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Age-Related Differences in Audiovisual Multisensory Integration

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Psychology

by

Denton Jack DeLoss

August 2015

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ABSTRACT OF THE DISSERTATION

Age-Related Changes in Audiovisual Multisensory Integration

by

Denton Jack DeLoss

Doctor of Philosophy, Graduate Program in Psychology
University of California, Riverside, August 2015
Dr. George J. Andersen, Chairperson

Recent research has demonstrated that multisensory integration, once thought to be isolated to later stages of processing in polysensory areas, may play a significant part in nearly all sensory processing. A large volume of research has also found a wide array of perceptual and cognitive changes with age. Given these sensory declines, we would also expect similar declines in multisensory integration. The present studies examined age-related changes in multisensory integration using the sound-induced flash illusion. The illusion is studied by presenting a number of visual flashes paired with a discrepant number of auditory beeps. The first experiment examined multisensory integration in younger and older individuals using the sound-induced flash illusion. Older individuals

were found to have stronger multisensory integration as compared to younger individuals. The second experiment examined whether this increased integration could be due to decreased inhibitory control in older individuals, or a decrease in their ability to ignore the auditory beeps. This was examined by including an unrelated task in the visual and auditory modalities. The results of the study found that the addition of the task did influence the strength of the illusion in both older and younger individuals. However, this did not differ by age, indicating that attentional differences are not the cause of increased integration in older individuals. The third experiment examined whether the strength of the visual and auditory stimuli influences the strength of integration and whether this differs for older and younger individuals. The strength of the stimuli was found to influence the strength of the illusion, with decreased stimulus strength increasing the strength of the illusion. No age-related differences were found for the sound-induced flash illusion. However, older individuals showed a greater change in integration with decreased stimulus strength for the reverse illusion in which participants report the number of beeps presented instead of the number of flashes. Lastly, the fourth experiment examined whether spatial disparity influences the illusion and whether this changes with age. Spatial disparity between the auditory and visual flashes was not found to influence the illusion to a high degree and no age-related differences were found.

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Age-Related Differences in Audiovisual Multisensory Integration

Imagine yourself standing on a street corner waiting at a crosswalk. As a red truck passes by, you not only see the vehicle pass, but you hear the noise from the engine, the tires, and the suspension as it travels over a pothole in the rough asphalt. You also feel the slight breeze produced by the passing vehicle while simultaneously feeling subtle vibrations in your feet. As this situation demonstrates, many of our sensory experiences in the environment involve a variety of senses, and in many cases, this input to multiple senses is tied to a single event in the world. Given the redundant nature of much of this sensory information, it would be beneficial for sensory systems to integrate these different information sources.

In this dissertation I will refer to this integration process as multisensory integration. Although a great deal of research has been conducted on multisensory integration, relatively little research has examined how multisensory integration changes with age. Many of those studies examined facilitation of reaction times in the presence of multisensory information (Diederich, Colonius, & Schomburg, 2008; Hugenschmidt, Peiffer, McCoy, Hayasaka, & Laurienti, 2009; Peiffer, Mozolic, Hugenschmidt, Laurienti, & Pei, 2007). A smaller number of studies have examined perceptual differences in multisensory tasks using multisensory illusions to explore age-related changes (Cienkowski & Carney, 2002; Setti, Burke, Kenny, & Newell, 2011). Understanding multisensory integration in older individuals is of great importance. Not only for possible interventions, such as perceptual learning, to counter-act age-related decline, but also for the design of devices such as crash avoidance systems in

automobiles. Older drivers are the fastest increasing population on the road and also are at increased risk for crashes (Waller, 1991). Properly designed multisensory vehicle warning systems have been suggested as one method to reduce this risk (Spence, Ho, & Taylor, 2008). For these reasons, the proposed study examined age-related differences in multisensory integration. The experiments: (1) examined whether multisensory integration is affected by age-related declines in sensory processing, similar to those seen in vision and audition; (2) investigated whether these changes are associated with changes in the spatial resolution of multisensory integration; and (3) determined if changes in multisensory integration with age may be due to declines in temporal resolution as has been previously suggested by previous research. This chapter is divided into four major sections: a brief review of research on multisensory integration, a brief examination of research on age-related sensory decline, and an exploration of the current state of research on multisensory integration and aging.

Multisensory Integration

Recent research has suggested a unique aspect of sensory processing — that sensory processing is strongly influenced by multisensory sensory inputs. This multisensory integration was once thought to be rare and confined to specific polysensory regions of cortex, but recently has been found to be more common in cortical processing than was previously believed. Indeed, studies have suggested that cortical processing is likely to be predominately multisensory in nature and that an independent encapsulated model of the senses is unlikely (Ghazanfar & Schroeder, 2006; Schroeder & Foxe, 2005). For example, direct connections have even been found between auditory cortex and

primary visual cortex (Clavagnier, Falchier, & Kennedy, 2004; Falchier, Clavagnier, Barone, & Kennedy, 2002a). Multisensory neurons, or neurons responding to stimuli in multiple modalities, have also been found in visual, auditory and somatosensory cortex, though they have been found in far greater concentrations in areas bordering these modality specific areas (Wallace, Ramachandran, & Stein, 2004). These findings demonstrate that multisensory integration is not restricted to higher-order association areas (e.g. Broca's and Wernicke's area in the case of language processing). It also supports a model of cortical processing that is heavily influenced by multisensory integration.

Many early studies examining the neural components of multisensory integration in felines and primates examined integration in the superior colliculus (Meredith & Stein, 1983; Meredith & Stein, 1986; Wallace, Meredith, & Stein, 1992, 1998). The superior colliculus receives direct input from the optic tract and other sensory areas. Its function is to help direct orienting behavior and attention through the initiation of saccadic eye movements (Munoz, Pélisson, & Guitton, 1991). The superior colliculus is also important in orienting the individual and localizing any environmental stimulus. The superior colliculus is well suited to this task, as it contains topographic representations (representations that are spatially organized), of the environment for multiple senses that are positioned based on a retinotopic map that is aligned based on eye movements. This allows proper orienting in sensory space based on the current position of the eyes and the orientation of the head. The results of these studies indicate the prevalence of

multisensory processing and the importance it plays in allowing us to localize stimuli quickly and accurately.

Response Properties of Multisensory Neurons. Multisensory neurons exhibit a number of properties that are uncommon to unimodal neurons (neurons responding and modulated by only a single modality). The first of these properties concerns how multisensory signals are combined into a single neuronal response. Multisensory neurons must combine information from multiple sensory modalities, and the simplest way to combine information is with a simple additive method. An additive model of a simple neuron that fires three impulses per second to a visual stimulus, and four impulses per second to an auditory stimulus, would yield seven impulses per second in response to both stimuli occurring simultaneously. In some cases, a superadditive response may be seen. A superadditive response is one in which the response rate of a multisensory neuron is greater in the presence of multisensory stimuli than the sum of the response of the neuron to both stimulus modalities in isolation. For example, consider a multisensory neuron that fires three times per second when its receptive field is stimulated by a visual stimulus. The same neuron fires two times per second when an auditory stimulus is presented. However, when both of these stimuli are presented simultaneously the neuron fires nine times per second. This is a much higher rate than would be expected if the neuron responded in a simple additive manner. Superadditivity was once considered one of the primary indicators of a multisensory interaction (Stanford & Stein, 2007). However, research has also challenged this criteria, particularly when assessed using functional imaging (Laurienti, Perrault, Stanford, Wallace, & Stein, 2005). Multisensory

neurons can also exhibit sub-additive responses, for example the response to multisensory stimuli would be inhibited to one that is weaker than that seen for either stimulus modality alone. These neurons can be highly selective in their response characteristics. For example, animal research has shown that while traditional bimodal neurons exist (neurons responding to two modalities), there also exist selective neurons that respond only when visual stimulation is present. However, these neurons have a response that is weakened below that of a unimodal visual response when paired with simultaneous auditory stimuli (Allman, Keniston, & Meredith, 2009). This result indicates the complicated nature of multisensory neurons in the brain.

Multisensory neurons can also be modulated by other aspects of a signal. For instance, a single multisensory neuron may in fact exhibit subadditive, additive and superadditive responses. This is because multisensory neurons also tend to exhibit what is referred to as inverse effectiveness, a decrease in the rate of a neuron's response as the strength of the stimuli is increased (M. A. Meredith & Stein, 1986a; Wallace & Stein, 1994). An example of this effect is shown in Figure 1. When the stimuli are weak, we see a superadditive response in the neuron. Conversely, when the stimuli are strong we see a simple additive response, or in some cases we may observe a subadditive response. This may be due to the maximum firing rate of the neuron itself. If a strong unimodal stimulus is sufficiently strong to reach the upper limits of the firing rate of a specific neuron then there may be a ceiling effect that prevents a superadditive response. An alternative possibility is that the ability of a multisensory response to provide any additional information decreases as unimodal strength increases. As the unimodal

stimulus gets stronger there is less uncertainty regarding its stimulus properties, so the need for combining information from multiple modalities to form a superadditive multisensory response is also diminished.

Multisensory neurons demonstrate significant inhibition when stimuli are spatially incongruent. This inhibition was identified early in research by Meredith and Stein (1986b), and is typically referred to as response depression. A hypothetical example of response depression is shown in Figure 2. When the visual and auditory stimuli are spatially coincident, we see a superadditive increase in the response of neurons in the overlapping region. However, when the visual and auditory stimuli are spatially incongruent we see a decrease in the response of the neurons, below that seen for the unimodal stimuli. This response depression indicates the complexity of multisensory systems by demonstrating a high degree of interconnectivity and inhibition of neurons in non-neighborhood regions.

While the majority of the properties governing the integration of multisensory stimuli in the environment have been identified in studies using invasive neurological procedures in animals, there is evidence that behavioral indices of these properties can also be observed. Research conducted by Stein, Meredith, Huneycutt, & McDade (1989) found strong evidence of behavioral indices of superadditivity, inverse effectiveness and response depression, which could all be observed in trained felines. In one condition the animals were trained to approach the source of visual and auditory stimuli (a speaker paired with a light-emitting diode). The percent of correct responses showed a significant superadditive increase in the presence of multisensory stimuli. The change in

performance was inversely related to the strength of the unimodal stimuli, exhibiting a behavioral correlate to the inverse effectiveness seen in multisensory neurons. The animals also showed evidence of response depression. These animals were trained in a second condition to approach only the source of the visual stimuli and to ignore any auditory presentation. These animals demonstrated significant decrements in performance when the visual stimulus was paired with a spatially incongruent auditory stimulus. While it is possible that the animals were confused in these conditions and were approaching a point between both stimuli, no relationship between the eccentricity between the visual and auditory stimuli and the amount of response depression was found. This finding suggests that the behavioral response depression found was not likely due to task confusion in cases of incongruent multisensory stimuli. The results of the study suggest that multisensory integration can be seen in behavioral as well as neurophysiological methods. The results also demonstrate that the properties present in multisensory neurons can also be observed in behavioral measures.

Multisensory Illusions. Measuring reaction time or accuracy using multisensory stimuli is one of the many ways to assess multisensory integration. The integration of information from multiple modalities can bias or alter perception in another modality resulting in a multisensory illusion. While many of the previously discussed studies have used neurophysiological techniques to examine multisensory integration, multisensory illusions can be used to behaviorally examine integration. Multisensory illusions that have previously been used to probe audiovisual multisensory integration include the ventriloquist effect (Alais & Burr, 2004; Bertelson & Radeau, 1981; Pick, Warren, &

Hay, 1969), the McGurk effect (McGurk & MacDonald, 1976; Rosenblum, Schmuckler, & Johnson, 1997; Saldaña, Rosenblum, & Saldana, 1993), the stream-bounce illusion (Sekuler, Sekuler, & Lau, 1997), the flicker-flutter illusion (Shipley, 1964; Welch, DuttonHurt, & Warren, 1986), and the sound-induced flash illusion (Shams, Kamitani, & Shimojo, 2000, 2002a). These illusions can also be used to assess age-related differences in multisensory integration to determine whether the degree of integration differs between older and younger individuals.

Studies demonstrating multisensory integration established that audition could be modulated by visual information. McGurk and McDonald (1976) found that when certain discrepant phonemes, such as an auditory “ba” paired with a visual “ga”, are presented to an individual, that the perceived phoneme (auditory and visual “da”) is based on the combination of both information sources. This finding challenged the previous view (e.g. Brooks, 1968) that perceptual systems are modular — that information from one sensory modality, such as vision, is not influenced by another sensory modality, such as audition. Previous experience with the McGurk effect and knowledge of the illusion do not alter the effect, suggesting that it is cognitively impenetrable (cannot be altered by conscious awareness) and therefore occurs at an early level of processing. Other research has demonstrated that this type of integration not only occurs for speech sounds but can also alter the perception of non-speech sounds, such as whether or not a stringed instrument was plucked or bowed (Saldaña and Rosenblum, 1993). Another illusion involving localization of a sound source provides further evidence of early-level sensory integration. Visual capture, and more specifically the ventriloquism effect, can cause

shifts in the perceived location of a sound source when spatially displaced sounds are temporally coincident with a visual stimulus. Recent research has demonstrated that auditory information can drive localization of a visual source in cases where visual information is degraded (Alais & Burr, 2004).

Conversely, existing research has shown that visual perception can also be influenced by auditory stimuli (Shams, Kamitani & Shimojo, 2000; Shams, Kamitani & Shimojo, 2002). These studies provide evidence that the number of perceived visual flashes of a white disk is influenced by the number of beeps played concurrently with the stimuli. For example a single flash paired with two auditory beeps is frequently reported as two distinct flashes. According to this research, a single visual flash is likely to be perceived as multiple flashes when paired with two to four beeps, providing evidence of multisensory integration. This illusion occurs even when participants were explicitly instructed to ignore the beeps and only respond to the number of flashes perceived. An magneto-encephalography (MEG) study performed by Shams, Iwaki, Chawla & Bhattacharya (2005) demonstrated that the auditory information modulated activity in occipital cortex and that this modulation of activity only occurred on trials in which the participants perceived the illusion (the number of perceived flashes differed from the actual number presented). Other research (Watkins, Shams, Josephs & Rees, 2007) has demonstrated that activity in early visual cortex (V1) is modulated by the illusion and that, in addition to increased activity when a single flash was paired with multiple beeps, activity was inhibited when two flashes were paired with a single beep (i.e., was perceived as a single flash). These results suggest that multisensory integration is not

likely due to the result of attentional changes or perceptual matching of auditory and visual information. These results also suggest that sound-modulated neural activity in early visual cortex is predictive of an individual's perception of visual stimuli.

Age-Related Sensory Decline

The capacity for multisensory integration to reduce uncertainty, particularly in cases where stimuli are weak, makes it important to consider with regards to sensory declines in aging. Older individuals demonstrate losses in sensitivity across multiple sensory domains. These sensitivity losses weaken the strength of stimuli and may increase the likelihood of multisensory integration via inverse effectiveness. These declines are well documented in the literature on aging and vision or audition.

Visual Decline. Age-related declines in vision have been found to be due to factors that include changes in the physical structure of the eye, the retina and the pathways leading to the brain. The cornea has been found to become more spherical and smaller with increasing age (Guirao, Redondo, & Artal, 2000). These corneal changes cause increased optical aberration leading to a loss of image quality at the retina. The aging lens has been shown to lose the ability to change focal length when stretched, with a complete loss of accommodation by age 60, which is a factor leading to age-related presbyopia (Glasser & Campbell, 1998). There is also evidence of age-related changes in the opacity of the lens, increasing absorption of light and causing a decreasing in retinal illuminance (the amount of light reaching the retina, Weale, 1988). Furthermore, studies have found age-dependent losses in photoreceptors (Curcio, Millican, Allen, & Kalina, 1993) and a loss of retinal ganglion cells (Curcio & Drucker, 1993). Animal studies have

revealed increased spontaneous neural firing and decreased selectivity in single-cell recordings in visual cortex (Hua et al., 2006; Schmolesky, Wang, Pu, & Leventhal, 2000a). This increased neural firing may be related to other studies demonstrating deterioration of gamma-aminobutyric acid (GABA) mediated neural inhibition in primary visual cortex (Leventhal, Wang, Pu, Zhou, & Ma, 2003).

Behavioral studies of aging have found a loss of visual acuity (Weale, 1975), decreased contrast sensitivity (Crassini, Brown, & Bowman, 1988), impaired motion perception (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Trick & Silverman, 1991), decreased detection of optical flow (Andersen & Enriquez, 2006), decrements in texture discrimination (Andersen, Ni, Bower, & Watanabe, 2010), and increases in orientation discrimination thresholds (Betts, Sekuler, & Bennett, 2007). These age-related declines in vision have also been found to be associated with an increase in crash risk during driving and are a contributing factor to the increased likelihood of falls that occur with age (R Q Ivers, Cumming, Mitchell, & Attebo, 1998; Owsley et al., 1998). Altogether, these declines can have a profound effect on the health and well-being of older individuals.

Auditory Decline. Age-related sensory decline is not limited to vision. Similar age-related declines have been observed for audition. Longitudinal research has found losses in sensitivity to pure-tone audiograms as high as 48.5 dB at low frequencies and as high as 84.5dB at high frequencies (Brant & Fozard, 1990a). However, the rate of loss is greatest in the human vocal range, 0.5-2 kHz, making these losses of particular concern for older individuals. Conversely, age-related changes in the ability to discriminate

frequency as well as intensity are greatest at lower frequencies, with older individuals requiring a significant greater difference in frequency or intensity to discriminate between two sounds (He, Dubno, & Mills, 1998a). A decreased ability to detect temporal gaps in auditory stimuli has also been observed in older individuals (Schneider & Hamstra, 1999; Snell, 1997), as well as large decrements in speech processing (Pichora-Fuller, Schneider, & Daneman, 1995). Given the declines in audition with normal aging, it is evident that age-related declines are not limited to a single stimulus modality.

Previous Research on Age-Related Differences in Multisensory Integration

These age-related declines in the senses and decreases in sensitivity with advancing age suggest that the strength of multisensory integration may also change with age. However, given the wide range of declines across the senses we would also expect some age-related decline in multisensory integration as well. Many aspects of multisensory integration have been investigated in the recent past, though relatively little research has been conducted examining age-related changes in multisensory integration.

Multisensory Integration, Aging and Audiovisual Speech. One of the earliest studies examining age-related differences in multisensory integration examined recall in the presentation of television news (Stine, Wingfield, & Myers, 1990). Older and younger adults were presented news segments in one of three conditions. The first condition was an auditory only presentation, the second included the addition of a written transcript and the third was a presentation of the full televised news segment consisting of the auditory and visual information. Younger adults demonstrated better recall compared to older individuals. Younger adults also demonstrated improved performance in the audiovisual

condition while older adults demonstrated no benefit. However, a study examining age-related differences in speech perception and the McGurk effect found different results (Cienkowski & Carney, 2002). The study examined auditory, visual and audiovisual identification of consonant-vowel syllables as well as sentence perception from the Central Institute for the Deaf Everyday Sentences (Silverman & Hirsh, 1955). The results showed that overall older adults were as successful as younger adults in integrating the auditory and visual information, though older adults did show larger standard deviations. No significant difference in the McGurk effect – as reflected by the fusing of conflicting auditory and visual syllables – was found between age groups. However, the younger participants showed a tendency towards choosing the auditory alternative, while older adults tended towards the visual alternative. Interestingly, older adults also demonstrated worse lip-reading performance compared to younger individuals. Other research has also demonstrated that older adults may rely more on visual information while processing speech (Thompson & Malloy, 2004; Thompson, 1995). While the results of these studies seem to contradict one another, with older individuals tending towards the visual alternative but being poorer at the lip reading task, it is likely that differences between the recall and identification tasks may have contributed to the differential outcomes.

Multisensory Integration, Aging and Visuotactile Influences. Age-related differences in multisensory integration between other modalities have also been observed. Spatial orientation differences in a subjective visual straight-ahead task (influenced by visual and tactile information) have also been observed between older and younger individuals (Strupp, Arbusow, Borges Pereira, Dieterich, & Brandt, 1999). In the

study, participants were asked to move a laser spot horizontally on a screen until it was perceived as being directly in front of the individual. On a subset of trials participants also received unilateral stimulation of the dorsal neck muscles. No age-related differences were observed in the condition without vibration of the neck muscles, with participants' responses from both age groups being highly accurate. A significant age-related increase in the displacement of the laser spot was found in the condition including vibration of the neck muscles. The results of this study suggest an increase in the integration of visuotactile information in older adults.

Research on aging, visuotactile integration, and crossmodal selective attention also found age-related differences (Poliakoff, Ashworth, Lowe, & Spence, 2006). The research examined the effect of spatially congruent and incongruent crossmodal distractors at two elevations (flash or vibration from the upper or lower portion of a sponge cube held in each hand) in a simple speeded response task. Three age groups were included in the study. These groups consisted of young participants (19-25 years), young-old participants (65-72 years), and old-old participants (76-92 years). Results showed that when attending to touch that the visual distractors caused a greater increase in errors for both older groups as compared to the young group. The old-old participants also showed no effect of spatial congruence for distractors, while the young-young and young-old groups showed greater impairments when the distractors were spatially congruent as compared to spatially incongruent distractors. The results indicate that older individuals suffer from decrements in crossmodal selective attention; older individuals also suffer from declines in crossmodal spatial selective attention.

Multisensory Integration, Aging and Semantic Congruence. Recent research has also demonstrated an increase in audiovisual integration in older adults in accordance with the results obtained by Cienkowski and Carney (2002). These studies examined age-related differences in the facilitation of accuracy and reaction times in a visual, auditory, or audiovisual two-alternative forced-choice discrimination task (Hugenschmidt, Peiffer, et al., 2009; Laurienti, Burdette, Maldjian, & Wallace, 2006). Prior research had indicated that in addition to multisensory integration occurring for temporally and spatially congruent stimuli, there was also integration for semantically congruent stimuli (Laurienti, Kraft, Maldjian, Burdette, & Wallace, 2004). Laurienti et al. (2006) presented participants with a blue or red disc, an auditory presentation of the word blue or red or the simultaneous presentation of both the visual and auditory stimuli. To examine whether improvements in performance are due to a simple additive model, or if some greater multisensory facilitation was occurring, an independent race model was used to analyze the cumulative distribution functions of the response time data. Unisensory conditions were compared to the statistical facilitation of the summed probabilities of the visual and auditory response. Cases in which the probability of responses to the multisensory stimuli were significantly greater than those predicted by the summed probability of the unisensory stimuli were argued to provide an indication that neural integration was occurring.

The results of the study by Laurienti et al. (2006) indicated that accuracy was above 94% for older and younger participants in all conditions and no significant differences between age groups in accuracy were found. However, a non-significant trend

for age was obtained, suggesting that older show a smaller change in accuracy with multisensory stimuli. A significant age group by presentation condition was found and post-hoc tests indicated a significant age group difference for visual discrimination accuracy with younger participants significantly more accurate than older participants. A significant effect of age group was found in the reaction time data, as well as a significant effect of modality, and a significant age by modality interaction. Older participants exhibited greater improvement of reaction times (87.5ms) compared to younger participants (53.2ms). Older individuals also exhibited multisensory facilitation, improvements in reaction times greater than that which would be expected for a simple additive effect, over a time window that was approximately twice that of younger participants. However, the longer time windows of integration seen in older individuals do not significantly differ from an optimal time window (the temporal window in which integrating information may benefit processing); these larger time windows have been proposed to imply higher prior probabilities in older observers (Colonus & Diederich, 2011). To examine whether this facilitation was multisensory in nature or whether it was merely due to an increase in the amount of sensory information presented, a dual-visual redundant target task was also examined, where two simultaneous visual stimuli appeared on the screen. Similar to the multisensory experiment a significant effect of modality was found, with both groups showing faster reaction times for visual stimuli. However, the interaction between modality and age group failed to reach significance. An analysis of a race model did show that younger participants exhibited significant facilitation for the redundant visual presentation condition, though this facilitation did not exceed 2% and no

facilitation was found for the older age group. The results of these experiments indicate that older individuals do show greater facilitation in reaction times for multisensory stimuli and that this facilitation is not merely the result of an increase in the amount of sensory information provided.

