dictate that the bimodal PSE should be weighted in favor of the vestibular estimate. However, older adults' bimodal PSE was pulled toward the visual heading estimate, meaning that the highly unreliable visual inputs still had a larger than predicted influence on their heading estimate. There are a number of plausible explanations as to why a more substantial spatial conflict had differential effects on the performance of older and younger adults in terms of relative cue weighting. In the following sections, several nonexclusive or exhaustive explanations are offered. First, we consider how aging may affect the interpretation of visual motion cues as being caused by self-motion or object motion. We then consider how age-related differences in cumulative experience may affect expectations pertaining to the spatial congruency between cues arising from self-motion. Finally, we discuss the potential role of broader age-related changes in terms of central multisensory integrative mechanisms.

A persistent challenge faced by the perceptual system is to determine which sensory inputs are caused by the same movement or event and should therefore be integrated versus those that are caused by independent movements or events and should be segregated (i.e., causal inference; see Kayser & Shams, 2015; Körding et al., 2007; Parise, Spence, & Ernst, 2012; Shams & Beierholm, 2010; Spence & Squire, 2003). Generally, sensory inputs that occur close together in space and in time are more likely to have originated from the same event and are more likely to be integrated (Körding et al., 2007; Shams & Beierholm, 2010; Wallace & Stevenson, 2014). The range of intersensory spatial and temporal discrepancies over which integration is likely to occur is commonly referred to as the spatial and temporal windows of integration, respectively (Diederich & Colonius, 2004; Wallace et al., 2004). However, much of the previous research concerning the spatial and temporal binding windows has focused on the integration of discrete visual and auditory inputs. The processes under-

lying visual-auditory integration and visual–vestibular integration, however, may be distinct. Visual and auditory stimuli are exteroceptive (i.e., generated externally), and therefore their spatial and temporal proximity can be used to make inferences about whether they are causally related and should be integrated (Blanke et al., 2015). However, the integration of interoceptive cues (i.e., those generated internally), such as vestibular and proprioceptive inputs, may be subject to additional constraints (see Blanke et al., 2015, for review). Visual and vestibular cues to self-motion may be unique in this respect, because under most natural conditions involving self-motion, the visual and vestibular systems will provide highly congruent information (Kaliuzhna et al., 2015; Prsa et al., 2012). There is some evidence to suggest that because dynamic visual and vestibular cues associated with self-motion are essentially redundant, observers may discard the individual visual and vestibular estimates (i.e., sensory fusion; Prsa et al., 2012). Previous work has demonstrated that visual–vestibular integration is robust to the introduction of different types of intersensory incongruencies, including conflicting heading angles (e.g., Butler et al., 2011, 2010; Fetsch et al., 2009), conflicting movement axes (i.e., forward translation vs. roll; Kaliuzhna et al., 2015), and conflicting velocity profiles (Butler et al., 2015). Taken together, this evidence suggests that visual and vestibular cues to self-motion may be integrated in a more mandatory fashion than exteroceptive cues.

Recent evidence indicates that although visual–vestibular integration may be robust to the introduction of various types and levels of multisensory incongruencies, integration is not observed under more significant visual–vestibular spatial conflicts (de Winkel et al., 2017). de Winkel and colleagues (2017) implemented an absolute heading estimation task in which they presented participants with a broad range of visual–vestibular spatial conflicts (up to 90°). At modest spatial conflicts ($<14°$), participants displayed optimal integration, but as the magnitude of the spatial conflict approached 90°, a single sensory modality captured the percept. This is presumably because as the magnitude of the spatial conflict increased, the probability that the two sensory cues were causally related decreased. This is consistent with the observation in the current study that younger adults continued to optimally integrate in the presence of a 5° spatial conflict but not a 20° conflict. At a 5° conflict, the probability that both cues were causally related to self-motion may have been sufficiently high that younger adults integrated them. A 20° conflict may have led to ambiguity as to whether the cues were causally related to self-motion or to object motion (Brandt, Bartenstein, Janek, & Dieterich, 1998; Brandt, Dichgans, & Koenig, 1973). This could also explain why younger adults' bimodal JNDs at $\Delta = 20°$ were suboptimal and were closer to their $\Theta = 20°$ visual JNDs than their vestibular JNDs. On bimodal trials where visual motion was attributed to the movement of external objects, they may have been judging which interval of object motion was more rightward, and therefore they were only as precise as their $\Theta = 20°$ visual alone estimate.