Multisensory Integration, Aging and Simple Detection Tasks. Research has also shown that older individuals exhibit increased facilitation for multisensory stimuli compared to younger individuals even in cases when unimodal differences between the two age groups were not observed (Peiffer et al., 2007). Peiffer et al. examined older and younger individuals' accuracy and reaction times in a simple detection task for two light-emitting diodes, broadband white noise from four speakers 41° equidistant from the diodes (to give the perception of a central source), or a combination of the visual and auditory stimuli. Participants were instructed to respond as quickly as possible when they saw or heard any stimulus. No differences between age group, sensory condition, or interaction between the two factors was found. An analysis of reaction times indicated that there was an effect of stimulus modality; reaction times for the multisensory presentations were significantly faster than those for the auditory or visual stimuli alone. No significant effect of age was found, though, a significant age by stimulus modality interaction was observed. Older individuals showed no differences in performance for the unimodal stimuli but they were significantly faster than younger individuals for multisensory stimuli. This suggests that multisensory integration in older individuals is stronger than in younger individuals. The data from the study were also analyzed using an independent race model. These improvements in performance were shown to be

greater than those predicted by the race model, indicating that multisensory integration was likely occurring. Improvements were not explained by a simple additive model (accounting for additional information in multisensory conditions), suggesting that these improvements were not simply due to a purely additive model.

Research examining age-related changes in multisensory processing for visual, auditory and somatosensory stimuli in a simple reaction time task has also been conducted (Mahoney, Li, Oh-Park, Verghese, & Holtzer, 2011). The study examined response time facilitation in younger and older individuals to multisensory audiovisual, auditory-somatosensory, and visual-somatosensory stimuli compared to unisensory auditory, visual, and somatosensory presentations. Participants were instructed to depress a foot pedal as fast as possible when any stimulus was detected. The results indicated that older adults showed greater facilitation compared to younger participants for the visual-somatosensory compared to unimodal stimuli. Both age groups showed facilitation for audiovisual and auditory-somatosensory stimuli, though no interaction of age was found for either condition. Contrast analyses demonstrated that both younger and older individuals showed greater facilitation for multisensory stimuli that included somatosensory stimulation (auditory-somatosensory and visual-somatosensory) compared to the audiovisual stimuli. While greater facilitation for older individuals in both studies using simple detection tasks was unexpected, it has been suggested that it is possible that increased facilitation for multisensory stimuli in older individuals may be related to changes in top-down processes that have been suggested to occur with increased age (Alain & Woods, 1999; Peiffer et al., 2007).

Multisensory Integration, Aging, and Attention. Another important issue is whether older individuals are able to filter crossmodal information using selective attention. A recent study examined how this ability may change with age (Hugenschmidt, Peiffer, et al., 2009). The study used a crossed design that included spatial and non-spatial tasks. Additional manipulations to examine endogenous (voluntary and internal) as well as exogenous (reflexive and external) attention were also included in the study. No significant difference in accuracy was observed in any of the four task types with accuracy at 96% or higher for both age groups in all conditions. Analyses included traditional mean comparisons as well as Cox proportional hazards models, models which examine the effect of covariates over time, that were proposed “to correct for concerns of general cognitive slowing” (Hugenschmidt, Peiffer, et al., 2009). The proportional hazards model also assessed the cost and benefits of valid, invalid and neutral cues. In the endogenous spatial task, the benefit of a valid endogenous cue was observed for both age groups for visual targets, though auditory targets showed a larger cost for invalid cues as compared to the benefit for valid cues. In the non-spatial endogenously cued task, a larger benefit was found for the auditory cues than for the visual cues. While they acknowledge that previous experiments have generally found larger benefits for the visual modality (Spence & Driver, 1997). They note that the complexity of the non-spatial task (in which participants categorized animals) used by Spence & Driver (1997) compared to the spatial location discrimination task used in their study may have contributed to the observed differences in the benefit of information in each modality. No significant differences for switch cost and age group were found in the exogenous spatial and non-

spatial tasks. These results suggest that older individuals, while in some cases are slower to respond, are able to filter crossmodal information using selective attention as well as younger individuals.

While the results of the study by Hugenschmidt, et al. (2009) suggests that age-related differences in multisensory integration are unlikely to be due to differences in crossmodal selective attention, it is not a direct test of whether age-related differences in multisensory integration and crossmodal selective attention exist. To examine this issue, a color discrimination task similar to that used by Laurienti et al. (2006) was employed that also included endogenous attentional cues. Attentional cues were visual pictographic representations of the sense to be attended presented on a white background. This consisted of either two eyes indicating that participants were to attend to the visual modality, two ears indicating that participants were to attend to the auditory modality or an eye and an ear indicating that they were to divide their attention between modalities. Participants were presented two pictographic cues that flanked the fixation point on the left and right sides. Targets could be unisensory, consisting of either the visual presentation of a blue or red disc, the auditory presentation of a vocalization of the word blue or red, or a multisensory presentation of both the visual and auditory stimuli. Multisensory presentations were always congruent and cues were always informative (the cue was always followed by a stimulus in the cued modality). However, cues to divide their attention between both modalities could consist of only the unisensory visual or auditory stimuli.

Analyses were similar to those conducted by Laurienti et al. (2006) and included traditional analyses of variance as well as race model analyses. Results indicated that older individuals responded slower than younger individuals, that reaction times were quicker for unimodal cues compared to divided cues, and that responses to multisensory targets were faster compared to unisensory targets. An interaction between age and target type was also found that indicated that older individuals demonstrated more facilitation on multisensory trials than younger participants. The interaction between attention type and target type was also significant indicating that both age groups showed the greatest facilitation for selective attention on visual trials. Race model analyses indicated significant effects of age and cue type for visual as well as auditory selective attention, though no interaction was found for either modality. Older individuals did show stronger facilitation in the presence of multisensory information when employing selective attention but the overall reduction in this facilitation for divided attention cases was equivalent to that obtained for younger individuals. The finding that older individuals showed improved reaction times in all selective attention conditions, compared to those conditions that required them to divide their attention between modalities, suggests that differences in top-down processing, as assessed by crossmodal selective attention, are not likely to be responsible for the increase in multisensory integration for older individuals.

Another recent study (Setti, Burke, et al., 2011) examined age-related changes in the sound-induced flash illusion and how these changes are linked to falls. They posited that older individuals with a history of falls would show integration when the signal onset asynchrony between the flashes and beeps was increased. Furthermore, they proposed

that older individuals with difficulties ignoring task-irrelevant information might be more likely to integrate distracting information which could lead to an increased risk of falls. The experiment used a mixed design that included three groups that consisted of younger individuals, healthy older individuals, and fall-prone older individuals. They also examined multiple beep SOA's from 30 to 270 ms. On flash trials participants were presented with 1-2 flashes paired with 0-2 beeps. This design only allowed the examination of fission, the perceptual splitting of 1 flash into 2 flashes, on illusion trials (trials with differing numbers of beeps and flashes). They also included auditory only trials with 2 beeps presented at one of the multiple SOA levels. Participants were told to report the number of beeps presented during trials in which they perceived no flashes. This inclusion of beep-only trials may have increased attentional load, as participants were required to switch tasks at certain points of the study, and previous research has shown age-related differences in cross-sensory tasks with varying levels of attentional load (Hugenschmidt, Mozolic, Tan, Kraft, & Laurienti, 2009).

Analyses were conducted on the mean number of correct trials across conditions for each participant. Trials with 2 flashes and/or 2 beeps were recorded as correct when they indicated 2 or more flashes, which may have influenced the analysis by restricting the range of possible answers. The data was analyzed using three separate mixed analyses of variance with data split by stimulus type (auditory only, visual only and audiovisual trials). The auditory only ANOVA used a 3(group) by 7(SOA) design. Effects of group and of SOA were both found to be significant. They found that younger participants were significantly more accurate than either older group, and that participants were

significantly less accurate when the SOA between beeps was 30ms compared to any other SOA. A significant interaction was also found, indicating that younger observers were significantly more accurate than older observers at the 30 ms SOA. No significant difference between the two older groups was found.

To analyze the visual only condition the data was further separated to examine 1-flash trials and 2-flash trials. No significant effect of group was found for the 1-flash condition but a significant difference was found in the 2-flash condition. Results demonstrated that younger adults were significantly more accurate than older adults with no difference between the fall-prone or normal older groups. An analysis of multisensory congruent and incongruent conditions showed that each group was found to be significantly more accurate on congruent trials compared to incongruent trials. They also analyzed group by stimulus sequence (positive or negative SOA) by SOA. Main effects of group and SOA were found, as well as an interaction of group and SOA. The results showed that fall-prone adults were significantly less accurate compared to younger or healthy older individuals. No difference was found between younger and healthy older adults. They also found that all three groups were significantly more accurate on congruent compared to incongruent trials. The results showed that participants were more accurate when the SOA was 30 ms compared to any other SOA. This finding suggests that the illusion was weakened by such a short SOA between the beeps which were argued to be mistaken for a single beep. They also found that fall prone older adults were significantly more susceptible to the illusion than healthy adults or younger participants

at SOAs greater than 110 ms. The healthy older adults were also found to be more susceptible than younger adults at SOAs of 150, 230 and 270 ms.

Overall the results of the study indicate that fall prone adults are more susceptible than younger or healthy older individuals (those older individuals without a history of falls) at all SOAs longer than 70 ms. This is in accordance with previous research showing that the illusion remains strong with SOAs of 70 ms and that it begins to diminish at SOAs greater than 115 ms (Shams et al., 2002a). While healthy older adults did demonstrate significantly lower accuracy in some of the SOA conditions, the differences in performance may be due to age-related declines in audition. A non-significant trend in the data indicated that healthy older adults actually outperformed younger participants in the 30 ms condition, with older adults and younger adults having accuracy levels of 81% and 66% correct, respectively. This may indicate that some of the variance in the results could be account for by the temporal resolution of audition between younger observers and healthy older participants. While the results of this study contribute to an examination of age-related perceptual changes in multisensory integration in the sound-induced flash illusion, the limitations of the design to only perceptual fusion and the nature of the task including auditory only trials require future study to rule out these issues as possible confounds.

More recent research has focused on age-related differences of multisensory cues on attention (Mahoney, Verghese, Dumas, Wang, & Holtzer, 2012). The study used a modified version of the attention network test which has been previously used to examine orienting, executive attention, and alerting in older participants (Mahoney, Verghese,

Goldin, Lipton, & Holtzer, 2010). The task requires participants to respond to the direction of a centrally located arrow that could be flanked by congruent or incongruent arrows. The target was laterally presented randomly to the left or right of fixation. Participants were presented unisensory or multisensory cues that were informative either temporally (cues presented bilaterally alerting participants that the stimuli would appear 100ms after the cue) or spatially and temporally (cues lateralized to the left or right, orienting participants to the side on which the stimuli would be presented and alerting them that the stimuli would be presented 100ms after the cue).

The results of the study indicated that there was no significant benefit of the alerting (temporal only) cues and no interaction between alerting cue and age. Younger individuals compared to older individuals showed a greater benefit of the orienting cues (spatially and temporally informative), however these orienting cues were found to be beneficial to both younger and older individuals for all sensory conditions. Further analyses examined the effects of multisensory as compared to unisensory orienting cues. Older adults demonstrated a significant benefit of audiovisual and visual-somatosensory orienting cues compared to unisensory cues, while younger adults exhibited a significant benefit of multisensory orienting cues in the auditory-somatosensory and visual-somatosensory multisensory conditions. In summary, the results showed that while older individuals exhibited slower reaction times and a diminished ability to resolve conflict between the orientation of the target and flankers, both age groups showed a benefit of multisensory orienting cues, but neither groups showed any benefit of either multisensory or unisensory alerting cues. The results of this study show that while there may be

performance differences between age groups, the benefits of multisensory cues on attention are maintained. The results of both studies taken together suggest that age-related differences in multisensory integration are unlikely to be due to differences in crossmodal attention.

In summary, the research examining multisensory integration in the context of aging indicates that older individuals exhibit greater integration of visual information during speech processing (Cienkowski & Carney, 2002; Thompson & Malloy, 2004; Thompson, 1995), as well as stronger visuotactile integration than younger individuals in a variety of tasks (Poliakoff et al., 2006; Strupp et al., 1999). Older individuals also show greater performance improvements in tasks requiring integration of audiovisual semantic information (Laurienti et al., 2006), and in simple detection tasks including multisensory stimuli (Mahoney et al., 2011; Peiffer et al., 2007). This increased integration is not likely to be due to differences in crossmodal attention (Deloss, Pierce, & Andersen, 2013; Hugenschmidt, Peiffer, et al., 2009; Mahoney et al., 2012). However, research has indicated that increased integration in the sound-induced flash illusion for temporally disparate stimuli is an indicator of fall risk in older individuals (Setti, Burke, et al., 2011).

Hypotheses, Proposed Studies and Analyses

Aging, Multisensory Integration, and the Sound Induced Flash Illusion

To examine age-related differences in multisensory integration, a series of experiments were conducted. These studies examined age-related differences in perceptual multisensory integration using the sound-induced flash illusion (Shams et al., 2000, 2002a). In the sound-induced flash illusion paradigm, observers are simultaneously

presented flashes and beeps. In some conditions, the number of flashes and beeps are identical (e.g., one, two or three flashes and beeps). In other conditions, the number of flashes and beeps are discrepant (e.g., one flash with either two or three beeps; two flashes with either one or three beeps, or three flashes with one or two beeps). An illusion is reported for discrepant trials when observers report a number of flashes that is different than the actual number of presented flashes, due to the discrepant number of auditory beeps (T. S. Andersen, Tiippana, & Sams, 2004; Shams, Ma, & Beierholm, 2005). Specifically, a greater number of flashes are reported than were presented when a greater number of beeps are presented; this illusion is typically referred to as a fission illusion. In addition, evidence of a fusion illusion has also been demonstrated, in which participants report seeing fewer flashes than were presented when the number of beeps is fewer than the presented number of flashes (Andersen et al., 2004; Shams, Iwaki, Chawla, & Bhattacharya, 2005). The illusion has been shown to be perceptual in nature and not merely due to a criterion shift (McCormick & Mamassian, 2008). Research has also demonstrated a flash-induced sound illusion in which the perceived number of beeps is influenced by the number of flashes presented (Andersen et al., 2004). Furthermore, research has suggested that the illusion may be due to feed-forward processes as indicated by early modulation of visual cortex (Shams, Iwaki, Chawla, & Bhattacharya, 2005; Watkins et al., 2007). Unlike previous studies examining age-related changes in multisensory integration using reaction times as an indicator of multisensory interactions (Laurienti et al., 2006; Peiffer et al., 2007), the sound-induced flash illusion can be used to assess changes in the visual percept. This avoids some of the complexity of speeded

tasks used in studies of aging that involve multiple stages of processing beyond perception, that may include cognition (Ratcliff, Thapar, & McKoon, 2001).

Hypotheses

The previous research on multisensory integration and aging reviewed earlier suggests that older individuals integrate multisensory information to a greater degree compared to younger individuals. The reasons for this increased integration are unclear. One possibility is that older individuals demonstrate greater multisensory integration as a way to help counteract age-related declines in sensory processing. However, another possibility is that this increased integration is itself due to age-related sensory decline. Setti et al. (2011b) found that there was greater integration in older individuals with increased age-related declines associated with an increased risk of falls. This integration continued to be strong at high SOA levels indicating that they were integrating information inappropriately, or information that has a low degree of temporal coincidence. The following hypotheses explore whether age-related changes in multisensory integration in older individuals are due to specific changes in multisensory processing. If these age-related declines in multisensory integration exist in older individuals they should exhibit less spatial and temporal selectivity when integrating multisensory information.

Aging, Reaction Time, and Multisensory Integration. Current research suggests that older individuals as compared to younger individuals show greater facilitation of reaction times when multisensory cues are presented (Hugenschmidt, Mozolic, & Laurienti, 2009; Hugenschmidt, Peiffer, et al., 2009; Laurienti et al., 2006).

Surprisingly, this facilitation was also found in tasks in which significant baseline differences between age groups were not found (Peiffer et al., 2007). The benefits of this multisensory information were found to be greater than those explained by age-related declines in the ability to filter task-irrelevant information (Alain & Woods, 1999; Fabiani, Low, Wee, Sable, & Gratton, 2006). Research has also shown that the latency (the time before a neuron exhibits a response to a stimulus) is significantly reduced for multisensory as compared to unisensory stimuli (Rowland, Quessy, Stanford, & Stein, 2007). These improvements in the speed of neural responses may be one of the underlying factors in reducing reaction times for behavioral responses when multisensory stimuli are present. Taken together, these findings suggest that if multisensory stimuli can improve performance in speeded response tasks in the laboratory, that it may also aid responses in other real-world tasks such as driving. While older individuals may suffer from age-related declines that affect accuracy in judging the exact location of a multisensory stimulus, these fine-grained spatial or temporal judgments are not necessary in many tasks. In real world driving conditions, tasks such as detecting an impending collision, and locating in the visual field a vehicle on a collision path does not typically require fine-grained discrimination with high precision, it does require attending to the incoming vehicle and reacting quickly and appropriately. Multisensory stimuli may be one possible way to improve performance for tasks in which reaction time is the primary measure of interest.

Hypothesis 1. Older individuals as compared to younger individuals will demonstrate greater benefits from the presentation of multisensory as compared to unisensory stimuli.

Prediction 1. Older individuals as compared to younger individuals will show a greater improvement in accuracy for multisensory stimuli as compared to unisensory stimuli.

Aging, Attention, and Multisensory Integration. As discussed earlier, older individuals suffer from age-related declines in vision and audition. However, they also suffer from attentional declines, specifically in their ability to suppress task-irrelevant information (Alain & Woods, 1999; Chao & Knight, 2000; Poliakoff et al., 2006). These declines in attentional control may influence the degree of integration in the sound-induced flash illusion. If older individuals are unable to suppress task-irrelevant auditory beeps to the same extent as the younger individuals then the degree of integration should be larger for older adults..

Hypothesis 2. Older individuals have decreased inhibitory control for cross-modal task-irrelevant information. Older individuals will exhibit smaller changes when making a task-irrelevant crossmodal stimulus task-relevant.

Prediction 2. Older individuals as compared to younger individuals will demonstrate a smaller change in the strength of the illusion when the auditory stimuli are made task-relevant, for example through the addition of a go/no-go task in the auditory domain.

Aging, Noise, and Multisensory Integration. As discussed earlier, older individuals suffer from age-related declines in vision as well as audition (for reviews of age-related declines in vision and audition see Andersen, 2012; Fitzgibbons & Gordon-Salant, 2010; Owsley, 2011; Schneider, Daneman, & Pichora-Fuller, 2002). These declines are likely related to findings that have also demonstrated that older individuals suffer from increases in internal noise, or noise within the system that is not present in the environment, as well as to a decrease in their ability to filter external noise, noise that is present in the stimuli (Lisa R. Betts et al., 2007; Bower & Andersen, 2011). These increases in internal noise and decreases in the ability to filter external noise serve to decrease the strength of the stimuli (see Figure 3 for a simplified model of sensory processing). Neurophysiological and behavioral studies have demonstrated that multisensory integration is affected by inverse effectiveness, an increase in the benefit of multisensory integration when stimuli are weak (Carriere, Royal, Wallace, & Carolina, 2008; Holmes, 2009; M. A. Meredith & Stein, 1986a; Senkowski, Saint-Amour, Höfle, & Foxe, 2011; Stevenson, Fister, Barnett, Nidiffer, & Wallace, 2012; Wallace, Carriere, Perrault, Vaughan, & Stein, 2006). If increased internal noise results in a weakening of the stimulus for older individuals then the degree of integration should increase due to inverse effectiveness.

Hypothesis 3. Older individuals have higher levels of internal noise compared to younger individuals. In addition to increasing external noise, a second method of decreasing the strength of a stimulus is by directly manipulating factors related to signal strength such as brightness or contrast. Older individuals have greater levels of internal

noise, which will degrade weak signals, such as low brightness or low contrast stimuli, to a greater degree as compared to strong signals.

Prediction 3. Older individuals as compared to younger individuals will demonstrate a greater change in sensitivity to detect low intensity multisensory stimuli as compared to low intensity unisensory stimuli.

Aging, Spatial/Temporal Acuity, and Multisensory Integration. Older individuals have demonstrated age-related declines in their ability to localize visual and auditory stimuli in the environment (Abel, Giguère, Consoli, & Papsin, 2000; Andersen, Ni, Bian, & Kang, 2011) and declines in their ability to perform temporal order judgments (Setti, Finnigan, et al., 2011). The strength of multisensory integration has been shown to be dependent on spatial and temporal congruency of the stimuli across modalities. When the spatial or temporal incongruence between the stimuli in these modalities is increased, response depression occurs (Jiang & Stein, 2003; Kadunce, Vaughan, Wallace, Benedek, & Stein, 1997; Meredith, Stein, & Stein, 1996; Stein et al., 1989; Wallace et al., 2006; Wallace & Stein, 1997) — a weakening of the strength of the neural or behavioral response below the strength of a unisensory stimulus. Younger individuals will exhibit higher response depression, due to their ability to accurately localize stimuli with regards to space and time. Subsequently, age-related declines in spatial and temporal acuity (the ability to accurately locate stimuli in the environment and determine the temporal order of events) in older individuals may decrease the magnitude of response depression. This may cause integration of multisensory stimuli to occur as spatial or temporal disparities are increased for older as compared to younger observers.

Due to a decrease in response depression, older individuals should exhibit smaller decreases in integration as spatial or temporal incongruence increases.

Hypothesis 4. Older individuals as compared to younger individuals will exhibit age-related declines in recovering multisensory spatial information.

Prediction 4. Older individuals as compared to younger individuals will exhibit a smaller decrease in the strength of the illusion with decreases in spatial congruence due to decreased response depression.

Studies

Sound-Induced Flash Illusion Methodology. All experiments examining the sound-induced flash illusion will include a pre-test examining participants' ability to discriminate the 1-2 beeps and 1-2 flashes in isolation. Participants will perform two blocks, one consisting of trials of 1-2 auditory beeps and one consisting of trials of 1-2 visual flashes. Participants will be required to pass each of these pre-tests before progressing to the experiment.

Experiments

Experiment 1. Experiment 1 examined the sound-induced flash illusion in younger and older individuals. It also assessed whether attentional differences between older and younger individuals may be responsible for any differences observed in the illusion. In experiment 1, participants discriminated between 1-3 visual flashes, 1-3 auditory beeps, or 1-3 flashes presented simultaneously with 1-3 auditory beeps. Stimulus conditions will be divided into three blocks — a flash only block, a beep only block, and a multisensory block consisting of both flashes and beeps. While previous research

suggests that attention is not a key factor in age-related changes in multisensory integration, no study has specifically examined whether this is also the case for the sound-induced flash illusion.

Expected Results. If hypothesis 1 is correct then older individuals will demonstrate improved accuracy for congruent multisensory as compared to unimodal stimuli (Prediction 1).

Experiment 2. To ensure that attention is not a factor in age-related changes in the sound-induced flash illusion Experiment 2 examined whether age-related differences in attention may be responsible any age-related difference in the sound-induced flash illusion. The experiment consisted of three blocks. The first block was the same as the multisensory condition from the first part of experiment 1. The additional two blocks included a go/no-go task in either the visual or auditory domain. In the block with the go/no-go task in the visual domain, participants were instructed to withhold their response on trials where the flashes are double their standard size. In the block with the go-/no-go task in the auditory domain, participants were instructed to withhold their response on trials when the beeps are presented at a lower frequency.

Expected Results. If hypothesis 2 is correct then older individuals will show greater multisensory integration as indicated by a greater effect of beeps on the perceived number of flashes (Prediction 1). Older individuals will also show a smaller increase in multisensory integration when required to attend to stimuli in the auditory domain during a go/no-go task (Prediction 2).

Experiment 3. Experiment 3 examined the effects of stimulus strength on multisensory integration in younger and older individuals. The experiment consisted of two blocks. In block 1 participants discriminated between 1 or 2 visual flashes presented on each trial. These flashes were accompanied by 0, 1, or 2 auditory beeps. A mixed design was used with 3 sound pressure levels for the auditory beeps and 3 stimulus brightness levels for the visual flashes. Participants' absolute auditory threshold was determined and 3 sound pressure levels (SPL) was used. These conditions will be based on their 70%, 82% and 94% correct thresholds. Participants' visual detection brightness thresholds for a visual flash were also determined. The three brightness levels used in the study were based on their 70%, 82% and 94% correct thresholds. Participants completed 10 trials at each level of auditory SPL (3 levels), visual brightness (3 levels), number of flashes (2 levels), and number of beeps (3 levels), for a total of 540 trials. Block 2 will be identical to block 1, however participants discriminated between 1 or 2 auditory beeps paired with 0, 1, or 2 visual flashes.

Expected Results. If hypothesis 3 is correct then older individuals will show greater multisensory integration as indicated by a greater effect of beeps on the perceived number of flashes (Prediction 1). Older individuals will also show a greater increase in multisensory integration as stimulus strength is decreased (Prediction 3). These effects will be observed for integration in the visual and auditory discrimination blocks with the auditory beeps and visual flashes showing a greater effect on the perceived number of flashes and beeps respectively.

Experiment 4. Experiment 4 examined the effects of spatial congruence on multisensory integration in younger and older individuals. During the experiment participants discriminated between 1-2 visual flashes. These flashes were accompanied by 0, 1 or 2 auditory beeps. These beeps were played at one of five locations. Five speakers were positioned so that one speaker was directly below the central presentation area, one speaker was placed 0.5m to left of this point, and another speaker was placed 0.5m to the right of this point, as well as one speaker 1 meter to the left and 1 meter to the right of the central presentation location. Beeps were presented at 72 dB SPL. Reaction times were recorded to determine whether there is any change in response time for spatially incongruent stimuli.

Expected Results. If hypothesis 4 is correct then older individuals will show greater multisensory integration as indicated by a greater effect of beeps on the perceived number of flashes. Older individuals will also show a smaller decrease in the strength of multisensory integration as the spatial separation between the beeps and flashes increases (Prediction 4).

Concluding Remarks

The objective of the research is to examine age-related differences in multisensory integration. The work studied multisensory integration and aging, as well as whether attentional differences between older and younger individuals may influence any differences found. The work assessed spatial changes in multisensory integration in older individuals. It also examined the effects of stimulus strength on multisensory integration in older and younger individuals. Few studies have explored how the integration of visual

and auditory stimuli changes in older individuals and this research adds to this body of research by examining age-related changes in multisensory integration.

Figures

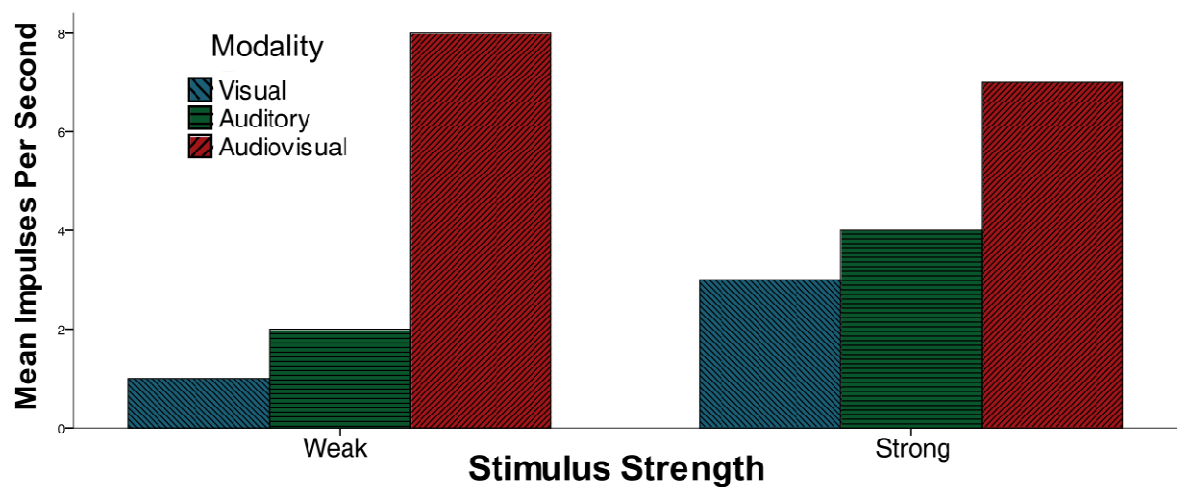


Figure 1. The firing rate of a multisensory neuron as a function of the modality of presentation and stimulus strength. This provides an example of the additive properties of multisensory neurons and the role of inverse effectiveness.

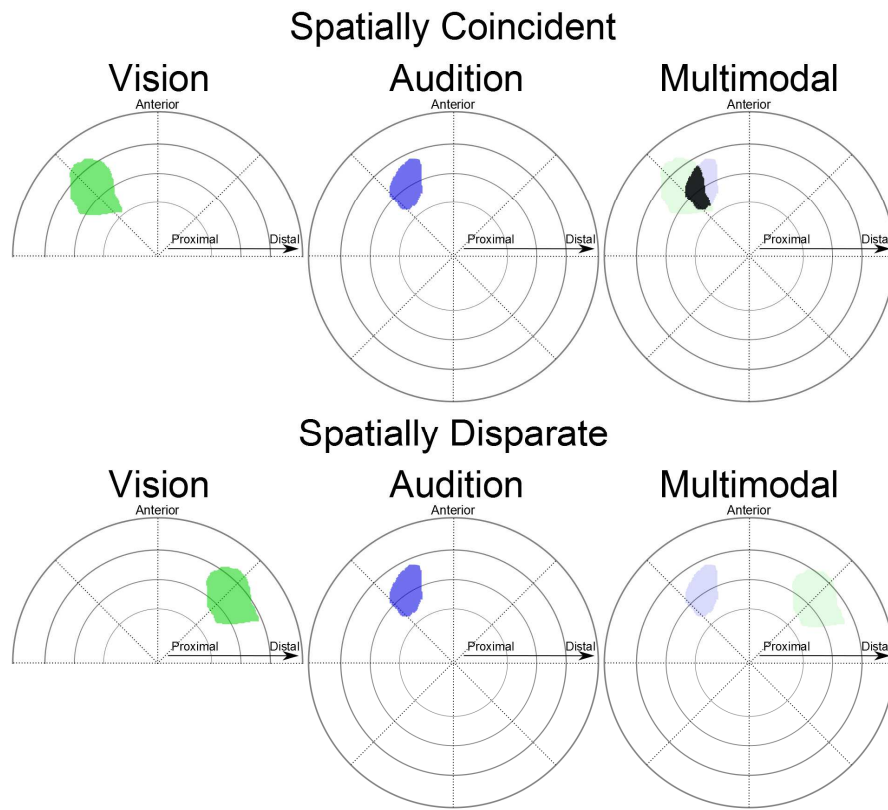


Figure 2. Responses of multisensory neurons to unimodal and multisensory presentations for spatially coincident and disparate stimuli. Response strength is indicated by opacity.

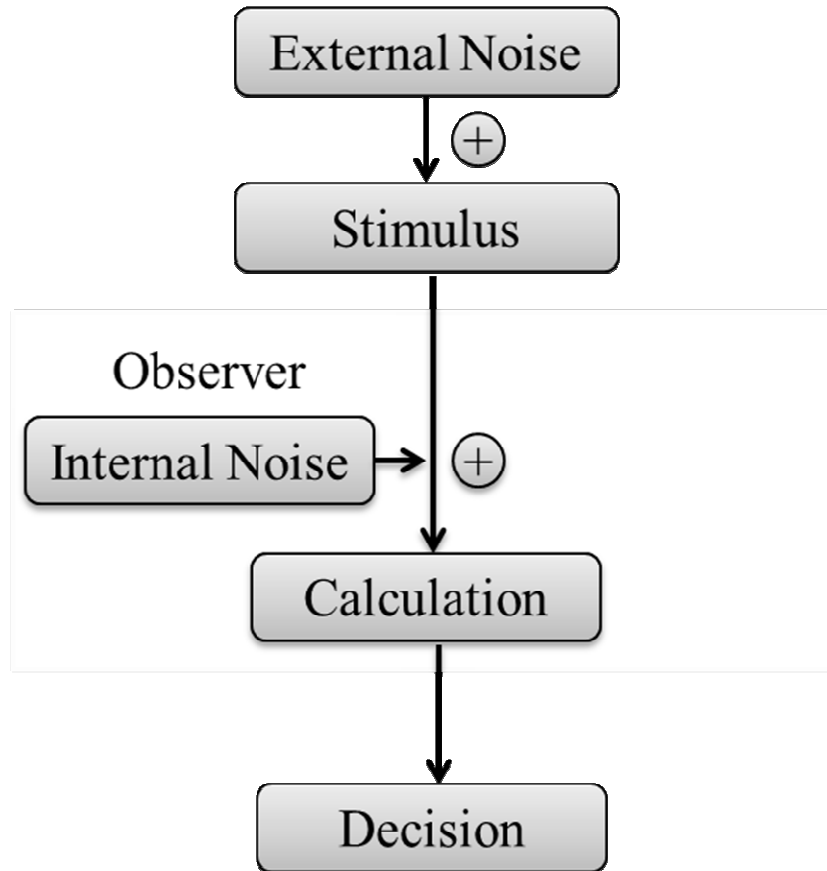


Figure 3. A simplified representation of a model demonstrating the effects of internal and external noise on processing. Plus signs indicate additive effects.

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Chapter 1: Aging, attention, and multisensory integration

This chapter was published in the academic journal *Psychology & Aging*. This section corresponds to Experiments 1 and 2 as described in the introduction. Copyright © 2013 by the American Psychological Association. Reproduced with permission. The official citation that should be used in referencing this material is: DeLoss, D. J., Pierce, R. S., & Andersen, G. J. (2013). Multisensory Integration, Aging, and the Sound-Induced Flash Illusion. *Psychology and Aging*, 28(3), 802–12.

Age-related sensory declines can have a profound effect on the health and well-being of older individuals. Epidemiological studies have shown that age-related declines in vision are associated with increased crash risk during driving and are a contributing factor to the increased likelihood of falls that occur with age (Rebecca Q. Ivers, Cumming, Mitchell, & Attebo, 1998; Owsley et al., 1998). Research also suggests that age-related declines in audition can lead to decreased quality of life (I Appollonio, Carabellese, Frattola, & Trabucchi, 1996). However, perceptual processing is not solely based on the information from one sensory modality. Research has shown that this processing is based on combined information from multiple sensory inputs or multisensory integration (Massaro & Friedman, 1990; Massaro, 1987; McGurk & MacDonald, 1976; M. A. Meredith & Stein, 1986a; Watkins et al., 2007). An important issue is whether age-related differences exist in the integration of multisensory sensory information that cannot be assessed in studies examining vision or audition in isolation. The experiments we report here aim to address this issue.

While early research on sensory processing proposed modularity of the senses until later stages of processing, more recent research has shown that this is unlikely to be the case and that cortical processing may be primarily multisensory (Ghazanfar & Schroeder, 2006; Schroeder & Foxe, 2005; Watkins et al., 2007). The integration of information from multiple sensory modalities into a unified multisensory percept may lead to more accurate processing of stimuli in the environment. Multisensory integration may prove to be of greater importance for older individuals due to a wide array of age-related declines in both vision and audition.

Age-related declines in vision have been observed for a wide range of different types of visual processing. These declines include decrements in visual acuity (Weale, 1975), discriminating luminance (Crassini et al., 1988), the detection and discrimination of motion (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Trick & Silverman, 1991; Bennett, Sekuler & Sekuler, 2007), the detection of an impending collision (Andersen & Enriquez, 2006), the perception of depth (Norman, Clayton, Shular & Thompson, 2004; Norman et al., 2008; Norman, Crabtree, Bartholomew & Feffell, 2009), the discrimination of texture (Andersen et al., 2010), and the discrimination of the orientation of stimuli (Lisa R Betts, Sekuler, & Bennett, 2007). In addition, physiological studies have found age-dependent reductions in the number of photoreceptors (Curcio et al., 1993), loss of retinal ganglion cells (Curcio & Drucker, 1993), and decreases in retinal illuminance (Weale, 1988). These perceptual and physiological changes are likely to be underlying factors in age-related declines in visual performance (see Andersen, 2012 and Owsley, 2011 for a more thorough review of the vision and aging literature).

Age-related declines in audition have also been observed for older individuals. These declines include pure-tone hearing thresholds, particularly at higher frequencies (Brant & Fozard, 1990a), frequency and intensity discrimination (He, Dubno, & Mills, 1998b), temporal gap detection (Schneider & Hamstra, 1999; Snell, 1997), and speech processing (Pichora-Fuller, Schneider, & Daneman, 1995). (For more detailed reviews of age-related declines in audition see Fitzgibbons & Gordon-Salant, 2010 and B. A. Schneider, Daneman, Pichora-Fuller, & Columbia, 2002.)

However, one possible way to reduce the negative effects of these declines is to use redundant information from multiple sensory modalities that can help to reduce false alarms. This would allow the system to maintain high levels of sensitivity while simultaneously reducing variance (Ernst & Bühlhoff, 2004; Spence & Driver, 2004). This capacity of multisensory integration to reduce uncertainty and improve accuracy is one of the many reasons why an investigation of how multisensory integration changes with advancing age is important.

Recently several studies have examined age-related differences in multisensory integration. Research has found faster reaction times (RT) for older and younger participants when presented with multisensory as compared to unisensory stimuli (Mahoney et al., 2011) or multisensory as compared to unisensory orienting cues (Mahoney et al., 2012). Studies have also found that older individuals demonstrate greater facilitation than younger individuals when multisensory information is present (Laurienti et al., 2006; Peiffer et al., 2007). Studies have found that older observers demonstrate greater integration of auditory and visual stimuli, and greater reliance on

visual information for spoken syllables (Thompson, 1995). The greater reliance on visual information was also found to be associated with the extent of visual-spatial attention (Thompson & Malloy, 2004). Other studies have found that presentation of multisensory information (visual presentation of a color and the spoken word of a color) in a simple color discrimination task resulted in faster performance for older as compared to younger observers (Laurienti et al., 2006). Even in tasks in which baseline age-related differences in reaction times are not present, older individuals still show greater facilitation for multisensory over unimodal stimuli than younger individuals (Peiffer et al., 2007). These results indicate a greater effect of multisensory stimuli in older as compared to younger individuals. Other research has found evidence of age-related differences in the temporal window of integrating multisensory information (Colonius & Diederich, 2011; Diederich et al., 2008) and suggested that a greater window of integration is associated with a greater risk of falls (Setti, Burke, et al., 2011).

A general conclusion of these studies, considered together, is that older individuals as compared to younger individuals show greater multisensory integration suggesting that age-related differences exist in early levels of sensory processing. Other research has found evidence of age-related differences in higher-level factors in multisensory processing. For example, previous functional imaging research has shown that older individuals have difficulty inhibiting task-irrelevant information, and that increased processing of this task-irrelevant information also predicted distractibility in a cross-sensory behavioral task (Hugenschmidt, Mozolic, Tan, et al., 2009). This increased difficulty in ignoring irrelevant information from other modalities may influence

judgments of older individuals in multisensory tasks, particularly when using measures, such as reaction times, that are sensitive to these decisional components.

In the present study we examined age-related differences in perceptual multisensory integration using the sound-induced flash illusion (Shams et al., 2000; Shams, Kamitani, & Shimojo, 2002b). In the sound-induced flash illusion paradigm, observers are simultaneously presented flashes and beeps. In some conditions, the number of flashes and beeps are identical (e.g., one, two or three flashes and beeps). In other conditions, the number of flashes and beeps are discrepant (e.g., one flash with either two or three beeps; two flashes with either one or three beeps, or three flashes with one or two beeps). An illusion is reported for discrepant trials when observers report a number of flashes that is different than the actual number of presented flashes, due to the discrepant number of auditory beeps (T. S. Andersen, Tiippana, & Sams, 2004; Shams, Ma, & Beierholm, 2005). Specifically, a greater number of flashes are reported than were presented when a greater number of beeps are presented. In addition, evidence of a fusion illusion has also been demonstrated, in which participants report seeing fewer flashes than were presented when the number of beeps is fewer than the presented number of flashes (Andersen et al., 2004; Shams, Iwaki, et al., 2005). The illusion has been shown to be perceptual in nature and not merely due to a criterion shift (McCormick & Mamassian, 2008). Research has also demonstrated a flash-induced sound illusion in which the perceived number of beeps is influenced by the number of flashes presented (Andersen et al., 2004). Furthermore, research has suggested that the illusion may be due to feed-forward processes as indicated by early modulation of visual cortex (Shams,

Iwaki, Chawla, & Bhattacharya, 2005; Watkins et al., 2007). Unlike previous studies examining age-related changes in multisensory integration using reaction times as an indicator of multisensory interactions (Laurienti et al., 2006; Peiffer et al., 2007), the sound-induced flash illusion can be used to assess changes in the visual percept. This avoids some of the complexity of speeded tasks that involve multiple stages of processing beyond perception, that may include cognition (Ratcliff et al., 2001).

Although previous research has demonstrated age-related differences in the facilitation of reaction times in the presence of multisensory information (Laurienti et al., 2006; Peiffer et al., 2007), relatively few studies have examined adult age-related differences in multisensory perceptual processing. There are two possible outcomes regarding aging and multisensory integration. One possibility is that age-related declines in multisensory integration will occur due to declines in vision and audition. This outcome would be consistent with a model in which the noise or error present in either vision or audition are combined when information is present in both modalities. However, a second possibility is that integration will be better for older participants as compared to younger participants because older individuals may rely on multisensory information because of degraded unisensory processing. Previous research has suggested a role of overactivation and neural recruitment as a method of compensation for age-related declines in cognition (see Reuter-Lorenz & Cappell, 2008 for a discussion). The greater reliance on multisensory information, and thus greater integration, may thus be another type of compensatory process for age-related declines in unimodal sensory processing.

Experiment 1

Experiment 1 examined whether there were unimodal age-related differences in the ability to detect 1-3 visual flashes or 1-3 auditory beeps. Once unimodal differences between the groups were examined, we explored the existence of perceptual age-related differences in multisensory integration as assessed by the strength of the sound-induced flash illusion.

Methods

Participants. Twelve college students, 7 male and 5 female (M age = 20.75 years, SD = 0.62 years), from the University of California, Riverside and twelve older participants, 6 male and 6 female (M age = 75.67 years, SD = 5.07 years), from the surrounding community participated in the experiment. Older participants were required to be 65 years of age or older. All observers were naïve concerning the experimental purpose and were paid for their participation in the experiment. All subjects were pre-screened for self-reported eye disease (e.g. macular degeneration, glaucoma, retinitis pigmentosa), neurological disorders (e.g. Alzheimers disease, Parkinson's disease, stroke), as well as for any significant hearing loss. After passing this pre-screening participants were then assessed using an array of visual (acuity and contrast sensitivity) and cognitive (forward and backward digit span; KBIT vocabulary) tests (see Table 1). Participants were required to have a log minimum angle of resolution of 0.40 or better, as well as log contrast sensitivity of 1.00 or better. Participants were also required to have digit-span scores no more than one standard deviation below the standards for cognitively normal individuals published by the Alzheimer's Disease Center (Weintraub et al., 2010).

Participants were allowed to wear hearing aids (however none of the participants came to the lab with hearing aids), and hearing was tested using the pre-test described in the experimental methods.

Apparatus. Stimuli were presented on a 22” Viewsonic PF817 CRT monitor at a resolution of 1024x768 at 100Hz (non-interlaced) driven by a Alienware Area-51 ALX equipped with an Intel Core i7 960 processor, and an NVIDIA Geforce GTX 480 graphics card, using the Microsoft Windows 7 (Service Pack 1) operating system. The background luminance of the display was 0.06 cd/m². Custom experimental software was written in MATLAB (The Mathworks, Inc., version 7.8.0.347); the Psychophysics Toolbox extensions were also utilized (Brainard, 1997; Pelli, 1997). Calibration and measurements of the monitor were performed using a ColorCal2 colorimeter (Cambridge Research Systems).

Stimuli. Stimuli consisted of 1-3 flashes of a uniform white disc paired with 0-3 auditory beeps. The radius of the flashed disc was 0.75° in visual angle in size and was presented at 127.97 cd/m². The flash duration was 10 milliseconds (ms) with a 70 ms inter-flash interval. Auditory beeps were 3.5 kHz sine wave tones. Beeps were 10 ms in length with 58 ms inter-beep intervals, and were presented at 74.2 dB. On trials that included both flashes and beeps, the onset of the first beep began 23 ms after the onset of the first flash. Previous research (Shams et al., 2002) has found no significant effect on the illusion with timing offsets of up to 70 ms. The stimulus parameters were identical to those used by (Shams, Ma, et al., 2005).

Experimental task and procedure. The monitor was viewed at a distance of 94 centimeters. Head position was stabilized with the use of a chin rest and stimuli were viewed binocularly. Any corrective lenses or contacts normally worn by the participants were allowed during the experiment. The only light source in the room during the experiment was the monitor. At the beginning of the study, participants were required to pass a pre-test to determine whether they understood the task and were able to discriminate the beeps or flashes in isolation. The pre-test consisted of two sections, the first assessed their ability to discriminate 1 to 3 beeps, and the second assessed their ability to discriminate 1 to 3 flashes. Participants fixated a 0.33° fixation crosshair, which was centered horizontally, presented 3.12° below the top of the screen. Participants then pressed any key to advance each trial. This was followed by the presentation of the stimuli; the flashes or beeps were then presented. During the flash pre-test the flashes were presented 12° below fixation. At the end of the trial participants were shown a blank response screen and entered the number of flashes or beeps perceived using the number row of the keyboard. Response periods ended if the participant failed to respond within 6000 ms. Participants were given a maximum of five 30-trial blocks in each section to get eight trials in a row correct to be eligible for the experimental portion. No significant differences ($p > 0.05$) in the number of trials to completion were observed between age groups for either pre-test. The experiment consisted of three experimental blocks, a flash only block, a beep only block, and a multisensory block. These unimodal blocks during the experiment were separate from the unimodal pre-tests. The order of these blocks was counter-balanced across participants, with two younger and two older participants

assigned to each possible block ordering. Each block was separated by a mandatory five-minute break. The entire experiment took approximately 1.5 hours. The flash-only block assessed participants' ability to discriminate 1 to 3 visual flashes. Each possible number of flashes was presented for 100 trials for a total of 300 trials in the flash-only block. The presentation order was randomized for each participant. The task of the participant was to report the perceived number of flashes (or the number of beeps if in a beep only block) using the number row of the keyboard. Participants were informed that the upcoming trials would occasionally be accompanied by a series of beeps, and that while these beeps may be distracting to remember to respond only to the number of flashes presented. On each trial participants fixated on a 0.33° white crosshair presented 3.12° below the top of the screen centered horizontally that was presented for 1000 ms. Then 1-3 visual flashes 12° below the fixation point were presented. The crosshair remained on the screen and participants entered their response. As in the pre-test, the response period ended if the participant failed to respond within 6 sec. Subsequent to their response or after 6 sec had elapsed, the crosshair vanished and a prompt instructed participants to press any key to continue to the next trial. The beep-only block was identical to the flash-only block, except that participants were presented and asked to respond to 1-3 beeps. Again, each number-of-beeps condition was presented for 100 trials for a total of 300 trials. The multisensory block was the same as the flash-only, except that each visual presentation was also paired with zero to three beeps. Trials with no beeps during the multisensory block were used in later analyses to examine whether congruent multisensory information improved performance over unimodal trials. Participants received 25 trials for each

possible combination of flashes (1,2 or 3) and beeps (0, 1, 2 or 3), for a total of 300 trials in the multisensory block.

Results

The results for each block were analyzed separately. Original degrees of freedom are reported, and Greenhouse-Geisser corrections were used where appropriate. Data from the flash-only block were analyzed using a 2 (age) by 3 (flashes) mixed repeated-measures analysis of variance (ANOVA). As expected, the number of flashes influenced the perceived number of flashes, $F(2, 44) = 384.87$, $MSE = 13.53$, $p < 0.001$. A significant age by flash interaction, $F(2, 44) = 3.90$, $MSE = 0.14$, $p < 0.05$, was also observed (see Figure 4A). Simple effects analyses were conducted using localized independent-samples t-tests. These indicated that the only significant difference between older and younger individuals occurred in the 2-flash condition, $t(23) = 3.61$, $p = 0.001$. Older participants tended to underestimate the number of flashes ($M = 1.89$, $SD = 0.23$), though this effect did not reach significance, $t(11) = 1.628$, $p = 0.132$, while younger participants significantly overestimated the number of flashes ($M = 2.17$, $SD = 0.16$), $t(11) = 3.659$, $p = 0.004$. Data from the beep-only block were analyzed using a 2 (age) by 3 (beeps) mixed repeated-measures ANOVA. There was a significant main effect of beeps, $F(2, 44) = 1798.46$, $MSE = 21.38$, $p < 0.001$. Older and younger individuals exhibited nearly veridical performance at all beep levels. No significant interaction between the number of beeps and age were observed. The multisensory block was analyzed using a 2 (age) by 3 (flashes) by 3 (beeps) mixed repeated-measures ANOVA. The zero-beep conditions were excluded from this analysis because these trials provide

no information concerning multisensory integration. The perceived number of flashes was influenced by the displayed number of flashes, $F(2,44) = 103.12$, $MSE = 10.23$, $p < 0.001$. A significant main effect of beeps was also observed, $F(2,44) = 132.13$, $MSE = 14.47$, $p < 0.001$. This finding suggests that the perceived number of flashes was influenced by the auditory information. A significant age by beep interaction was also found, $F(2, 44) = 8.51$, $MSE = 0.93$, $p < 0.01$. Older individuals exhibited greater integration of the cross-modal auditory information, as their average responses were lower than that of younger individuals in the one-beep condition, and higher than that of younger participants in the three beep condition (see Figure 4B). One way to analyze this interaction is through an analysis of individual slopes obtained through a linear regression predicting the perceived number of flashes from the number of beeps for each participant. This allows examination of the strength of the illusion. If the presence of beeps had no effect on the perceived number of flashes then we would expect a slope of zero with a mean of two (due to an equal number of trials at each possible level of 1-3 flashes). A greater slope indicates a larger effect of the illusion as the 1-beep and 3-beep conditions are respectively greater than or less than the mean. According to these results, older individuals showed a significantly steeper slope ($M=0.66$, $SD=0.15$) compared to younger individuals ($M=0.48$, $SD=0.12$), as indicated by a two-tailed independent-samples t-test, $t(22)=3.187$, $p=0.004$. A flash by beep interaction was also observed, $F(4, 88) = 17.03$, $MSE = 0.48$, $p < 0.001$. As incongruence between the actual number of flashes and beeps increased, the effect of the beeps on the perceived number of flashes decreased (see Figure 5).