There have been no comparable studies that have introduced large visual–vestibular conflicts to older adults. In the current study, unlike younger adults, older adults did not demonstrate evidence of optimal integration during large or even subtle visual–vestibular conflicts. It is conceivable that as older adults accumulate a lifetime of exposure to self-motion experiences and the associated congruency between visual and vestibular cues, they may develop more rigid expectations that these temporally con-

gruent visual and vestibular cues are related to self-motion. This may result in a greater sensitivity to spatial discrepancies and, thus, reduced tolerance to even modest spatial conflicts.

Previous work in other sensory domains has also shown that multisensory integration may be broadly heightened in older age and that when older adults are presented with incongruent or task-irrelevant cues, they may continue to combine them in an obligatory fashion, resulting in greater performance decrements than younger adults (DeLoss, Pierce, & Andersen, 2013; Guerreiro, Murphy, & Van Gerven, 2013; McGovern, Roudaia, Stapleton, McGinnity, & Newell, 2014; Sekiyama, Soshi, & Sakamoto, 2014). In the current task, older adults may have attempted to incorporate both the visual and vestibular cues into their heading percept, even during spatial conflicts, despite the comparatively low reliability of the visual cues. Previous evidence of heightened multisensory integration with older age has largely been derived from visual-auditory and visual-somatosensory stimulus detection and discrimination tasks, and therefore the results described here are some of the first similar observations for visual–vestibular integration and in the context of self-motion perception.

Potential Implications for Safe Mobility

The current findings suggest that older adults are less tolerant to intersensory spatial conflicts than younger adults, as older adults did not demonstrate reliability-based heading estimation when faced with large spatial conflicts. This observation may help to better characterize previous observations pertaining to age-related differences in performance on tasks involving multisensory self-motion perception and mobility. In the context of gait and balance control, it has been demonstrated that when older adults are presented with incongruent cues to self-motion, they experience greater postural instability (e.g., Berard et al., 2012; Deshpande & Patla, 2007; Jeka, Allison, & Kiemel, 2010). A prominent hypothesis has been that this may reflect age-related differences in the ability to down-weight unreliable visual cues specifically, perhaps due to a bias toward visual cues to self-motion (e.g., Berard et al., 2012; Simoneau et al., 1999; Sundermier et al., 1996). The current study suggests that age-related differences in multisensory self-motion perception are more nuanced as older adults integrate congruent cues to self-motion optimally and are able to account for cue reliabilities when forming their multisensory self-motion percept under these typically conditions. However, in the presence of an intersensory spatial conflict, younger adults continue to account for relative cue reliabilities in forming their self-motion percept, whereas older adults demonstrate nonoptimal cue weightings. Older adults may incorporate all available cues to self-motion into their percept in a more obligatory fashion. Under most real-world situations, this approach may be advantageous given that self-motion is typically experienced with congruent visual and vestibular cues. However, older adults may be more susceptible to performance declines during instances for which the available cues to self-motion happen to be unreliable, discrepant, or irrelevant to the task at hand. This includes experimental conditions for which incongruent cues to self-motion are presented, including the abovementioned studies on gait and posture control and the current experiment. This pattern of performance also has important implications for how sensory interactions support mobility in older adults. Critically, older adults may be more susceptible to perfor-

mance decrements during real-world circumstances where they are confronted with large-field visual motion that is unrelated to their own movement. This could include everyday scenarios such as walking through moving crowds, maneuvering on public transit (trains, buses), walking while viewing digital signage, or negotiating busy intersections while driving. Under these circumstances, older adults' tendency to incorporate incongruent visual motion cues into their estimates of self-motion could lead them to misjudge the rate and/or direction of self-motion. This could, in turn, increase the risk of costly behavioral errors such as a loss of stability while walking or colliding with other objects or vehicles while driving.

These results may also have implications with respect to how older adults interact with virtual reality environments such as HMDs and driving simulators. Driving simulators, in particular, are now being regarded as a viable alternative to on road driving when assessing or training older drivers for the purpose of driver recertification (see Ball & Ackerman, 2011). However, it will be important for those designing driving simulators for training and assessment purposes to consider that the presence of and/or incongruency of the sensory cues that the simulator provides will have a differential impact on the performance of older and younger adults. For instance, our previous research has shown that when either auditory or vestibular cues to self-motion are omitted from a driving simulation and only visual cues to self-motion are available, older adults display greater differences in performance than younger adults (see Ramkhalawansingh et al., 2016).