A 2 (age) by 3 (number of flashes) by 2 (congruent multisensory information versus unimodal flashes) mixed repeated-measures ANOVA was conducted on the response data to determine whether age-related differences exist for congruent beep information during the multisensory block as compared to the unimodal flash trials during the multisensory block. We found a significant main effect of congruency, $F(1, 22) = 627.67$, $MSE = 41.004$, $p < 0.001$), in which performance was more veridical on trials with congruent multisensory information. The actual number of flashes significantly influenced the perceived number of flashes, $F(2,44) = 236.33$, $MSE = 6.48$, $p < 0.001$. We also found a significant congruency by flash interaction, $F(2,44) = 31.01$, $MSE = 0.80$, $p < 0.001$). Specifically, congruent beep information resulted in improved performance as the number of flashes was increased. Finally, we found a congruency by flash by age interaction, $F(2, 44) = 7.12$, $MSE = 0.18$, $p = 0.002$. Older individuals showed a greater improvement in performance with congruent multisensory information than younger individuals. Older participants showed significant improvement ($p < 0.05$) in the 2 and 3-flash conditions, in which the mean reported number of flashes was closer to veridical when congruent multisensory information was present. Younger participants only showed a significant improvement in the 2-flash condition (see Figure 6).

Experiment 2

The results of Experiment 1 indicated a greater effect of the sound-induced flash illusion in older as compared to younger observers. Previous research (Alsius, Navarra, Campbell, & Soto-Faraco, 2005; Mishra, Martínez, & Hillyard, 2010; Talsma, Doty, & Woldorff, 2007) has found evidence that attention is a critical factor in multisensory

integration. In addition, research has found that older individuals have a decreased capacity to ignore irrelevant information within, and across modalities, and this may be an alternative explanation for the age-related differences in integration (Poliakoff et al., 2006; Schmitz, Cheng, & De Rosa, 2010). Specifically, if there are age-related differences in the ability to ignore irrelevant auditory information, then greater encoding of the auditory stimuli by older individuals for multisensory trials may have led to an increased effect of the illusion for older as compared to younger observers. To examine whether these age-related differences may be due to an age-related difference in the capacity to ignore the irrelevant auditory stimuli, a go/no-go task was used. Three conditions were examined---a condition including an auditory go/no-go cue, a condition with a visual go/no-go cue, and a condition with no cue condition. The no-cue condition was a replication of the conditions in Experiment 1. For the auditory go/no-go cue condition participants were instructed to withhold a response if the beeps were presented at a lower frequency. For the visual go/no-go cue condition participants were instructed to withhold a response if the flashed disk was increased in size. If the age-related results of Experiment 1 were due to differences in attending to irrelevant information, then older observers may show little or no change in the sound-induced flash illusion when an auditory cue is used or no cue is present. This outcome would suggest that older participants are attending to auditory information in both of these conditions. In contrast, cuing younger individuals to attend to the auditory information with an auditory cue should result in a greater sound-induced flash illusion than in trials without the go/no-go task because participants are prompted to attend to auditory information. We also

included a go/no-go task in the visual modality with a visual cue for comparison purposes.

Methods

Participants. Twenty-four college students, 11 male and 13 female, from the University of California, Riverside ($M\ age = 21.96$ years, $SD = 0.75$ years) and twenty-seven older participants, 15 male and 12 female, from the surrounding community ($M\ age = 72.50$ years, $SD = 4.30$ years) participated in the experiment. Three older participants were unable to pass the pre-test (see methods below) and were not included in the study. Older participants were required to be 65 years of age or older. All observers were paid for their participation in the experiment, were naïve concerning the purpose of the Experiment and had not participated in Experiment 1. Subjects were screened using the same procedures as those used in Experiment 1 (see Table 2).

Apparatus. The apparatus used was the same as that in Experiment 1.

Stimuli. Stimuli were the same as those in the first experiment, with the following exceptions. The standard frequency for beeps during the go and control trials was 4.5 kHz. On visual no-go trials, the radius of the flashed disc was increased on 12% of the trials during the visual go/no-go block to 1.5° to indicate that the subject should not respond during that trial. On auditory no-go trials, the frequency of the tones was decreased to 2.5 kHz. This occurred on 12% of the trials in the auditory go/no-go block to indicate that the subject should not respond to the trial. The percentage of no-go trials (12%) was chosen to increase the attentional demand due to the low frequency of no-go trials.

Experimental task and procedure. The pre-test for inclusion in the study was the same as that used in Experiment 1. Experiment 2 consisted of three blocks, a multisensory block without any additional task, a multisensory block with a go/no-go task in the visual domain, and a multisensory block with a go/no-go task in the auditory domain. The order of the blocks was counter-balanced across participants such that two younger and two older participants were tested at each possible block order. Participants were allowed to take a break between each block. One of the blocks was the same as the multisensory block from Experiment 1. A block with a go/no-go task in the visual domain required participants to withhold their response when the flashes were presented at twice their standard size. One block with a go/no-go task in the auditory domain was also included. During this block, participants were to withhold their responses when the beeps were presented at a frequency 2 kHz lower (2.5 kHz) than the standard beep frequency (4.5 kHz). Similar to Experiment 1, if the participant failed to respond the response period ended after 6000 ms in all three blocks. Participants received 25 trials of each combination of flashes and beeps in random order, for a total of 300 trials within each block. The duration of the experiment was approximately 1.5 hours.

Results

Results were analyzed using a 2 (age) by 3 (block) by 3 (flashes) by 3 (beeps) mixed repeated-measures ANOVA. Focused analyses that examined whether age-related differences could be influenced by manipulating selective attention were also conducted. Trials in which participants withheld their response were removed from the primary analysis. Separate analyses were conducted examining accuracy for correctly withheld

responses, as well as false alarms for blocks including the go/no-go tasks. All analyses report original degrees of freedom and Greenhouse-Geisser corrections were used where appropriate. The zero beep conditions were dropped from this analysis, as they provide no information concerning multisensory integration. They were included in the blocks to ensure participants were continuing to perform the task, and were used to assess whether congruent multisensory information improved performance over unimodal trials and whether this was dependent on the attentional manipulation. A significant main effect of flashes was found, $F(2,92) = 164.26$, $MSE = 152.23$, $p < 0.001$, indicating that the number of flashes influenced the number of perceived flashes. A significant main effect of beeps, $F(2,92) = 156.80$, $MSE = 127.32$, $p < 0.001$, was also observed, indicating that the beeps had an effect on the perceived number of flashes. We also found a significant age by beep interaction, $F(2,92) = 9.42$, $MSE = 7.65$, $p = 0.002$. Similar to Experiment 1, older individuals showed a greater effect of auditory information on visual judgments. An analysis of the slopes (number of beeps relative to perceived number of flashes) indicated that older participants had a significantly greater slope ($M=0.52$, $SD=0.26$) compared to younger participants ($M=0.32$, $SD=0.17$), as indicated by a two-tailed t-test, $t(46) = 3.16$, $p = 0.003$. A significant interaction between flashes and beeps, $F(4,184) = 18.44$, $MSE = 2.65$, $p < 0.001$, was also found, indicating that the effect of the beeps on the perceived number of flashes decreased as the number of beeps became more incongruent with the number of presented flashes. In addition, we also found that the attentional manipulation did influence the sound-induced flash illusion as indicated by a block by beep interaction, $F(4, 184) = 3.57$, $MSE = 0.18$, $p = 0.02$, and a block by flash by beep interaction, $F(8,$

368) = 3.89, $MSE = 0.06$, $p = 0.001$. The interaction between age and cue condition was not significant, $F(2, 92) = 1.05$, $MSE = 0.10$, $p = 0.354$. However, we found that the modality of the attentional manipulation did influence the strength of the illusion (see Figure 7). A repeated-measures mixed ANOVA--analyzing the slopes (i.e. examining the perceived number of flashes relative to number of beeps) of the two attention manipulations and age--indicated an increase in slope for the auditory go/no-go task ($M=0.44$, $SD=0.26$) as compared to the visual go/no-go task ($M=0.38$, $SD=0.24$), $F(2,46) = 8.41$, $p = 0.006$. Though, this change in the degree of integration by modality of the go/no-go cue did not significantly differ with age, $F(1, 46) = 0.41$, $p = 0.53$. The presence of the auditory go/no-go task increased the strength of the illusion, while the presence of the visual go/no-go task resulted in a decrease in the strength of the illusion. This finding suggests that an attentional cue can alter the illusion, with the increase in illusion strength for the auditory go/no go task suggesting greater integration whereas the decrease in illusion strength for the visual go/no-go task suggesting a decrease in integration. However, we failed to find evidence that the impact of the go/no-go cue varied with age. No-go trials were analyzed using the proportion of correctly withheld responses with a 2 (go/no-go signal domain) by 2 (age) mixed repeated-measures ANOVA. A significant effect of block was found, $F(1, 46) = 40.96$, $MSE = 0.31$, $p < 0.001$. Participants showed a significant decrease in performance in their ability to withhold responses for the visual go/no-go task ($M = 0.86$, $SD = 0.13$) compared to the auditory go/no-go task ($M = 0.97$, $SD = 0.05$). No main effect or interaction of age was found. An analysis of the proportion correct of go trials that participants correctly responded showed no significant main effect

of block or age. This indicates that both older and younger individuals were correctly performing the go/no-go task in both conditions, and that high performance in the blocks including the attention manipulation was not merely due to a high rate of withholding responses by either group. An analysis of the effect of congruent multisensory versus unimodal information on responses was performed using a 2 (age) by 3 (block) by 3 (flashes) by 2 (congruency) mixed repeated-measures ANOVA. A significant effect of flashes $F(2,92) = 1275.23$, $MSE = 194.77$, $p < 0.001$ was found. We also found a significant effect of congruency $F(1,46) = 47.68$, $MSE = 4.58$, $p < 0.001$, indicating that performance was closer to veridical when congruent multisensory information was available. A significant congruency by age interaction, $F(1,46) = 15.71$, $MSE = 1.51$, $p < 0.001$, was also observed, with a greater improvement in performance with congruent multisensory information for older observers. The block by flashes interaction $F(4,184) = 5.65$, $MSE = 0.10$, $p < 0.001$ was also significant. As previously described the go/no-go task altered responses such that performance in the primary task was greater in the visual go/no-go condition compared to the auditory go/no-go condition. We also observed a significant, $F(2,92) = 32.32$, $MSE = 1.44$, $p < 0.001$, flash by congruency effect. As the number of flashes increased so did the benefit of the congruent multisensory information. Finally, we found a significant, $F(2,92) = 12.15$, $MSE = 0.54$, $p < 0.001$, age by flash by congruency effect. As the number of flashes increased older participants showed a greater benefit of congruent multisensory information than younger participants (see Figure 8). Older participants again showed a significant improvement ($p < 0.05$) in the 2 and 3-flash

conditions whereas younger participants only showed a significant improvement in the 3-flash condition.

Discussion

In the present experiments, we found evidence of age-related perceptual differences in multisensory integration. In Experiment 1, we examined whether age-related differences in multisensory integration exist using the sound-induced flash illusion. In addition to completing a multisensory sound-induced flash illusion block, participants also completed beep-only and flash-only blocks. We found that the auditory beeps had a greater influence on the perceived number of flashes for older as compared to younger participants. We also examined the unimodal data to determine whether this difference could be explained by age-related differences in vision or audition. There were no significant age-related differences in accuracy for the beep-only condition. However, we did find a significant effect of age in the 2-flash condition of the flash-only block. Older participants tended to overestimate the number of flashes while younger participants significantly underestimated the number of flashes. Nevertheless, the observed age-related differences in the multisensory effects were found to be the greatest in the 1-flash and 3-flash conditions — conditions in which the difference between the presented number of flashes and beeps was the largest. Therefore, it is unlikely that the observed age-related differences in multisensory integration could be due to age-related differences in vision or audition alone. This conclusion is supported by the finding that the greatest age-related differences were found in different conditions of the multisensory blocks as compared to the single significant age effect in the 2-flash condition. In

addition, we found that fusion, the combining of flashes due to a smaller number of auditory beeps, occurred for both age groups. We also found that fission, the splitting of a single flash due to a larger number of auditory beeps, occurred for both age groups (see Andersen et al. 2004 for similar findings of fission and fusion for younger observers). In the unimodal flash condition, we only found a decrease in the reported number of flashes for older individuals. We did not find an increase in the 3-flash condition of the multisensory block. The decrease for the 1-flash condition of the multisensory condition was also much greater than that seen in the unimodal condition. For these reasons, we do not believe that unimodal differences in vision or audition contributed to the results found in the present study. In addition, we examined age-related differences in the advantages conveyed by congruent multisensory stimuli by comparing performance in the multisensory block on the flash-only trials to performance during the same block in which the number of flashes and beeps were congruent. In both experiments, we found that older participants showed a greater benefit of congruent multisensory information compared to younger individuals, particularly as the number of flashes increased. This finding is in accord with the results of other studies demonstrating that older individuals show greater performance gains in the presence of redundant multisensory information than younger individuals (Hugenschmidt, Peiffer, et al., 2009; Peiffer et al., 2007). In the second experiment, we examined the effects of attention on the sound-induced flash illusion. Previous research has shown that older individuals have difficulties inhibiting task-irrelevant information (Hugenschmidt, Mozolic, Tan, et al., 2009; Schmitz et al., 2010; Sweeney, Rosano, Berman, & Luna, 2001). In our study, it was possible that older

individuals were exhibiting differences in integration due to an inability to inhibit the auditory information. To examine this possibility we included a go/no-go component in the second experiment to encourage younger and older participants to attend to specific aspects of each stimulus domain. Similar to the results of Experiment 1, we found that older individuals as compared to younger individuals demonstrated greater integration of auditory and visual information. We found that congruent multisensory information was more beneficial to older as compared to younger individuals. In addition, we found that the go/no-go task had an effect on the strength of the illusion, and that this effect changed in accordance with the sensory domain of the go/no-go signal. Specifically, we found a decrease in the strength of the illusion when the go/no-go task was in the visual domain, and we found an increase in the strength of the illusion when the go/no-go task was in the auditory domain. This suggests that the strength of the illusion was modulated by attention. However, the effect of attention on the illusion did not vary with age. This suggests that attention was not the basis of the age-related difference in the magnitude of the illusion. This finding is consistent with previous research (Hugenschmidt, Mozolic & Laurienti, 2009) that found that multisensory integration increased with age, with the effect modulated by directing attention to either visual or auditory information for both younger and older participants.

In summary, these results suggest that age-related differences in multisensory integration are not the result of age-related differences in the ability to ignore irrelevant information or increased attention of older individuals under multisensory conditions. The finding of an attention effect is interesting. While previous research has proposed

that the sound-induced flash illusion may be driven by an early processing component through feed-forward connections to visual cortex (Shams, Iwaki, et al., 2005; Watkins et al., 2007), other studies have found that the illusion can be influenced by higher-level processes (Setti & Chan, 2011). The results of the present study also suggest the possible influence of higher-level processes. Evidence in support of higher-level factors has been previously suggested by research that found audio-visual interactions identified as temporally “moderately early” and “late” in frontal cortex (Shams et al., 2005a). The results of Experiment 2 further support the influence of higher-level factors (beyond sensory cortex) on the sound-induced flash illusion. While these results support prior research showing little age-related change in the ability to engage selective attention (Hugenschmidt, Peiffer, et al., 2009), further study will be needed to explore the mechanisms involved in these higher-level processes. The results of the present experiments, considered together with the findings of other studies (e.g., Mahoney et al., 2011; 2012; Thompson, 1995; Laurienti et al., 2006), suggest that multisensory integration is maintained with increased age. In fact, older as compared to younger individuals showed greater integration of multisensory information. While this may indicate a compensatory mechanism to aid processing to offset unimodal processing declines, it may also be due to decreased selectivity in multisensory networks. This may be similar to selectivity losses seen in neurophysiological studies of animal visual cortex (Hua et al., 2006; Schmolesky et al., 2000a). While older participants were more susceptible to the illusion, our results also indicated greater facilitation for older participants in cases of congruent multisensory stimuli. In natural environments, it is

unlikely that visual and auditory stimuli that are spatially collocated will provide conflicting information. Outside of artificial conditions, such as that used in the sound-induced flash illusion, this increased integration may be beneficial. For example, in other audio-visual illusions, such as the McGurk effect, research has shown that older participants demonstrate a trend towards the visual alternative while simultaneously exhibiting a decrease in lip-reading performance (Cienkowski & Carney, 2002; McGurk & MacDonald, 1976). This suggests that while there is a decline in visual lip-reading performance older observers are still integrating that visual information into the auditory stimuli. The literature considered together suggests an overall increase in multisensory integration in older individuals. However, an important issue for further research will be to examine whether these age-related differences in multisensory integration indicate increases in the sensitivity of multisensory networks, possibly to compensate for unimodal declines, or if this increased integration may reflect a decrease in temporal and spatial selectivity such that integration is occurring for a broader range of non-coincident stimuli.

Tables

Experiment 1	Younger		Older	
Variable	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Age(years) ¹	20.75	0.62	75.67	5.07
Years of Education	15.08	0.67	14.92	1.88
Log Contrast Sensitivity ²	1.48	0.15	1.30	0.44
LogMAR Acuity ¹	0.01	0.11	0.15	0.12
Digit Span Forward	12.25	1.91	10.50	2.43
Digit Span Backwards ¹	8.83	2.62	6.83	1.90
WAIS – Matrix Reasoning ¹	20.33	3.09	16.67	4.91

Table 1. Means and standard deviations of participant demographics and results from cognitive and perceptual tests for Experiment 1. Note: ¹Differences between age groups were significant as indicated by a two-tailed t-test ($p < 0.05$). ²Contrast sensitivity measured using the Pelli Robson Test (Pelli, Robson & Wilkins, 1988).

Experiment 2	Younger		Older	
Variable	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Age(years) ¹	21.96	0.75	72.50	4.30
Years of Education	15.50	1.02	16.71	4.96
Log Contrast Sensitivity ²	1.45	0.50	1.36	0.48
LogMAR Acuity	0.02	0.10	0.07	0.12
Digit Span Forward	10.54	2.47	10.75	2.77
Digit Span Backwards	7.50	1.96	7.75	2.44
WAIS - Matrix Reasoning ¹	20.04	3.01	17.08	2.83

Table 2. Means and standard deviations of participant demographics and results from cognitive and perceptual tests for Experiment 2. Note: ¹ Differences between age groups were significant as indicated by a two-tailed t-test ($p < 0.05$). ² Contrast sensitivity measured using the Pelli Robson Test (Pelli, Robson & Wilkins, 1988).

Figures

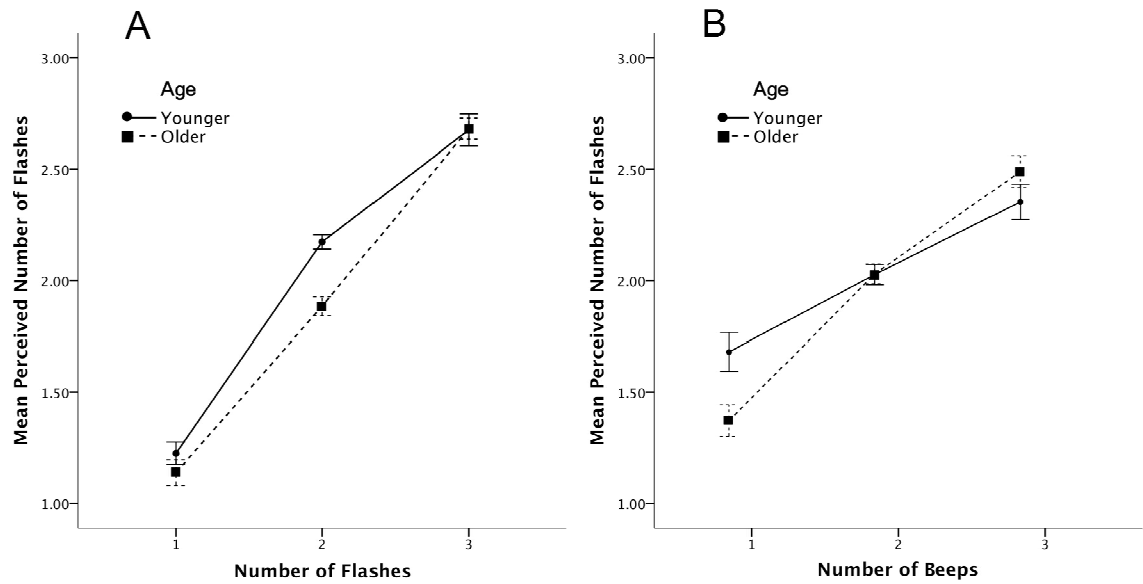


Figure 4. Panel A shows the mean perceived number of flashes as indicated by age group and number of flashes for the flash only block for Experiment 1. Panel B shows the mean perceived number of flashes as indicated by age group and number of beeps for the multisensory block for Experiment 1. Error bars indicate ± 1 SEM.. Error bars indicate ± 1 SEM.

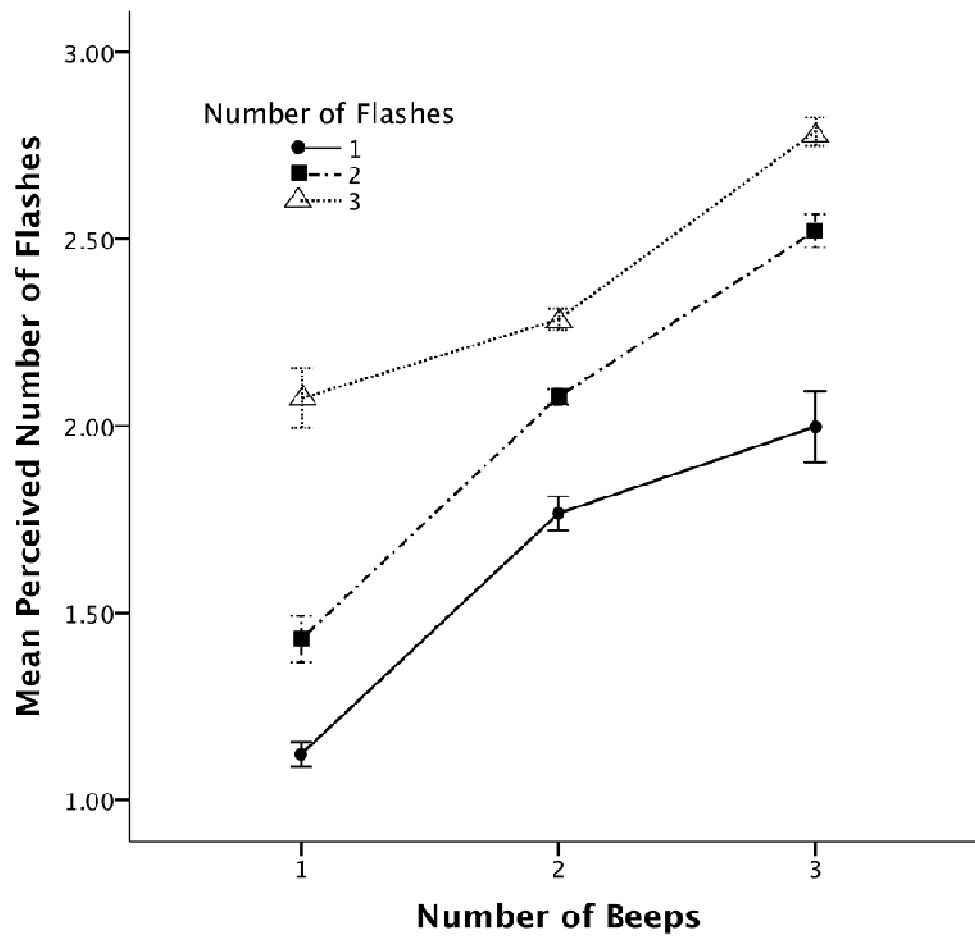


Figure 5. Mean perceived number of flashes as indicated by number of flashes and number of beeps for the multisensory block for Experiment 1. Error bars indicate ± 1 SEM.