Future Directions

A key consideration when interpreting the results of the current investigation is the inequality of the two unimodal reliabilities of the older adults' estimates (apart from the 5° offset conditions), which may have limited the sensitivity with which any reductions in perceptual variance may have been observed. Although the stimulus parameters were carefully selected to coincide with previous investigations (Butler et al., 2010), and pilot testing verified comparable psychometric properties of visual and vestibular estimates on a small group of pilot younger participants, the older adult group ultimately demonstrated a different pattern of responses. That said, by not intentionally equating unimodal performance in each group, this allowed us to examine typical age-related changes to sensory integration strategies without artificially "normalizing" the age groups for unimodal performance, thereby potentially increasing the generalizability of these results to more natural conditions. In this regard, the current investigation provides interesting first evidence to suggest that age-related sensory/perceptual declines (even within nonclinical cut points) might affect the integration strategies that older adults utilize. Baseline measures of visual, cognitive, and physical functioning did not predict performance under unimodal conditions in this sample; however, this may have been due to our relatively modest sample size. Thus, future work should seek to better disentangle the effects of central and peripheral age-related changes to sensory functioning. One method of accomplishing this is to artificially degrade the more reliable of the two estimates by adding noise to the signal such as introducing incoherent motion into the flow field (e.g., Fetsch et al., 2009) or adding noise to the vestibular cues via subtle lateral oscillations or using galvanic vestibular stimulation. It will

also be important for future work to carefully consider how other individual characteristics such as sex influence multisensory self-motion perception, given that there is some evidence that older male and female observers exhibit differences in object motion perception (e.g., Gilmore, Wenk, Naylor, & Stuve, 1992).

Because the congruent bimodal cue trials were embedded within a larger set of trials that included both small and large spatial conflicts, these constant changes in the spatial congruency between cues over the course of the experiment itself may have also impacted the weighting strategies that participants utilized (e.g., through rapid recalibration, which is known to change with older age; Noel, De Niear, Van der Burg, & Wallace, 2016). Previous research in multisensory traveled distance estimation has demonstrated that when a sensory cue is more stable across trials, it receives greater weight in the final estimate than when it is constantly changing relative to another sensory cue (Campos, Butler, & Bülthoff, 2014). In the current study, during incongruent trials, the vestibular heading was always 0° and the visual cues were either congruent or offset by 5° or 20°. Therefore, because the vestibular cues were comparatively stable across the experiment, observers may have learned to assign more weight to the vestibular estimate. Using an experimental design in which both visual and vestibular cues are manipulated equally as often, and/or examining trial-by-trial effects on how cue congruencies affect immediately subsequent trials, could provide more nuanced insights into the dynamics of any age-related differences in multisensory integration during self-motion.

Finally, the nature and length of the stimuli may have contributed to some of the age-related differences in reliability-based cue weighting under larger conflicts. Specifically, previous evidence indicates that older adults are able to appropriately reconcile or adapt to conflicting cues to self-motion but that they are slower to do so. For instance, when older adults are presented with oscillatory visual cues while attempting to maintain a stable posture, they are more susceptible to postural sway than younger adults (e.g., Deshpande & Patla, 2007; Jeka et al., 2006); however, when older adults are exposed to the conflicting cues over a longer duration, they eventually adapt (e.g., Jeka et al., 2010). It is conceivable that in the current study, if motion cues were presented over a longer duration, older adults' response to spatial conflict may have been different. Stereoscopic cues are also very important for optimal visual–vestibular integration (Butler et al., 2011), and older adults do not typically benefit from stereoscopic cues to self-motion unless the duration of exposure is longer than 2 s (Lich & Bremmer, 2014). Therefore, future studies should seek to examine the effect that motion cues of a longer duration have on older adults' visual–vestibular integration.

Conclusions

The objective of the current investigation was to determine whether there are age-related differences in multisensory integration within the context of self-motion perception. When presented with spatially congruent cues, younger adults' heading estimates were generally consistent with optimal integration. For the first time, we demonstrated that older adults also integrate congruent cues to self-motion in a manner that is consistent with optimal integration. When presented with a subtle spatial conflict, only younger adults demonstrated optimal bimodal reductions in vari-

ance. In the presence of a large spatial conflict, (a) younger and older adults did not demonstrate optimal reductions in variance for bimodal compared with unimodal conditions, and (b) older adults no longer weighted visual and vestibular cues according to their relative reliabilities but were instead biased toward the less reliable visual cues. Age-related changes in the integration of multisensory cues to self-motion could have important implications for older adults, as they could contribute to age-related changes in performance on critical everyday mobility-related tasks like standing, walking, and driving.

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