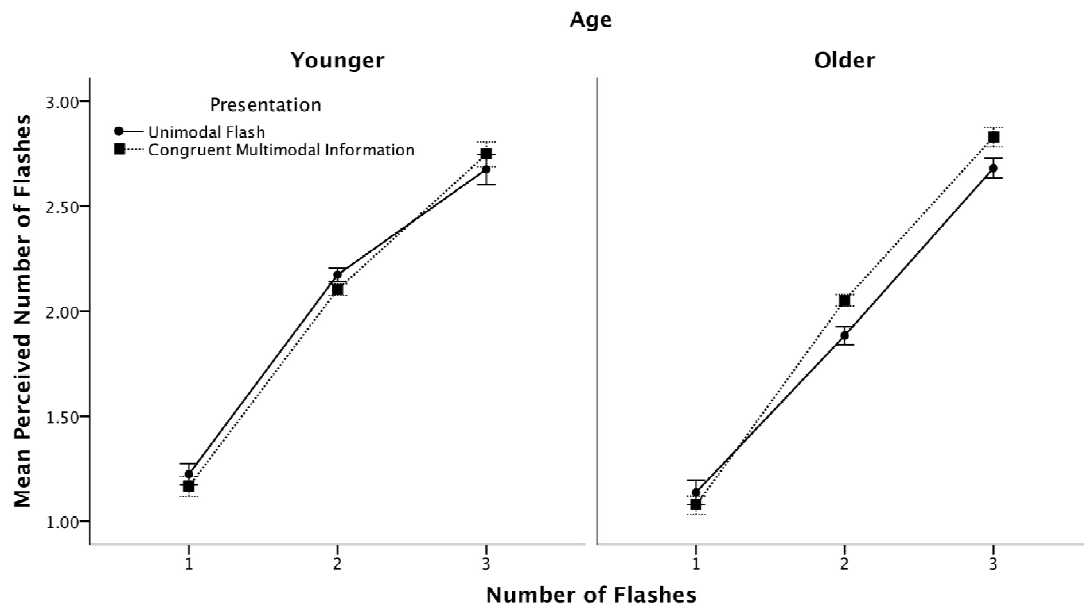


Figure 6. Mean perceived number of flashes as indicated by number of flashes, modality and age for the multisensory block for Experiment 1. Error bars indicate ± 1 SEM.

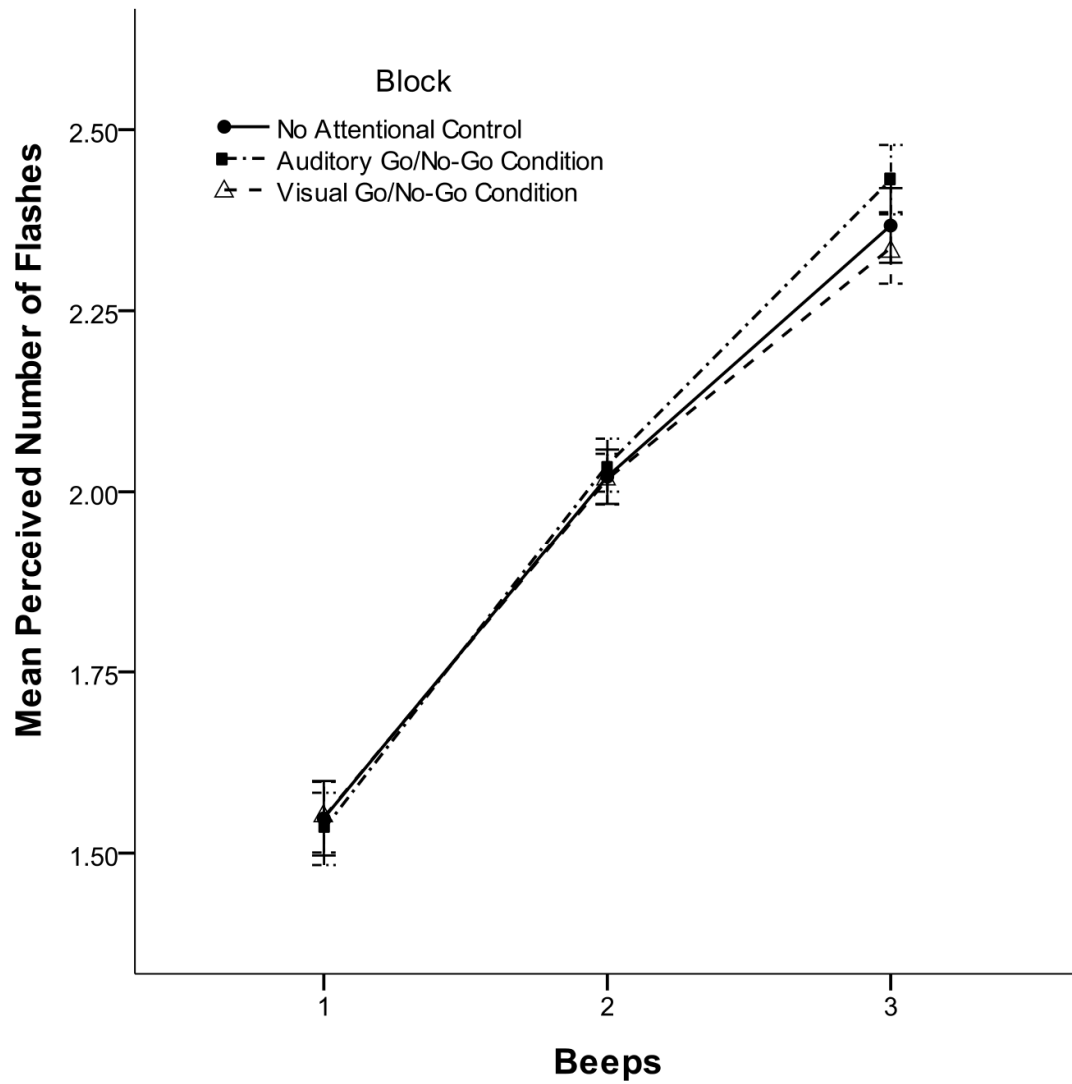


Figure 7. Mean perceived number of flashes as indicated by number of beeps and block for Experiment 2. Error bars indicate ± 1 SEM.

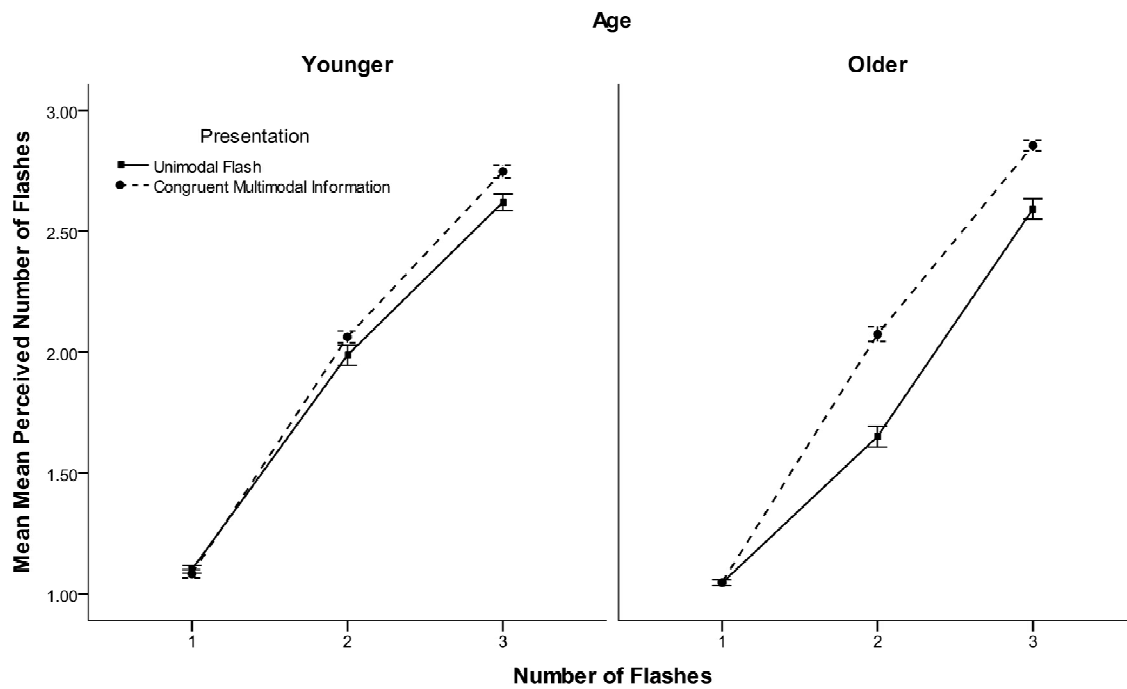


Figure 8. Mean perceived number of flashes as indicated by age and presentation type for Experiment 2. Error bars indicate ± 1 SEM.

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Chapter 2: Aging, Stimulus Strength, and the Sound-Induced Flash Illusion

This chapter is currently submitted to the academic journal *Acta Psychologica* and corresponds with Experiment 3 as described in the introduction.

Introduction

There are a wide range of age-related declines in sensory processing that occur with normal aging. Consider the age related declines in vision. Previous research has found that physiological changes including increased lens density (Xu, Pokorny, & Smith, 1997), loss of retinal ganglion cells (Curcio et al., 1993), decreased retinal illuminance (Weale, 1988), and a reduction in photoreceptors (Curcio & Drucker, 1993). Other studies have found declines in sensory processing that include low-level tasks such as orientation discrimination (Lisa R Betts et al., 2007) and masking (Andersen et al., 2010), to higher-level tasks such as motion perception (Bennett, Sekuler, & Sekuler, 2007; Trick & Silverman, 1991) and optical flow (Andersen & Enriquez, 2006; Atchley & Andersen, 1998). These declines in visual function can have serious consequences and have been suggested to be a factor in an increased likelihood of falls and increased crash risk while driving in older individuals (Rebecca Q. Ivers et al., 1998; Owsley et al., 1998); for a review of age-related declines in vision see Andersen, 2012 and Owsley, 2011).

Age-related declines in audition are also well documented in the literature. For example, older individuals show declines ranging from difficulties in low-level processing of pure-tone detection thresholds (Brant & Fozard, 1990b; Corso, 1963) and frequency and intensity discrimination (He et al., 1998a), to higher level processing such

as speech (Pichora-Fuller et al., 1995). Age-related declines in audition have been found to decrease the quality of life for older adults (Ildebrando Appollonio, Carabellese, Frattola, & Trabucchi, 1996). For a review of age-related declines in audition see Fitzgibbons & Gordon-Salant, 2010 and Schneider, Daneman, & Pichora-Fuller, 2002. While a significant body of research has been devoted to age-related unisensory declines, only recently has research begun to focus on how multisensory processing changes with age.

A number of recent studies have shown increased multisensory enhancement in older adults compared to younger individuals (Deloss et al., 2013; Diederich et al., 2008; Laurienti et al., 2006; Peiffer et al., 2007). While a small number of studies have shown decreased integration in older individuals (Roudaia, A. Sekuler, Bennett, & Sekuler, 2013; Stephen, Knoefel, Adair, Hart, & Aine, 2010). One possibility is that this increased multisensory integration in older individuals is a compensatory mechanism to deal with the significant age-related declines in unisensory processing. However, an alternative explanation is that this increased processing is itself another type of age-related decrement. In fact, older individuals have been shown to integrate information across much larger temporal windows than younger individuals (Diederich et al., 2008; Setti, Burke, et al., 2011; Stapleton, Setti, Emer P. Doheny, Kenny, & Newell, 2014). An increase between the onsets of a stimulus in one modality versus another modality should result in a decrease in integration, as the likelihood that the stimuli were from a single source decreases with decreased temporal coincidence. However, older individuals seem to be much less sensitive to these timing discrepancies. These temporal integration effects

have been suggested to have consequences for real world safety. For example, increased temporal windows of integration have been associated with an increased risk of falls and postural instability in older individuals (Setti, Burke, et al., 2011; Stapleton, Setti, Emer P. Doheny, et al., 2014). Though, recent research has shown that this decline in temporal sensitivity in older individuals can be improved through training (Setti et al., 2014).

The sound-induced flash illusion (Shams et al., 2002a) has been used in a number of these studies to assess age-related differences in multisensory integration (DeLoss et al., 2013; McGovern, Roudaia, Stapleton, McGinnity, & Newell, 2014; Setti, Burke, et al., 2011). The sound-induced flash illusion demonstrates that the presentation of simultaneous auditory beeps can influence the perception of visual flashes. The most basic form of the illusion consists of either the fission of a single visual flash into two perceived flashes when paired with two beeps (referred to as a fission illusion), or the fusion of two visual flashes into a single perceived flash when paired with a single beep (referred to as a fusion illusion). Older individuals have shown a stronger effect of this illusion, as well as increased temporal windows of integration (DeLoss et al., 2013; Setti et al., 2011).

In the present study, we examined the effects of age on one important characteristic of multisensory integration — inverse effectiveness. Inverse effectiveness refers to an increase in the effectiveness of multisensory integration when the individual sensory stimuli are weak. Consider the effect of stimulus intensity in one modality (vision) that occurs with a fixed stimulus in a second modality (audition). If a high-intensity visual stimulus is presented, then the presence of a paired auditory stimulus will

be unlikely to increase stimulus detection, as it is already near ceiling. However, if that visual stimulus is extremely weak, then a much stronger increase in stimulus detectability (or responsiveness of a neuron) will occur when paired with an auditory stimulus (Senkowski et al., 2011). This effect is referred to as inverse effectiveness (Holmes, 2007; Wallace et al., 1998). Inverse effectiveness has been found at the level of single multisensory neurons, as well as at the behavioral level in humans and cats (Holmes, 2007; Stein et al., 1989; Wallace, Meredith, & Stein, 1993; Wallace et al., 1998). To our knowledge, only a single study has examined the effect of auditory stimulus strength on the sound-induced flash illusion. T. S. Andersen, Tiippana, & Sams (2004) included an experiment assessing the use of near threshold auditory stimuli (10 dB) on the illusion. They found that the fission illusion still occurred at low auditory intensities, but the fusion illusion was not found. They also examined the illusion with an opposite strength of modality pairing, by examining whether the flashes influenced the perceived number of low intensity beeps. They found that fission occurred in all conditions, with fusion only occurring in one condition.

The present study examined how visual and auditory stimulus intensity influences the sound-induced flash illusion in older and younger individuals. For each participant the 70%, 82% and 94% correct detection thresholds for a visual flash and auditory beep were determined prior to multisensory presentation. These thresholds were then used to assess how stimulus intensity influences the illusion. To our knowledge, this is the first study to examine how both visual and auditory stimulus intensity influence the sound-induced flash illusion, and how these differences in intensity differentially affect the

performance of older and younger individuals. Due to increased internal noise in older individuals, they should show a greater effect of inverse effectiveness, as low intensity multisensory stimuli should demonstrate a greater benefit for older individuals as compared to younger individuals.

Methods

Subjects. Twelve college students, 7 male and 5 female (M age = 20.75 years, SD = 0.62 years), from the University of California, Riverside and twelve older participants, 6 male and 6 female (M age = 75.67 years, SD = 5.07 years), from the surrounding community participated in the experiment. Older participants were required to be 65 years of age or older. All observers were naïve concerning the experimental purpose and were paid for their participation in the experiment. All subjects were pre-screened for self-reported eye disease (e.g. macular degeneration, glaucoma, retinitis pigmentosa), neurological disorders (e.g. Alzheimer's disease, Parkinson's disease, stroke), as well as for any significant hearing loss. After passing this pre-screening participants were then assessed using an array of visual (acuity and contrast sensitivity) and cognitive (forward and backward digit span; WAIS Matrix Reasoning) tests (see Table 3). Participants were required to have a log minimum angle of resolution of 0.40 or better, as well as log contrast sensitivity of 1.00 or better. Participants were also required to have digit-span scores no more than one standard deviation below the standards for cognitively normal individuals published by the Alzheimer's Disease Center (Weintraub et al., 2010). Hearing was tested using the pre-test described in the experimental methods.

Apparatus. Stimuli were presented on a 22” Viewsonic PF817 CRT monitor at a resolution of 1024x768 at 100Hz (non-interlaced) driven by a Alienware Area-51 ALX equipped with an Intel Core i7 960 processor, and an NVIDIA Geforce GTX 480 graphics card, using the Microsoft Windows 7 (Service Pack 1) operating system. A Bits++ system (Cambridge Research Systems) was also used, which allowed the system to achieve 14-bit grayscale. The background luminance of the display was 0.06 cd/m². Auditory stimuli were presented using Audio Technica ATH-M50 headphones. Custom experimental software was written in MATLAB (The Mathworks, Inc., version 7.8.0.347); the Psychophysics Toolbox extensions were also utilized (Brainard, 1997; Pelli, 1997). Calibration, measurements and linearization of the lookup table of the monitor were performed using a ColorCal2 colorimeter (Cambridge Research Systems).

Stimuli and Procedures

Stimuli.

Pre-test. Stimuli during the pre-testing phase of the study consisted of either 1-2 visual flashes of a uniform white disc or 1-2 auditory beeps. The radius of the flashed disc was 0.75° in visual angle in size and was presented at 127.97 cd/m². The flash duration was 10 milliseconds (ms). Auditory beeps were 3.5 kHz sine wave tones. Beeps were 10 ms in length and were presented at 72dB.

Visual and Auditory Thresholding. Stimuli during thresholding consisted of a single visual flash or a single auditory beep. Stimulus parameters were the same as those used in the pre-test aside from the stimulus strength which was determined by QUEST.

Multisensory Presentation. Stimuli during the visual multisensory block of the

study consisted of 1-2 visual flashes paired with 0-2 auditory beeps. Stimuli during the auditory multisensory block consisted of 1-2 auditory beeps paired with 0-2 visual flashes. The strength of the stimuli was determined based on the 70%, 82% and 94% correct thresholds derived during thresholding. All possible stimulus combinations were presented for 10 trials each.

Experimental task and procedure. The monitor was viewed at a distance of 94 centimeters. Head position was stabilized with the use of a chin rest and stimuli were viewed binocularly. Any corrective lenses or contacts normally worn by the participants were allowed during the experiment. The only light source in the room during the experiment was the monitor.

Pre-Test. The pre-test consisted of two sections, the first assessed their ability to discriminate 1 to 2 beeps, and the second assessed their ability to discriminate 1 to 2 flashes. The pre-test took approximately 15 minutes. Participants fixated a 0.33° fixation crosshair, which was centered horizontally, and displaced vertically upwards 2.5° from the center of the screen. Flashes were presented at maximum brightness (127.97 cd/m^2), the background of the display was set to the mid-grey level of the monitor (63.71 cd/m^2). A mid-grey background was used throughout the study to avoid dark adaptation that may have been necessary for low threshold stimuli presented on a black background. Participants then pressed any key to advance the trial. The stimuli were then presented. During the flash pre-test the flashes were presented 5° below fixation. At the end of each trial participants were shown a blank response screen and entered the number of flashes or beeps perceived using the left arrow key of the keyboard to indicate that one flash was

presented, or the right arrow key to indicate that two flashes were present. Participants were given a maximum of five 16-trial blocks for each beep/flash pre-test condition to get a minimum of 13 trials correct within a single block to be eligible for the experimental portion. No significant differences ($p > 0.05$) in the number of trials to completion were observed between age groups for either pre-test.

Visual and Auditory Thresholding. The thresholding portion of the study consisted of two experimental blocks, a flash block and a beep block. The order of these blocks was counter-balanced across participants and each block was conducted on the first day of the study after the pre-test with a single break provided in between the two blocks. Each thresholding session of the experiment took approximately 1 hour. The flash block assessed participants' ability to discriminate a single visual flash on a mid-grey background that was presented in one of two intervals. Flash thresholds were assessed using a two-interval forced-choice task¹. Each interval lasted for 1500ms, with the onset of the stimulus occurring after a random delay of 500-1000ms. This delay was to eliminate any temporal cue that may help participants identify when the flash was presented. One interval contained the flash, and the other interval contained no stimulus. The task of the participant was to report which interval contained the flash using the left arrow key to indicate that the flash was displayed in the first interval, or the right arrow key to indicate that it was presented in the second interval. On each trial participants fixated on a 0.5° white crosshair presented 2.5° above the center of the screen centered

¹ The two-interval forced-choice task was used as pilot studies using a two-alternative forced choice task with one or two visual flashes showed high lapse rates which made reliable thresholding difficult.

horizontally. The two intervals were then presented, with the flash occurring 5° below the fixation point. The crosshair remained on the screen and participants entered their response using the keyboard, using the left arrow key to indicate that the flash occurred in the first interval, and the right arrow key to indicate that it occurred in the second. Subsequent to their response a prompt instructed participants to press any key to continue to the next trial. Participants 70%, 82%, and 94% thresholds were determined using QUEST. Three QUEST objects were initialized in MATLAB, one for each of the difficulty levels, all with a beta value of 3.52, a delta value of 0.01, and a gamma value of 0.5. Each block consisted of 360 trials, 120 trials for each threshold. The beep thresholding block was identical to the flash-only block, except that participants were presented a single beep and asked to identify which interval it was presented in.

Multisensory Presentation. The second and third day of the study consisted of the two multisensory blocks, a visual multisensory block and an auditory multisensory block, each presented on a separate day. The order of these blocks was counter-balanced across participants. Each block took approximately 1 hour. The visual multisensory block assessed participants' ability to discriminate 1-2 visual flashes in the presence of 0-2 auditory beeps. The flashes and beeps were presented at the 70%, 82%, and 94% correct thresholds derived during the thresholding blocks. Participants were presented 1-2 visual flashes after a delay of 250-1250ms. This delay was intended to prevent participants from using the length of each trial to determine the number of flashes presented. The task of the participants was to report the number of flashes presented. On each trial participants

² The beta value was determined during a pilot study.

fixated on a 0.5° white crosshair presented 2.5° above the center of the screen centered horizontally. The flashes were then presented, with the flashes occurring 5° below the fixation point. The crosshair remained on the screen and participants entered their response using the keyboard, using the left arrow key to indicate a single flash, or the right arrow key to indicate that two flashes were presented. Subsequent to their response a prompt instructed participants to press any key to continue to the next trial. The block consisted of 420 trials, 10 trials for each condition. The auditory multisensory block was identical to the visual multisensory block, except that participants were presented 1-2 auditory beeps paired with 0-2 visual flashes and asked to identify the number of beeps presented.

Results

Visual Multisensory Block. The results for the visual multisensory block were analyzed using an Age (2) x Flashes (2) x Beeps (2) x Flash Strength (3) x Beep Strength (3) analysis of variance. The no beep category was not included in the analysis as the auditory stimulus strength could not be manipulated for the no beep condition. It was included for comparison and to ensure participants were performing the correct task. Original degrees of freedom are reported, and Greenhouse-Geisser corrections were used where appropriate. Two older subjects were removed from the analysis as a stable threshold could not be reached during the thresholding blocks in at least one condition, resulting in a total of 10 older subjects used in the following analyses. As expected, the number of flashes influenced the perceived number of flashes, $F(1,20) = 125.89$, $MSE = 73.46$, $p < 0.001$. A significant effect of beeps was also found $F(1, 20) = 15.67$, $MSE =$

7.00, $p = 0.001$, indicating that the beeps did influence the perceived number of flashes. This can be seen in the decrease in slope in the illusion trials compared to the congruent trials shown in Figure 9. A slope of one would indicate no effect of the beeps on the perceived number of flashes, whereas a slope of negative one would indicate that the illusion was perceived on every multisensory trial. An auditory strength by beeps interaction was found, $F(2, 40) = 12.91$, $MSE = 0.19$, $p < 0.001$. The strength of the illusion increased with the strength of the beeps, and this effect was stronger for fission trials, in which two flashes and one beep are perceived as a single flash. There was also a flash strength by beeps by age interaction, $F(2, 40) = 4.33$, $MSE = 0.02$, $p < 0.02$. According to this result, older individuals showed greater susceptibility to the illusion in the lowest flash strength condition, while younger individuals showed the larger illusion in the mid flash strength condition (see Figure 10). A beep strength by flashes interaction was also found, $F(2, 40) = 3.66$, $MSE = 0.03$, $p < 0.035$, with the strength of the illusion increasing with the strength of the beeps (see Figure 11). Lastly, a beep strength by flash strength by flashes interaction was found, $F(4, 80) = 4.79$, $MSE = 0.03$, $p < 0.002$, the strength of the illusion decreased to a greater degree for fusion trials, one flash and two beeps perceived as two flashes, than fission trials (see Figure 12).

Auditory Multisensory Block. The results for the auditory multisensory block were analyzed using a Age (2) x Beeps (2) x Flashes (2) x Flash Strength (3) x Beep Strength (3) analysis of variance. The no flash category was not included in the analysis as the flash stimulus strength could not be manipulated for the no flash condition. It was included for comparison purposes and to ensure participants were performing the correct

task. Original degrees of freedom are reported, and Greenhouse-Geisser corrections were used where appropriate. As expected, the number of beeps influenced the perceived number of beeps, $F(1,20) = 172.99$, $MSE = 65.70$, $p < 0.001$. A significant effect of flashes was also found, $F(1, 20) = 20.92$, $MSE = 0.76$, $p = 0.001$, indicating that the flashes did influence the perceived number of beeps, as evidenced by the decrease in slope in illusion trials shown in Figure 13. A significant effect of beep strength was found, $F(2, 40) = 22.90$, $MSE = 1.23$, $p < 0.001$. A significant effect of flash strength was also found, $F(2, 40) = 12.88$, $MSE = 0.14$, $p < 0.001$. A beeps by age interaction was found, $F(1, 20) = 5.89$, $MSE = 2.24$, $p = 0.03$ (see Figure 14). Older individuals significantly underestimated the number of beeps on trials containing two beeps as compared to younger subjects. There was also a flash strength by flashes interaction, $F(2, 40) = 8.44$, $MSE = 0.06$, $p = 0.001$. The effect of the flashes on the perceived number of beeps was greater for fission trials, one beep and two flashes perceived as two beeps, was greater as the strength of the flashes increased (see Figure 15). A beep strength by beeps interaction was also found, $F(2, 40) = 57.27$, $MSE = 1.74$, $p < 0.001$, with the strength of the illusion decreasing to a greater degree for fusion trials, where two beeps and one flash is perceived as a single beep, as the strength of the beeps increased (see Figure 16). A beep strength by flash strength by beeps illusion was also found, $F(4, 80) = 2.89$, $MSE = 0.02$, $p = 0.027$. However, younger individuals showed little effect of the illusion beyond the lowest beep strength. This was further indicated by a beep strength by flash strength by beeps by age interaction, $F(4, 80) = 2.84$, $MSE = 0.02$, $p = 0.029$. Older individuals showed a greater increase in the illusion with an increase in flash strength for fission

trials, though as the strength of the beeps increased the strength of the illusion decreased to greater degree for younger individuals. This can be seen in Figure 12 by comparing older and younger individuals in the 94% correct threshold flash-strength condition as beep strength increases.

Discussion

The results of the present study suggest several important findings regarding multisensory integration in general, and the effects of age on multisensory integration. First, the results suggest that the sound-induced flash illusion may not truly be the result of multisensory integration, or that multisensory integration may not be the most appropriate term with regards to the illusion. Multisensory integration refers to the binding of sensory input from multiple modalities into a unified percept (Schmiedchen, Freigang, Nitsche, & Rübsamen, 2012; Spence, Senkowski, & Röder, 2009). One example of multisensory integration is the McGurk effect (McGurk & MacDonald, 1976), in which the pairing of a heard syllable “ba” and a video of an actor pronouncing the syllable “ga” results in the perception of the syllable “da.” This combination of information, across the two modalities in the McGurk effect, results in a perception of a syllable that was not presented in either modality, thus indicating binding and multisensory integration. A crossmodal interaction is the influence of one modality on the processing of another modality and may be a more appropriate description of the illusion given that the auditory and visual illusions examined here show highly discrepant results in terms of the strength of the illusion for visual compared to auditory judgments. However, research has shown that early processing is altered by the illusion, which

suggests that neuronal multisensory integration may be a significant factor in the illusion (Shams, Iwaki, et al., 2005; Watkins, Shams, Tanaka, Haynes, & Rees, 2006). In the present study, we also found evidence that the visual and auditory strength of the stimuli in the sound-induced flash illusion influence the strength of the illusion. For the visual illusion, the strength of the auditory beeps was found to increase the strength of the illusion for both younger and older individuals. A decrease in slope in Figure 9 indicates an increase in the strength of the illusion. Younger individuals showed less sensitivity to the illusion at the lowest flash strength level compared to older individuals. The auditory stimulus strength was found to significantly influence the illusion, with a decrease in the strength of the illusion for fission trials as the visual stimulus strength increased. This result is interesting, as it suggests that there may be a difference between the mechanisms behind fission and fusion illusions. Both groups showed behavioral evidence of inverse effectiveness as indicated by a decrease in slope as stimulus strength was increased.

For the auditory illusion, we found that there was a small but consistent effect of the flashes on the perceived number of beeps. However, this illusion seems to be stronger for fusion trials than for fission trials. Older individuals demonstrated greater integration than younger individuals. Older individuals also showed a greater effect of this illusion at higher auditory stimulus strengths than younger individuals. Interestingly, fission trials showed a greater effect than fusion trials at high auditory stimulus strengths. This trend is opposite of that found in the visual illusion, which suggests that the visual and auditory illusions may be the result of different mechanisms. Again, both age groups showed

behavioral evidence of inverse effectiveness. However, older individuals showed a smaller decline in the fission illusion with increased auditory stimulus strength.

The results of the present study demonstrate decreased behavioral inverse effectiveness in older individuals. This result combined with prior research showing declines in temporal sensitivity to multisensory stimuli suggest that changes in multisensory and crossmodal processing in older individuals may indeed be another form of age-related decline (McGovern et al., 2014; Setti, Burke, et al., 2011). One possible explanation for the age-related differences in integration — seen here in the visual and auditory illusions — may be due to age-related changes in neural inhibition. Previous research has found that decreased inhibition is a significant factor in properties of visual processing that decline in senescent animals, and that the administration of GABA agonists was found to significantly improve processing (Leventhal et al., 2003; Schmolesky, Wang, Pu, & Leventhal, 2000b). This decreased inhibition may be important for multisensory and crossmodal processing. Age-related decreases in inhibition could result in decreased spatial and temporal sensitivity of multisensory neurons, which may explain the increased temporal window of integration found in older subjects (McGovern et al., 2014; Setti, Burke, et al., 2011). Further research will be needed to determine whether this is a factor in increased multisensory integration and crossmodal interactions in older adults.

In summary, the present study demonstrates that older individuals show declines in inverse effectiveness compared to younger individuals as evidenced by the sound-induced flash illusion. Older individuals also showed a stronger effect of auditory

stimulus strength in the traditional sound-induced flash illusion for fission as opposed to fusion illusions. Evidence of the illusion in the opposite direction, with visual flashes influencing the number of perceived beeps, was also found in both age groups. However, fission illusions were found to be stronger than fusion illusions for this “flash-induced beep illusion” in both age groups. This suggests that the sound-induced flash illusion and the “flash-induced beep illusion” may rely on different mechanisms.

Tables

Variable	Younger		Older	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Age(years) ¹	22.25	2.3	76.00	7.42
Log Contrast Sensitivity ^{1,2}	1.42	0.10	1.31	0.10
LogMAR Acuity ¹	-0.09	0.07	0.17	0.17
Digit Span Forward ¹	11.08	2.06	9.27	1.56
Digit Span Backwards ¹	8.33	1.61	5.73	1.42
WAIS – Matrix Reasoning ¹	19.5	3.94	13.09	5.54

Table 3. Means and standard deviations of participant demographics and results from cognitive and perceptual tests. Note: ¹ Differences between age groups were significant as indicated by a two-tailed t-test ($p < 0.05$). ² Contrast sensitivity measured using the Pelli Robson Test (Pelli, Robson & Wilkins, 1988).

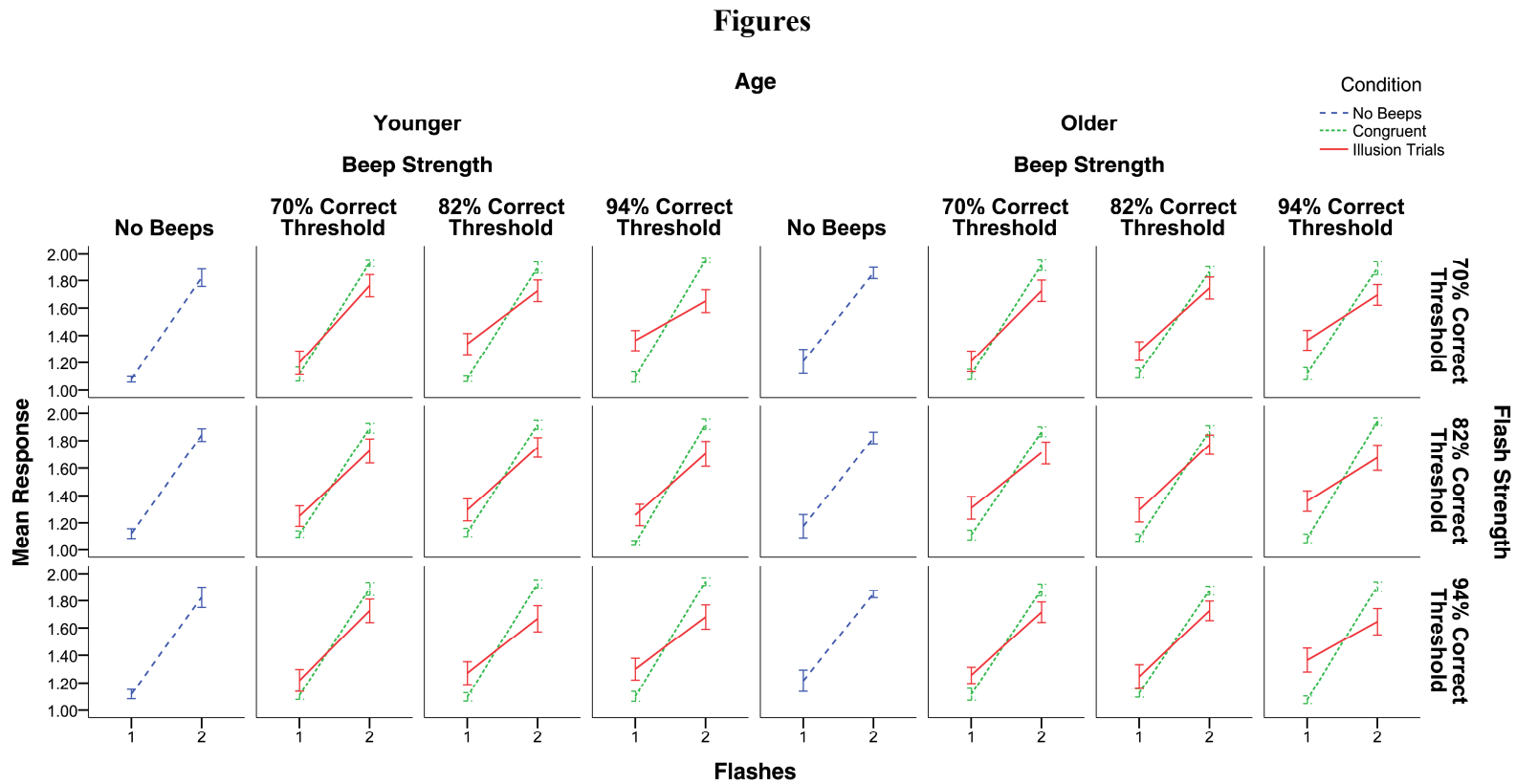


Figure 9. Mean perceived number of flashes as indicated by age group, number of flashes, flash strength, beep strength, and condition for the visual multisensory block. Error bars indicate ± 1 SEM.

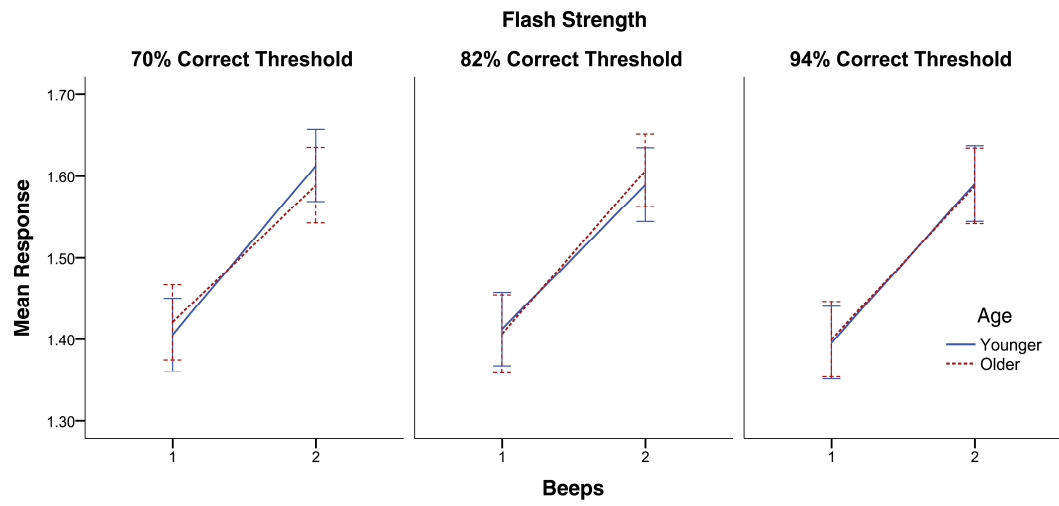


Figure 10. Mean perceived number of flashes as indicated by flash strength, age and beeps for the visual multisensory block. Error bars indicate ± 1 SEM.

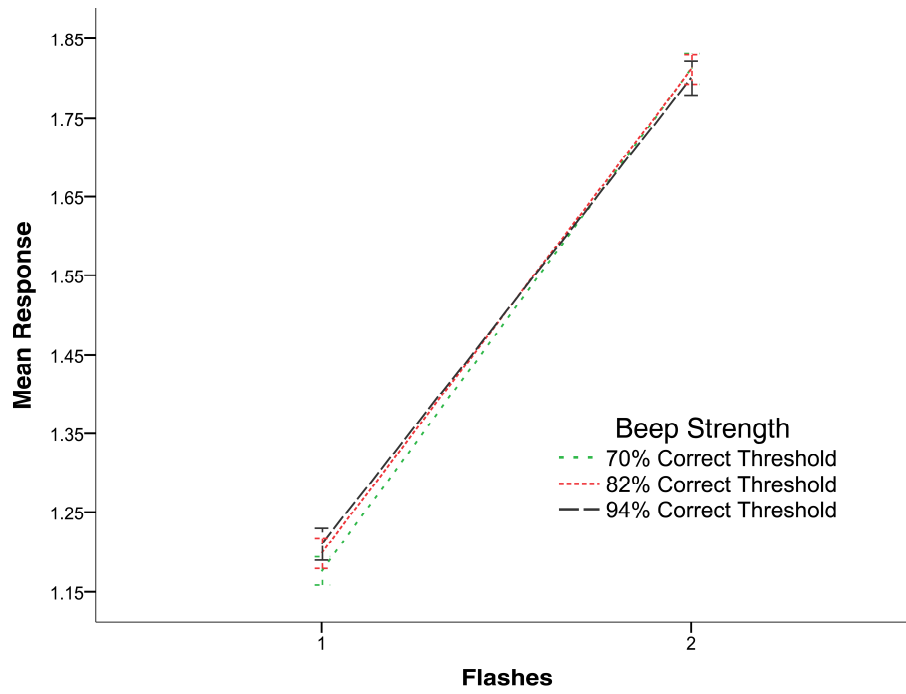


Figure 11. Mean perceived number of flashes as indicated by number of flashes and beep strength for the visual multisensory block. Error bars indicate ± 1 SEM.

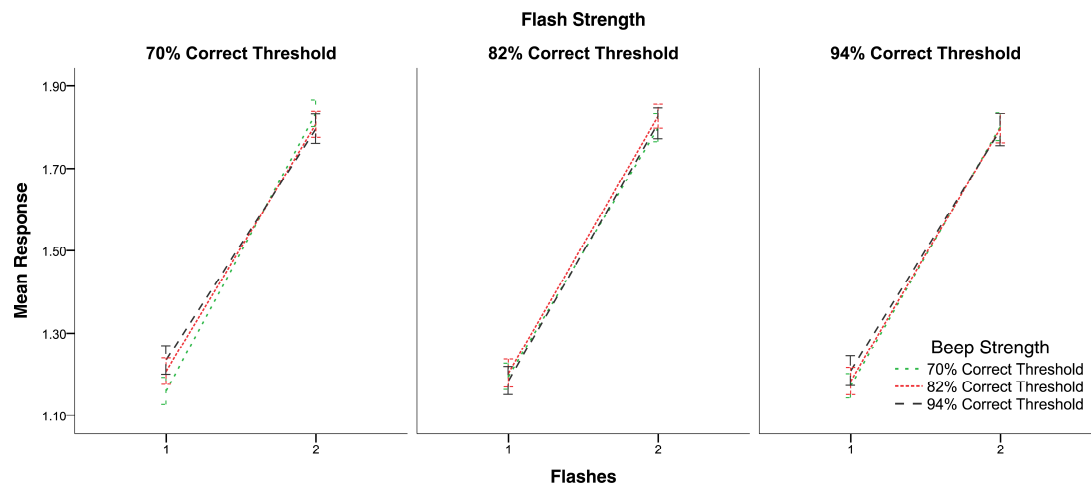


Figure 12. Mean perceived number of flashes as indicated by number of flashes, flash strength, and beep strength for the visual multisensory block. Error bars indicate ± 1 SEM.

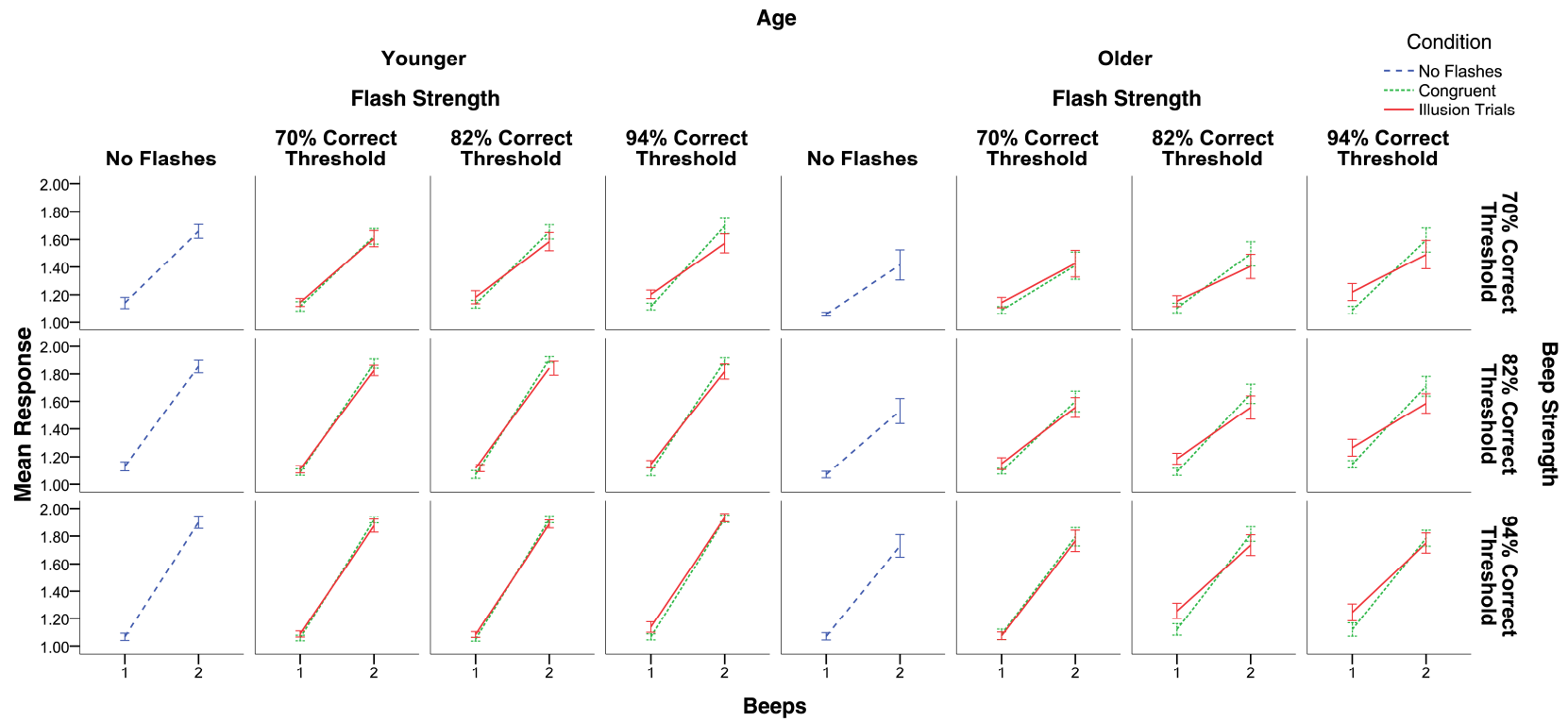


Figure 13. Mean perceived number of beeps as indicated by number of beeps, age group, beep strength, flash strength, and condition for the auditory multisensory block. Error bars indicate ± 1 SEM.

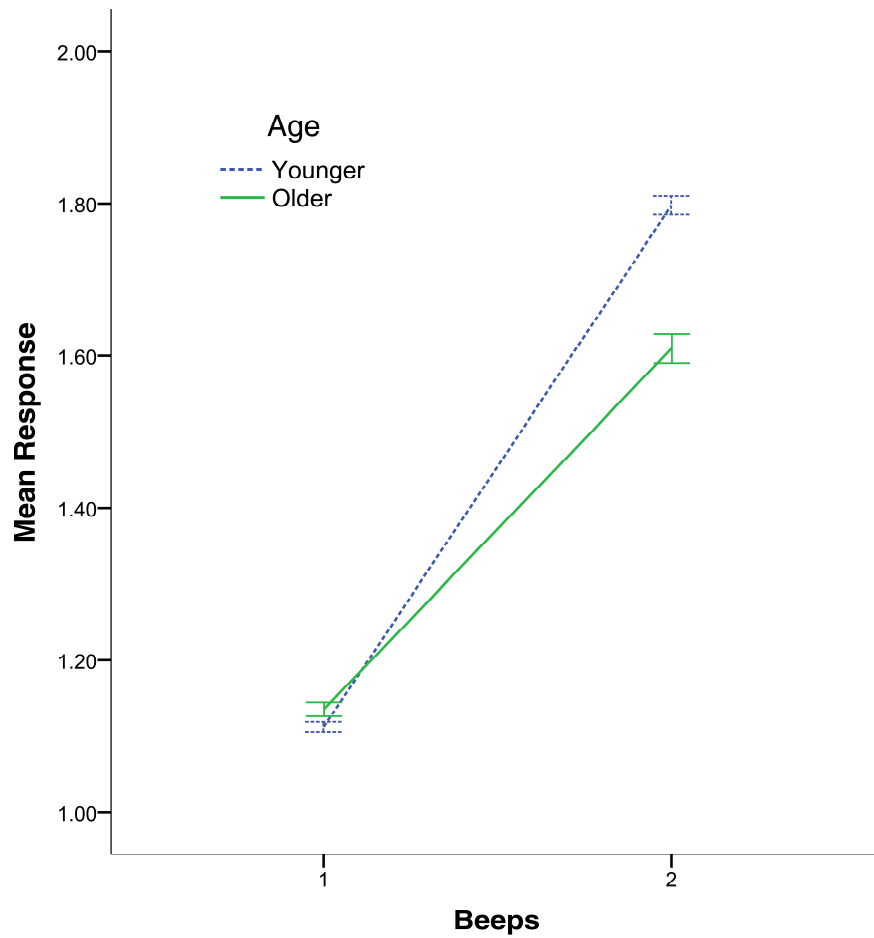


Figure 14. Mean perceived number of beeps as indicated by number of beeps and age group for the auditory multisensory block. Error bars indicate ± 1 SEM.

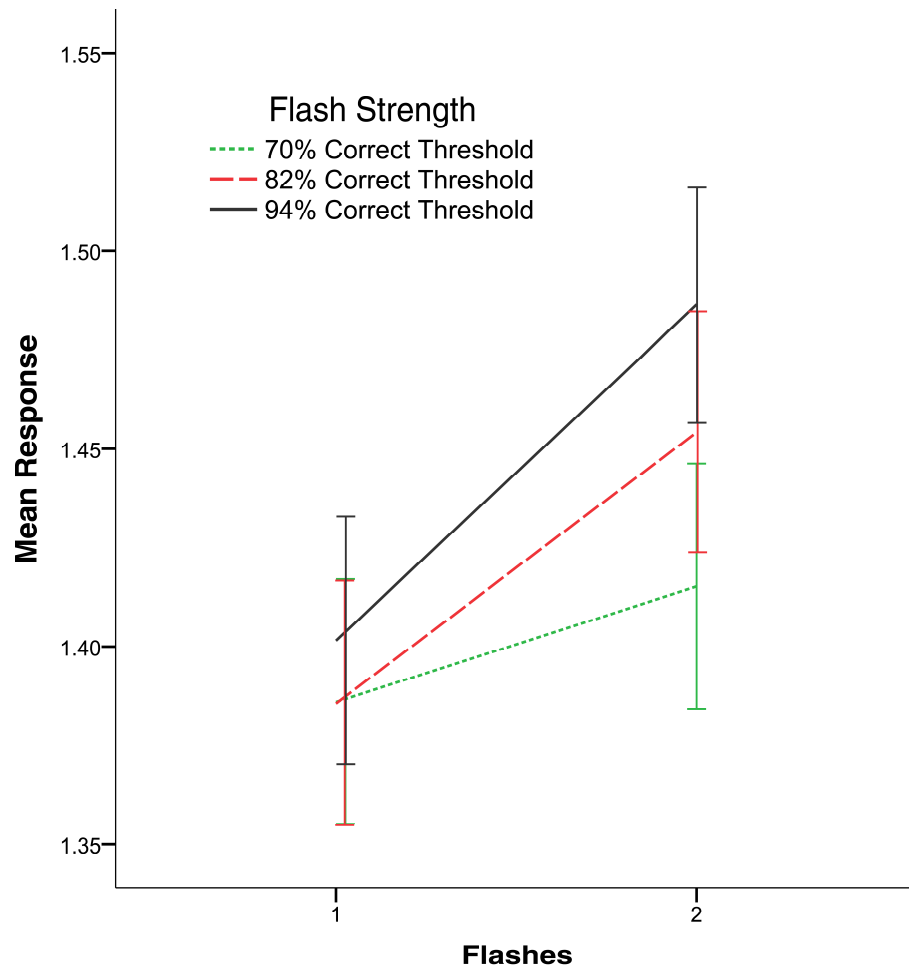


Figure 15. Mean perceived number of beeps as indicated by number of flashes and flash strength for the auditory multisensory block. Error bars indicate ± 1 SEM.

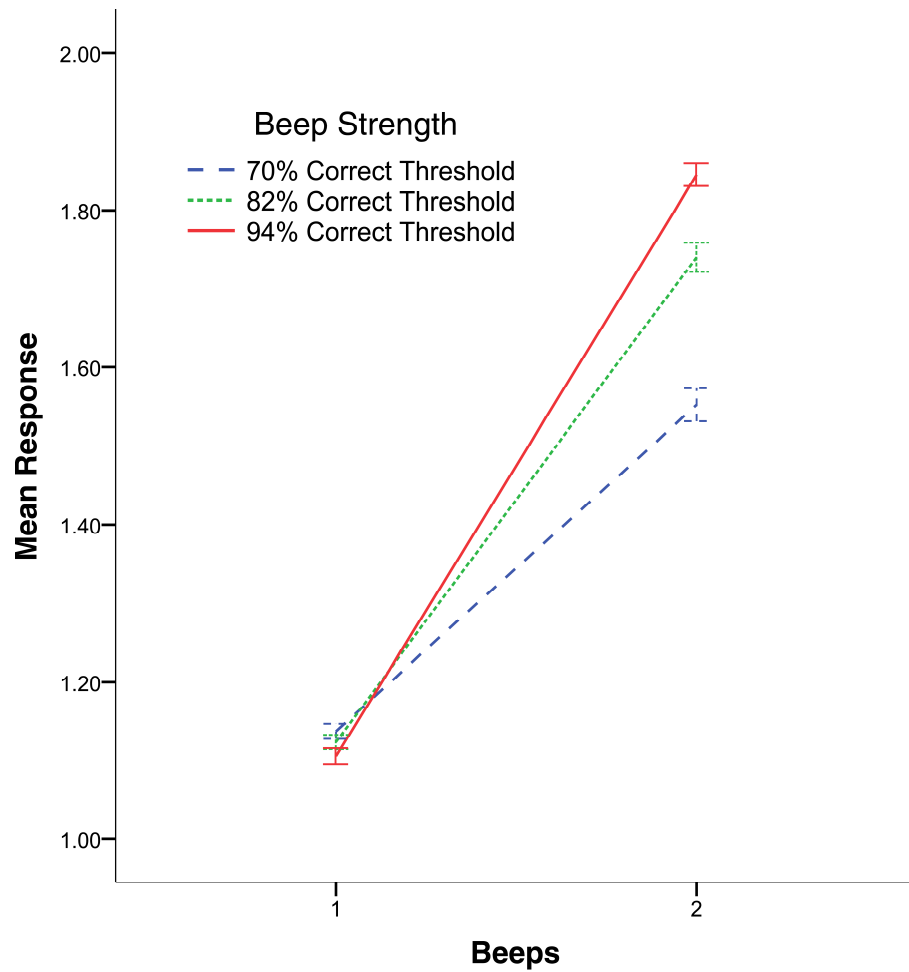


Figure 16. Mean perceived number of beeps as indicated by number of beeps and beep strength for the auditory multisensory block. Error bars indicate ± 1 SEM.

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Chapter 3: Aging, spatial disparity, and the sound-induced flash illusion

This chapter has been submitted to the academic journal PLOS One and corresponds with Experiment 4 as discussed in the introduction.

Introduction

Our senses were once believed to be modular and encapsulated, with information from one sensory modality being inaccessible by the other senses. Any integration of information across the senses was thought to occur in specific “polysensory” areas of the brain (Jones & Powell, 1970; Treisman & Gelade, 1980). However, recent research has shown that this is incorrect and sensory processing has been proposed as being primarily multisensory in nature (Ghazanfar & Schroeder, 2006). Direct connections from auditory cortex (A1) to primary visual cortex, as well as from somatosensory cortex to auditory cortex have also been found (Falchier, Clavagnier, Barone, & Kennedy, 2002b; Foxe et al., 2002). These findings suggest that unisensory processing independent from other sensory modalities is increasingly unlikely. Given that sensory processing has been found to be influenced by information from other sensory modalities, research on how the senses interact is important in understanding sensory processing.

Older individuals suffer from a wide range of sensory declines that occur over the course of normal aging. These declines have a significant influence on the aging population’s health and quality of life (Ildebrando Appollonio et al., 1996; Keidser, Seeto, Rudner, Hygge, & Rönnberg, 2015). Given these sensory declines in older individuals, changes in multisensory processing are also likely. Indeed, research has

shown that older individuals demonstrate a wide range of changes in processing multisensory stimuli. Older individuals have been found to have greater difficulty inhibiting irrelevant cross-modal information (Guerreiro, Murphy, & Van Gerven, 2013; Guerreiro & Van Gerven, 2011). Older individuals have also demonstrated increased multisensory integration in a variety of studies (Deloss et al., 2013; Diederich et al., 2008; Laurienti et al., 2006; Peiffer et al., 2007). However, a number of recent studies have also found a decrease in integration in older individuals as compared to younger individuals (Roudaia, A. B. Sekuler, Bennett, & Sekuler, 2013; Stapleton, Setti, Emer P Doheny, Kenny, & Newell, 2014).

These changes in integration in older individuals may reflect a compensatory mechanism that exhibits increased multisensory integration in an effort to help counteract age-related declines in vision and audition. However, given the wide range of declines in vision and audition, it seems unlikely that multisensory processing would be spared. Another possibility is that these changes in integration in older individuals also reflect a decline in functionality. Indeed, research has shown that older individuals have larger temporal windows of integration (Diederich et al., 2008; Stapleton, Setti, Emer P. Doheny, et al., 2014). Multisensory integration is dependent on spatial and temporal coherence, as spatial or temporal disparity increases the degree of integration decreases (Stein & Meredith, 1993). If integration occurs for large spatial and temporal disparities, the system would be highly inefficient and the likelihood of integrating information from separate events in the environment could cause erroneous integration. This increased

temporal window of integration suggests that older individuals may also suffer from declines in the efficient integration of multisensory information.

One recent method used to examine changes in multisensory integration in older individuals is by examining the sound-induced flash illusion. An illusion trial consists of a discrepant number of beeps that are paired with a number of visual flashes, the illusion is said to have occurred when the beeps influence the perceived number of flashes (Shams et al., 2000, 2002a). The illusion can influence the perceived number of flashes in two ways. The first is the fission illusion, when a single flash is paired with two beeps and is perceived as two flashes. The second is the fusion illusion when two flashes are paired with a single beep and perceived as a single flash. This illusion has been used to show that older individuals demonstrate greater integration than younger individuals (Deloss et al., 2013). It has also been used to show that older individuals have larger temporal windows of integration (McGovern et al., 2014; Setti, Burke, et al., 2011). However, to date, no study has examined whether spatial disparity in the sound-induced flash illusion is altered in older individuals.

To our knowledge, only a single study has examined the role of spatial disparity in the sound induced flash illusion (Innes-Brown & Crewther, 2009). This study assessed the role of spatial disparity on the illusion in young adults by presenting the flashes at one of two locations, offset from the center of the display by 10 degrees. Speakers were placed directly below the two possible flash locations. This allowed for a maximum spatial disparity of 20 degrees. The study found no effect of spatial disparity on the illusion. However, spatial disparity has been found to influence multisensory integration

in a number of human and animal studies (Bizley & King, 2008; M Alex Meredith & Stein, 1986; Teder-Sälejärvi, Di Russo, McDonald, & Hillyard, 2005; Van Wanrooij, Bell, Munoz, & Van Opstal, 2009). The present study examined the effect of spatial disparity on the sound-induced flash illusion in younger and older individuals at larger spatial disparities than used in the previously mentioned studies. While 20 degrees is sufficient for detecting a change in auditory location, multisensory integration has shown varying sensitivity to spatial disparity (Perrott & Saberi, 1990; Slutsky & Recanzone, 2001). To examine whether spatial disparity differentially influences the sound-induced flash illusion for younger and older adults the horizontal disparities used in this study were greater than the disparity used in previous research, with disparities in the present study at approximately 25 and 50 degrees. Reaction times were also recorded to examine whether any changes in processing occur with increased spatial disparity in older and younger individuals.

Methods

Participants. Twelve college students, 6 male and 6 female ($M\ age = 23.17$ years, $SD = 4.26$ years), from the University of California, Riverside and twelve older participants, 6 male and 6 female ($M\ age = 71.45$ years, $SD = 3.08$ years), from the surrounding community participated in the experiment. Older participants were required to be 65 years of age or older. All observers were naïve concerning the experimental purpose and were paid for their participation in the experiment. All subjects were pre-screened for self-reported eye disease (e.g. macular degeneration, glaucoma, retinitis pigmentosa), neurological disorders (e.g. Alzheimers disease, Parkinson's disease,

stroke), as well as for any significant hearing loss. After passing this pre-screening participants were then assessed using an array of visual (acuity and contrast sensitivity) and cognitive (forward and backward digit span; WAIS matrix reasoning) tests (see Table 4). Participants were required to have a log minimum angle of resolution of 0.40 or better, as well as log contrast sensitivity of 1.00 or better. Participants were also required to have digit-span scores no more than one standard deviation below the standards for cognitively normal individuals published by the Alzheimer's Disease Center (Weintraub et al., 2010). Visual and cognitive test data was lost for one older participant. Participants were allowed the use of hearing aids (only one participant required the use of a hearing aid), and hearing was tested using the pre-test described in the experimental methods. Any corrective lenses or contacts normally worn by the participants were also allowed during the experiment.

Apparatus. Stimuli were presented on a 22" Viewsonic PF817 CRT monitor at a resolution of 1024x768 at 100Hz (non-interlaced) driven by an Alienware Area-51 ALX (Intel Core i7 960 processor, NVIDIA Geforce GTX 480 graphics card, Microsoft Windows 7 Service Pack 1). The background luminance of the display was 0.06 cd/m². The experimental software was custom written in MATLAB (The Mathworks, Inc., version 7.8.0.347) and the Psychophysics Toolbox extensions were also used (Brainard, 1997; Pelli, 1997). Calibration and measurements of the monitor were performed using a ColorCal2 colorimeter made by Cambridge Research Systems. Dell A215 speakers were used in the study.

Stimuli. Stimuli consisted of 1-2 flashes of a uniform white disc paired with 0-2 auditory beeps. The radius of the flashed disc was 0.75° in visual angle in size and was presented at the monitors maximum brightness level (127.97 cd/m^2). The flashes had a duration of 10 milliseconds (ms) with a 70 ms inter-flash interval. Auditory beeps were 3500 Hz sine wave tones. The beeps were also 10 ms in duration with 70 ms inter-beep intervals, and were presented at 72 dB sound pressure level. All beeps had a 2 ms onset and offset ramp. On trials that included both flashes and beeps, the onset of the first beep began 20 ms before the onset of the first flash. Previous research (Shams et al., 2002) has found no decrease in the strength of the illusion with temporal offsets of up to 70 ms.

Experimental task and procedure. The monitor was viewed at a distance of 106 centimeters and head position was stabilized with the use of a chin rest. The only light source in the room during the experiment was the monitor. All stimuli were viewed binocularly. At the beginning of the study all participants were required to pass a pre-test to ensure that they were able to discriminate the unimodal beeps and flashes that would be used in the study. The pre-test consisted of two blocks, the first assessed their ability to discriminate 1 or 2 beeps, and the second assessed their ability to discriminate 1 or 2 flashes. Beeps were presented from a single speaker 1m in front of the participants that was placed directly below the front of the monitor. On each trial participants fixated a 0.5° crosshair, which was centered horizontally and presented 2.5° above the center of the screen. Participants then pressed any key to advance each trial. The stimuli were then presented which consisted of either flashes or beeps. During the flash pre-test block the flashes were presented 5° below the fixation crosshair. At the end of the trial participants

were shown a blank response screen and entered the number of flashes or beeps perceived using the left arrow key to indicate one flash or beep and the right arrow key to indicate two flashes or beeps. Participants were given up to five 16-trial blocks to pass the pre-test. The pre-test ended when they were able to get 13 of the 16 trials correct within a single block to be eligible for the study. The experiment consisted of the two pre-tests and a single experimental block. The entire experiment took approximately 1 hour. The experimental block assessed participants' ability to discriminate 1 to 2 visual flashes when paired with 0-2 beeps. The beeps came from one of five speakers placed 1m from the observer along a semi-circle (see Fig. 17). This configuration was used to control for the effect of distance. All speakers were calibrated so that the beeps were presented at 72dB at the observer. Each possible combination of flashes, beeps and speaker displacement was presented 20 times during the experimental block, for a total of 560 trials. Presentation order was randomized for each participant. The task of the participant was to report the perceived number of flashes using the left and right arrow keys, with the left arrow key indicating one flash and the right arrow key indicating two. Participants were informed that the trials would frequently be accompanied by a series of beeps, and that while these beeps may be distracting to remember to respond only to the number of flashes presented. On each trial participants fixated on a 0.5° white crosshair presented 2.5° above the center of the screen that was presented for 250-1250 ms randomized on each trial. This variable onset timing was implemented to eliminate any strategy using the temporal length of each trial as a cue to the number of flashes presented. After the delay 1-2 visual flashes were presented 5° below the fixation cross.

The crosshair then disappeared and text appeared on the screen instructing the participants to “Please enter ← if you saw one flash or → if you saw two flashes.” Participants then entered their response.

Results

Response Analysis. Response data was analyzed using an Age (2: Younger, Older) x Flashes (2: 1 flash, 2 flashes) x Beeps (2: 1 beep, 2 beeps) x Speaker Displacement (3: 0m, 0.5m, 1m) mixed analysis of variance. For any effects that violated sphericity Greenhouse-Geisser corrections were used. Original degrees of freedom are reported. As expected the number of flashes significantly influenced the perceived number of flashes ($F(1,22) = 28.847, p < .001$, see Fig. 18). There was also a significant effect of beeps ($F(1,22) = 308.02, p < .001$, see Fig. 18). The beeps showed a significant effect on the perceived number of flashes for both fusion, fission, and congruent trials (see Fig. 19). Congruent multisensory information improved performance for two flash trials to a greater degree than for single flash trials. This effect was greater for older individuals for the two flash condition, as they tended to underestimate the number of flashes presented in the unisensory two flash condition. A significant interaction between beeps and speaker displacement was also found ($F(2,44) = 3.36, p = .044$, see Fig. 20). A simple effects analysis of speaker displacement split by number of beeps revealed that there is a significant effect of speaker displacement for trials with a single beep ($F(2,32) = 4.268, p = .023$). Localized analyses using paired two-tailed t-tests revealed a significant difference between the 0.5 meter speaker displacement and the 1 meter speaker displacement ($t(16) = 2.90, p = 0.01$), the difference between the 0 meter and 1

meter speaker displacements did not reach significance ($t(16) = 2.05, p = 0.057$).

Surprisingly, the single beep condition analyzed above had a stronger effect on responses with a 1 meter displacement as compared to 0.5 meters. At 0.5m there was a small, albeit non-significant shift towards a decrease in both the fission and fusion illusion. However, at 1m this shift showed a significant increase in the fusion illusion as compared to the 0.5m condition.

Reaction Time Analysis. Reaction time data was analyzed using an Age (2: Younger, Older) x Flashes (2: 1 flash, 2 flashes) x Beeps (2: 1 beep, 2 beeps) x Speaker Displacement (3: 0m, 0.5m, 1m) mixed analysis of variance. For any effects that violated sphericity Greenhouse-Geisser corrections were used. Original degrees of freedom are reported. There was a significant effect of beeps on reaction time ($F(1,22) = 4.864, p = 0.038$, see Fig. 21). Reaction times for trials with two beeps were greater than those for one beep trials. There was also a significant flashes by beeps interaction ($F(1,22) = 5.012, p = 0.036$). Interestingly, fusion illusion trials showed reaction times nearly 100ms longer than non-illusion congruent trials for both age groups. However, fission illusion trials showed nearly no RT difference in younger individuals, and a small but non-significant difference in older individuals (see Fig. 21). Lastly, a significant effect of age was found ($F(1,22) = 7.421, p = 0.012$). Responses for older individuals were found to be significantly slower than the response times for younger individuals.

Discussion

The results of the response data in the present study provide further support that the sound-induced flash illusion is resistant to differences in spatial disparity. This is not

entirely surprising, as a number of audiovisual illusions have shown a lack of sensitivity to spatial disparity (Jones & Jarick, 2006; Slutsky & Recanzone, 2001). No significant difference in the effect of disparity was found between older or younger individuals in the present study. Both older and younger individuals showed highly significant fusion and fission illusions. Congruent flashes and beeps increased accuracy for both older and younger individuals as well. While older individuals did seem to show some sensitivity to audiovisual disparity this failed to reach significance (see Fig. 19). Additionally, there was a small change in the strength of the illusion at the 0.5m speaker location, but this change was not seen at the 1m speaker location.

The reaction time results indicate an interesting increase in reaction time for fusion illusion trials for both older and younger individuals (see Fig. 21). Fusion illusion trial reaction times were nearly 100ms slower than those for congruent single flash trials. No significant difference in reaction times for fission illusion trials was found. These may suggest that there are separate processes involved for the two illusion types, as a significant increase in processing time was only found for the fusion illusion. Another possibility is that there is more ambiguity in single flash trials where it may have seemed that they missed seeing the second flash. However, for two flash trials this ambiguity would be lessened on trials where both flashes were perceived by the observers. Conversely, the frequency data suggests that this may not be the case (see Fig. 20). Both younger and older observers made more mistakes on flash only trials with two flashes than one. This lends support to the two types of illusions possibly being the result of different processes. Previous research examining the role of intensity on the sound-

induced flash illusion in both younger and older individuals has also found evidence that the two illusions may be the result of two distinct processes (DeLoss & Andersen, 2015).

Overall, the results of the present study suggest that the sound-induced flash illusion is not influenced by spatial disparity. Similar results for spatial disparity were obtained for both younger and older individuals. In addition, the reaction time results suggest that the illusion may be due to separate processes. No significant differences were found with regards to spatial disparity between younger and older individuals for the response data or reaction time data. Whether increased integration in older individuals is the result of declines in multisensory processing will require further study. Future research will also be needed to examine whether fusion and fission illusions are the result of two separate processes.

Tables

Variable	Younger		Older	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Age(years) ¹	23.17	4.26	71.45	3.08
Log Contrast Sensitivity ^{1,2}	1.46	0.13	1.35	0.07
Near LogMAR Acuity	0.11	0.18	0.21	0.14
Far LogMAR Acuity ¹	-0.02	0.12	0.13	0.16
Digit Span Forward	10.67	2.10	9.64	1.86
Digit Span Backwards	6.17	1.53	6.45	1.13
WAIS – Matrix Reasoning	20.58	3.37	14.82	5.44

Table 4. Means and standard deviations of participant demographics and results from cognitive and perceptual tests. Note: ¹ Differences between age groups were significant as indicated by a two-tailed t-test ($p < 0.05$). ² Contrast sensitivity measured using the Pelli Robson Test (Pelli, Robson & Wilkins, 1988).

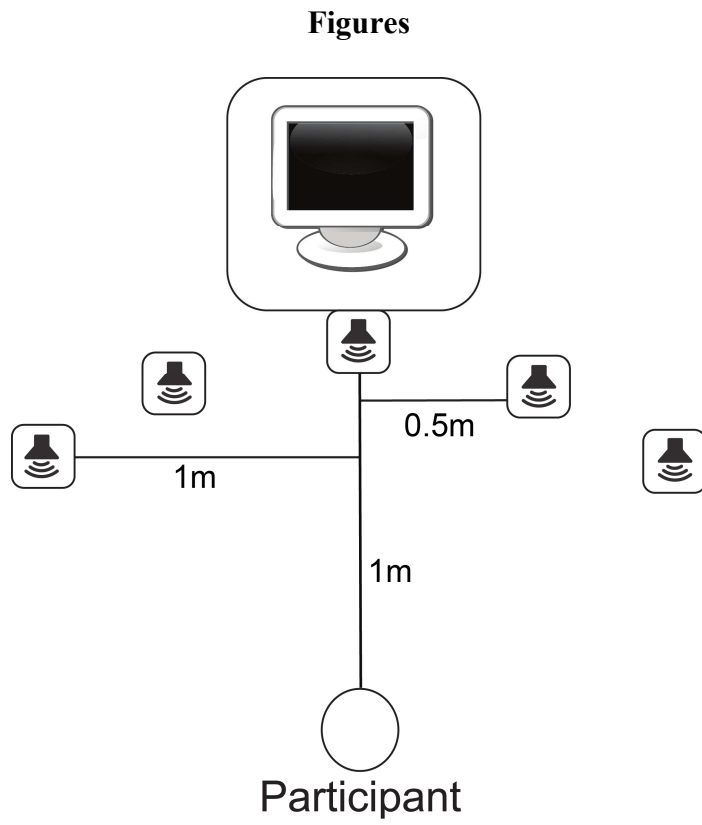


Figure 17. The experimental layout including the participant, monitor and speakers.

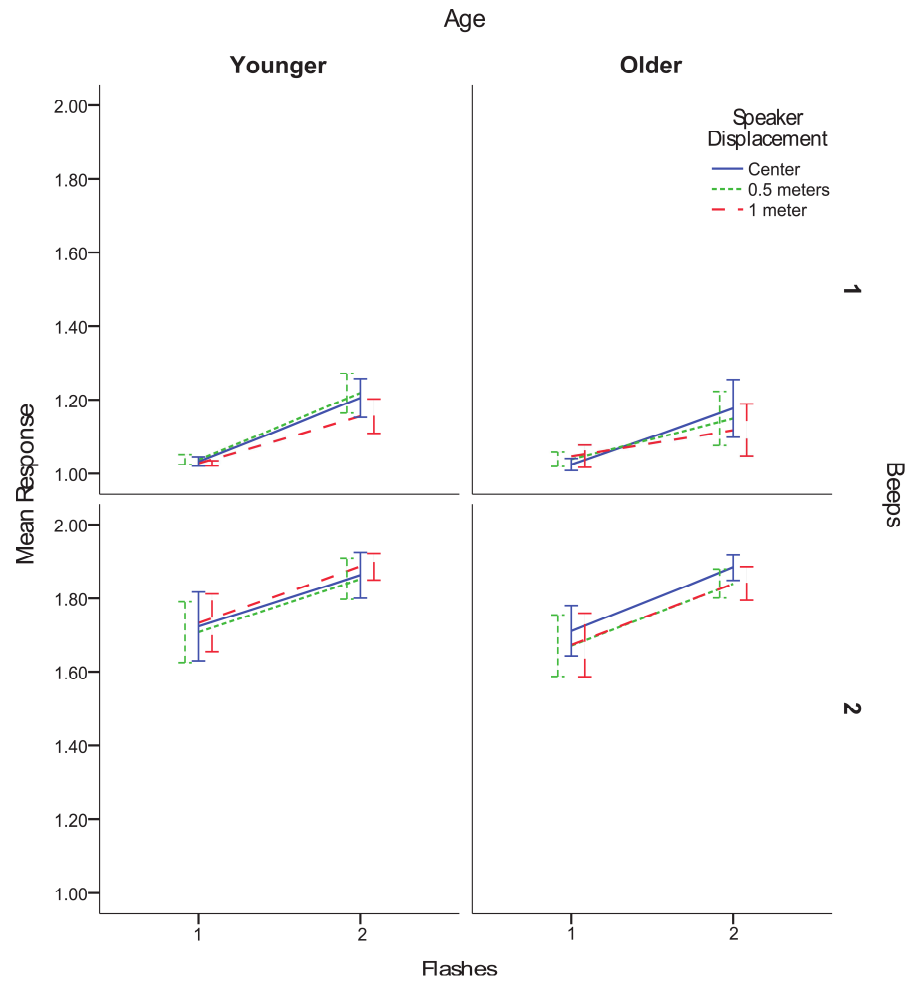


Figure 18. Mean response as indicated by the number of flashes, number of beeps, age, and speaker displacement. Error bars indicate ± 1 standard error of the mean.

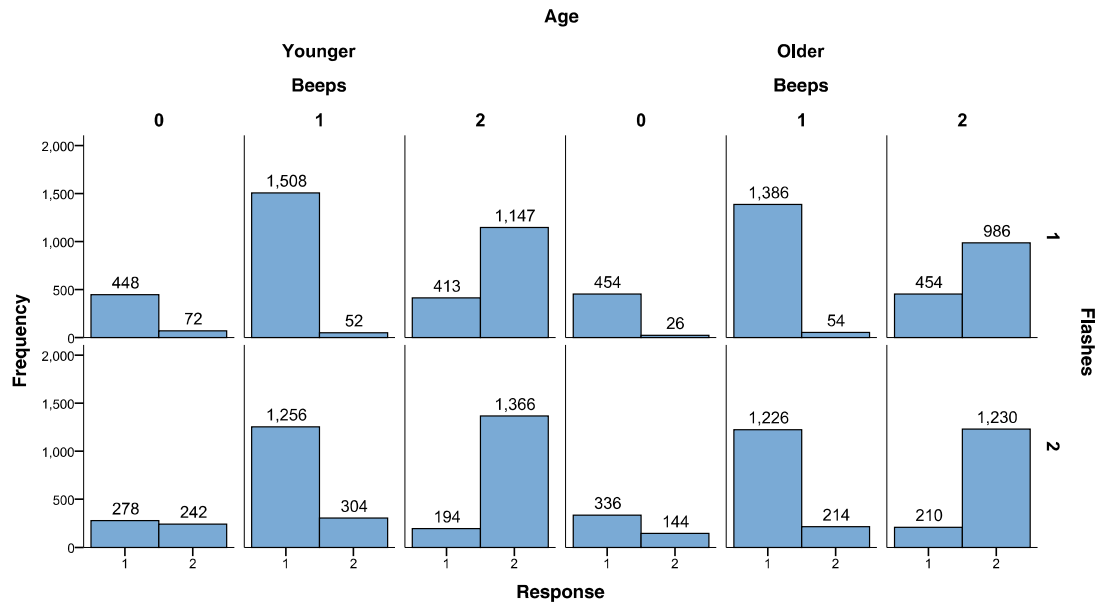


Figure 19. Response frequency as indicated by age, the number of flashes, and the number of beeps. Error bars indicated ± 1 standard error of the mean.

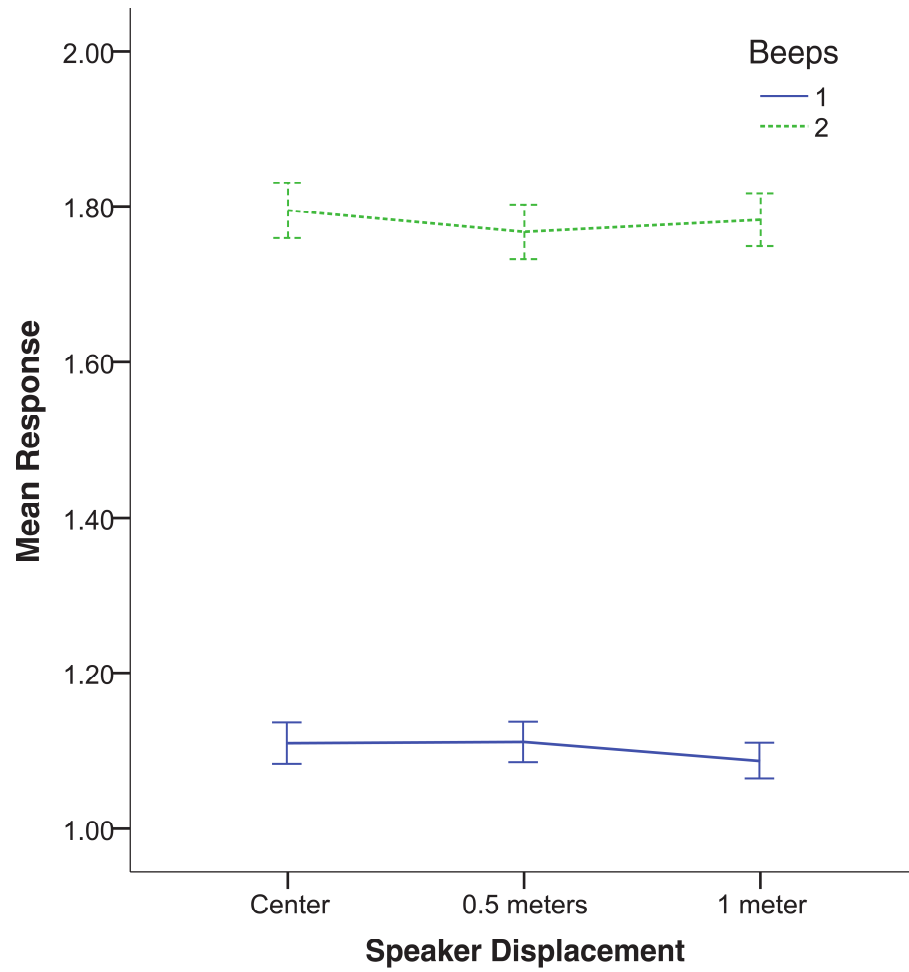


Figure 20. Mean response as indicated by speaker displacement and number of beeps.

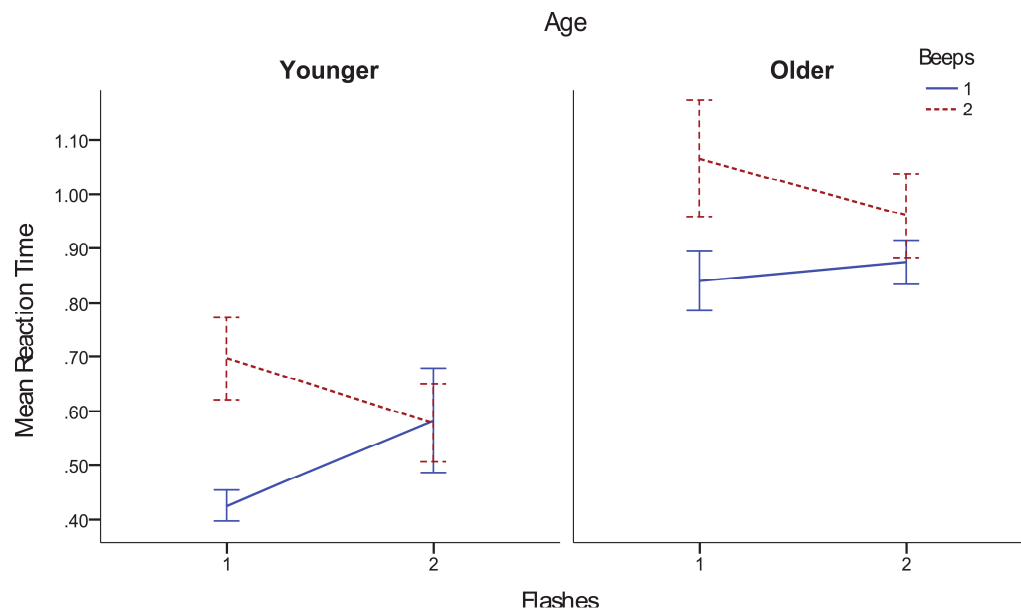


Figure 21. Reaction times as indicated by age, number of flashes, and number of beeps.

Error bars indicate ± 1 standard error of the mean.

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General Discussion

The goal of these studies was to examine age-related differences in multisensory integration with age. Multisensory integration has been broadly studied in younger college-aged populations. The present studies were designed to increase our understanding of how multisensory integration differs between younger and older individuals. Improving our understanding of multisensory integration in older subjects could help advance research in a number of ways. It is currently estimated that by 2025 fatalities in older drivers will nearly triple compared to those in 1995 (Hu, Reuscher, Schmoyer Jr., & Truett, 2000). Multisensory warning signals for collision avoidance while driving have been shown to be extremely promising in alerting drivers to impending collisions (Ho, Reed, & Spence, 2007a; Spence & Ho, 2008). Increased knowledge of how multisensory integration differs between younger and older individuals will help to develop appropriate multisensory warning signals. Recent research has also shown that computer-based behavioral training can improve eyesight in older individuals (DeLoss, Watanabe, & Andersen, 2015). The type of training used in this research can be accelerated through the use of multisensory stimuli (Seitz, Kim, & Shams, 2006). An improved understanding of multisensory integration in older individuals could increase the rate of learning in these behavioral interventions being used to improve sensory processing in the aging population.

The present study examined 4 hypotheses examined age-related differences in multisensory integration, attention, stimulus intensity, and spatial disparity. Hypothesis 1

examines a difference in the influence of congruent multisensory information on judgments made by older and younger individuals.

Hypothesis 1. Older individuals as compared to younger individuals will demonstrate greater benefits for multisensory as compared to unisensory stimuli.

This hypothesis was examined in Chapter 1. In Chapter 1, an analysis was conducted examining accuracy for unimodal trials versus multisensory trials that included a congruent number of flashes and beeps. This analysis was conducted by comparing the unisensory block that consisted solely of unimodal flashes to the congruent multisensory trials within the multisensory block which consisted of both flashes and beeps. The results of the analysis showed a significant increase in accuracy when congruent multisensory information was present, $F(1, 22) = 627.67$, $MSE = 41.004$, $p < 0.001$. A significant interaction between congruency and age was also found, $F(2, 44) = 7.12$, $MSE = 0.18$, $p = 0.002$. Older individuals were found to benefit to a greater degree when congruent multisensory information was presented as compared to unimodal flashes. The results of this study are consistent with Prediction 1, older individuals did show a greater improvement in performance when congruent multisensory information was present.

Experiment 1 in Chapter 1 demonstrated that older individuals show increased multisensory integration as assessed by the sound-induced flash illusion. Older individuals also show improved accuracy for congruent multisensory trials as compared to unimodal stimulus presentation. This is important for developing future technologies, such as collision avoidance systems where high accuracy and speeded reaction times are of importance. While previous research has shown improved performance for audiotactile

multisensory warning systems (Ho, Reed, & Spence, 2007b), and multisensory warning signals have been suggested as a possible aid for older drivers (Spence & Ho, 2008), no study to date has examined their use. The present study provides evidence that older individuals can integrate multisensory audiovisual information, and in fact show greater integration than younger individuals. This provides further support for the investigation of multisensory warning signals as an aid for older individuals, as well as the possible inclusion of a visual warning to aid the driver in the detecting of impending hazards.

The second hypothesis involves age-related differences in inhibitory control for task-irrelevant cross-modal information.

Hypothesis 2. Older individuals have decreased inhibitory control for cross-modal task-irrelevant information. Older individuals will exhibit smaller changes when making a task-irrelevant crossmodal stimulus task-relevant.

This hypothesis was tested in Experiment 2 of Chapter 1. To examine whether older individuals demonstrate a smaller change in performance in the illusion a go/no-go task was included along with the same experimental methods used to examine the sound-induced flash illusion and aging in Experiment 1 of Chapter 1. By making the visual and auditory stimuli task-relevant on certain trials it was possible to examine whether attentional differences in inhibitory control may explain the differences between older and younger observers seen in Experiment 1.

The results of Experiment 2 of Chapter 1 confirmed the age-related difference in integration found in Experiment 1 as indicated by a significant interaction between age and the number of beeps presented, $F(2,92) = 9.42$, $MSE = 7.65$, $p = 0.002$. The presence

of the go/no-go task in the visual or auditory modality was also found to influence the strength of the illusion as indicated by a significant interaction between the modality of the go/no-go cue and the number of beeps presented, $F(4, 184) = 3.57$, $MSE = 0.18$, $p = 0.02$. The presence of the go/no-go task in the auditory modality was found to result in a significantly stronger illusion than in the visual modality as indicated by a change in slope of the illusion, $F(2, 46) = 8.41$, $p = 0.006$. However, an interaction between the modality of the attentional manipulation and age was not significant, $F(2, 92) = 1.05$, $MSE = 0.10$, $p = 0.354$, nor was interaction of modality of the go/no-go cue and age examining the change in slope, $F(1, 46) = 0.41$, $p = 0.53$. These results are contrary to Prediction 2 and the expected results presented in the introduction, suggesting that attentional factors are fail to provide evidence for age-related differences in integration as assessed using the sound-induced flash illusion.

The findings from Experiment 2 of Chapter 1 also demonstrated increased integration in older individuals. However, previous research has shown decreased inhibitory control in older individuals (Alain & Woods, 1999; Sweeney et al., 2001). Decreased inhibition of the auditory beeps during the sound-induced flash illusion could be a possible explanation for increased integration in older adults. However, older and younger adults showed no difference in the change in strength of the illusion when required to attend to the visual or auditory modality in blocks containing the go/no-go task. Older individuals also showed no difference in accuracy for the go/no-go task, which could have possibly influenced the interpretation of these results. For these

reasons, it is concluded that increased integration in older adults is not due to changes in inhibitory control.

Hypothesis 3 suggests that age-related differences on differing stimulus strengths are influenced by increased internal noise.

Hypothesis 3. Older individuals have greater levels of internal noise, which will degrade weak signals, such as low brightness or low contrast stimuli, to a greater degree as compared to strong signals.

This hypothesis was examined in Chapter 2. To determine whether changes in internal noise may result in age-related changes in integration with differing stimulus strengths a study was conducted that examined the sound-induced flash illusion at multiple stimulus strengths. The study initially measured both younger and older participants' visual and auditory detection thresholds at their 70%, 82% and 94% correct levels. While unimodal performance was matched across age groups, multisensory processing would still be subject to increased internal noise. The sound-induced flash illusion was then presented at all possible combinations of these visual and auditory stimulus strengths to examine age-related differences in the strength of the illusion for different stimulus strength values. It also examined age-related changes in the role of stimulus strength on the flash-induced beep illusion, in which the number of flashes presented influences the perceived number of beeps, or the flash-induced beep illusion.

The results of the experiment conducted in Chapter 2, for the standard sound-induced flash illusion, demonstrated a significant interaction between the stimulus strength of the visual flashes, the number of beeps presented and age, $F(1, 20) = 15.67$,

$MSE = 7.00, p = 0.001$. Older individuals showed the strongest illusion in the lowest flash strength condition. The strength of the beeps was also found to influence the illusion as indicated by a beep strength by beeps interaction, $F(2, 40) = 12.91, MSE = 0.19, p < 0.001$, with the strength of the illusion increasing with decreased beep strength, as would be expected based on inverse effectiveness. No significant interaction between age and beep strength was found.

Contrasting the results for the sound-induced flash illusion, the flash-induced beep illusion, in which participants attended to and reported the number of beeps presented, showed a significant influence of stimulus strength on the illusion as indicated by an interaction between auditory stimulus strength and the number of beeps, $F(2, 40) = 57.27, MSE = 1.74, p < 0.001$. This was also supported by an interaction between the visual stimulus strength, the auditory stimulus strength, and the number of beeps, $F(4, 80) = 2.89, MSE = 0.02, p = 0.027$. Most importantly an interaction between the strength of the flashes, the strength of the beeps, the number of beeps, and age was also found, $F(4, 80) = 2.84, MSE = 0.02, p = 0.029$. The results from both forms of the illusion partially support Prediction 3, as there was a significant age-related difference in the strength of the illusion with a change in stimulus strength. However, with increased stimulus strength older individuals showed a smaller change in inverse effectiveness than younger individuals.

While the findings of Chapter 2 for the sound-induced flash illusion failed to show any significant age-related change in the strength of the illusion at decreased stimulus intensity, the flash-induced beep illusion did show evidence of increased inverse

effectiveness. The difficulty of stimulus detection was equal for both younger and older individuals, so a secondary factor must be influencing inverse effectiveness. The increased multisensory integration in older individuals at lower stimulus strengths may be due to increased internal noise, as inverse effectiveness would indicate an increase in integration as stimulus strength is decreased by internal noise. Previous research has examined internal noise through the manipulation of stimulus contrast in an orientation discrimination task at varying levels of external noise (Lisa R. Betts et al., 2007). To determine whether this increased inverse effectiveness is due to increased internal noise future research should measure internal noise in older individuals and examine whether the level of internal noise is correlated with an increase in inverse effectiveness.

Hypothesis 4 concerns age-related differences in spatial factors on multisensory integration.

Hypothesis 4. Older individuals as compared to younger individuals will exhibit age-related declines in recovering multisensory spatial information.

This hypothesis was examined in Chapter 3. To examine whether age-related differences exist in the recovery of multisensory information a study examining the role of spatial disparity on the sound-induced flash illusion was conducted. A sound-induced flash illusion paradigm was implemented with five speakers positioned equidistant from the participant. One speaker was placed directly under the visual flash source, two speakers were placed 0.5m to the left/right of the flash source, and two speakers were placed 1m to the left/right of the flash source. An equal number of trials were run for all possible combinations of number of flashes, number of beeps and single auditory source.

The results of the experiment indicated a small effect of spatial disparity. Spatial disparity was collapsed into the 3 horizontal distances from the flash source, as laterality was not found to significantly influence the illusion. An interaction between beeps and speaker displacement was found, $F(2,44) = 3.36, p = .044$. Trials with a single beep were found to be significantly influenced by speaker displacement, $F(2,32) = 4.268, p = .023$. This difference was found to be the result of a difference in the strength of the illusion between the 0.5m and 1m speaker displacements, $t(16) = 2.90, p = 0.01$. This change in the strength of the illusion at these locations was quite small, on the order of a change of 1 in 20 trials, providing further support that there is relatively little change in the strength of the illusion with increased spatial disparity. In addition, an analysis of reaction times showed a significant increase in reaction times for fusion trials, $F(1,22) = 5.012, p = 0.036$. Fusion trials increased reaction times by nearly 100ms for both older and younger participants. Older individuals were found to have significantly longer reaction times than younger individuals, as older individuals typically have increased reaction times when compared to younger individuals. The results from this study does not support Prediction 4, as older individuals were not shown to differ from younger individuals with increases in spatial disparity.

While spatial disparity was not found to greatly influence the strength of the illusion or cause a significant increase in reaction times, other experimental methods may still reveal a difference in processing of spatially congruent as compared to spatially incongruent flashes and beeps. Recent research has shown that spatially disparate trials may not show any significant difference in reaction times as compared to spatially

congruent trials in a visual-somatosensory task (Mahoney et al., 2015). However, they did find, using event-related potentials, a significant change in how early the multisensory effects on processing could be detected. Multisensory stimuli showed the same decrease in reaction time as compared to unisensory stimuli independent of spatial disparity, but the disparity was found to alter processing in sensory cortex. The present study may not have shown changes in the strength of the illusion, or reaction times for spatially disparate stimuli for younger or older participants, but changes in neural processing may be present. Future research on the effects of spatial disparity on age-related changes in multisensory integration should include electroencephalography to examine whether processing of spatially congruent as compared to disparate multisensory stimuli differ between younger and older individuals.

Overall, the findings presented here demonstrate that older individuals show increased integration in the sound-induced flash illusion. This increased integration was not found to be caused by differences in attention. Though, forcing participants to attend to the visual or auditory domain using a go/no-go task was found to influence the strength of the illusion, but this did not differ by age. Older individuals were also shown to exhibit increased behavioral inverse effectiveness, but this was only found for the flash-induced beep illusion. While both age groups showed inverse effectiveness in the sound-induced flash illusion, this was not found to differ by age. Lastly, the influence of spatial disparity on the sound-induced flash illusion was not found to differ by age.

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Appendix A

Cell Means for Experimental Data

Chapter 1

Experiment 1

Older	Mean	SD
Beep Only	2.022	0.812
1 Beep	1.016	0.013
2 Beeps	2.091	0.196
3 Beeps	2.957	0.059
Flash Only	1.911	0.685
1 Flash	1.138	0.242
2 Flashes	1.890	0.220
3 Flashes	2.704	0.222
Multisensory	1.912	0.612
1 Flash	1.524	0.538
1 Beep	1.077	0.121
2 Beeps	1.770	0.236
3 Beeps	2.144	0.510
No Beeps	1.103	0.096
2 Flashes	1.869	0.549
1 Beep	1.210	0.207
2 Beeps	2.058	0.174
3 Beeps	2.548	0.293
No Beeps	1.660	0.259
3 Flashes	2.343	0.452
1 Beep	1.845	0.403
2 Beeps	2.289	0.266
3 Beeps	2.812	0.182
No Beeps	2.425	0.293

Chapter 1 Continued

Younger	Mean	SD
Beep Only	2.013	0.771
No Flashes	2.013	0.771
1 Beep	1.076	0.183
2 Beeps	2.052	0.129
3 Beeps	2.910	0.091
Flash Only	2.024	0.649
1 Flash	1.224	0.285
2 Flashes	2.173	0.164
3 Flashes	2.675	0.220
Multisensory	2.010	0.561
1 Flash	1.508	0.504
1 Beep	1.166	0.273
2 Beeps	1.764	0.385
3 Beeps	1.88	0.572
No Beeps	1.223	0.314
2 Flashes	2.072	0.386
1 Beep	1.646	0.332
2 Beeps	2.103	0.212
3 Beeps	2.478	0.255
No Beeps	2.06	0.194
3 Flashes	2.450	0.308
1 Beep	2.273	0.312
2 Beeps	2.256	0.216
3 Beeps	2.746	0.183
No Beeps	2.526	0.229

Chapter 1 Continued

Experiment 2

Older	Mean	SD
Auditory Go/No-Go		
Condition	1.970	0.733
1 Flash	1.473	0.672
1 Beep	1.029	0.092
2 Beeps	1.731	0.620
3 Beeps	2.087	0.789
No Beeps	1.043	0.098
2 Flashes	1.950	0.614
1 Beep	1.291	0.330
2 Beeps	2.161	0.367
3 Beeps	2.571	0.400
No Beeps	1.775	0.477
3 Flashes	2.488	0.529
1 Beep	1.937	0.644
2 Beeps	2.492	0.317
3 Beeps	2.908	0.092
No Beeps	2.615	0.359
No Attentional Control	1.914	0.696
1 Flash	1.377	0.507
1 Beep	1.061	0.152
2 Beeps	1.528	0.405
3 Beeps	1.862	0.623
No Beeps	1.058	0.141
2 Flashes	1.882	0.600
1 Beep	1.224	0.309
2 Beeps	2.164	0.336
3 Beeps	2.473	0.482
No Beeps	1.666	0.327
3 Flashes	2.484	0.481
1 Beep	1.996	0.602
2 Beeps	2.454	0.309
3 Beeps	2.848	0.152
No Beeps	2.637	0.272

Chapter 1 Continued

Older	Mean	SD
Visual Go/No-Go Condition	1.893	0.696
1 Flash	1.375	0.584
1 Beep	1.031	0.059
2 Beeps	1.582	0.582
3 Beeps	1.855	0.743
No Beeps	1.032	0.063
2 Flashes	1.861	0.567
1 Beep	1.326	0.334
2 Beeps	2.138	0.364
3 Beeps	2.315	0.593
No Beeps	1.664	0.332
3 Flashes	2.443	0.479
1 Beep	1.996	0.586
2 Beeps	2.460	0.306
3 Beeps	2.828	0.148
No Beeps	2.487	0.374

Younger	Mean	SD
Auditory Go/No-Go Condition	1.979	0.656
1 Flash	1.326	0.379
1 Beep	1.059	0.067
2 Beeps	1.534	0.310
3 Beeps	1.643	0.445
No Beeps	1.066	0.084
2 Flashes	2.048	0.445
1 Beep	1.653	0.474
2 Beeps	2.067	0.245
3 Beeps	2.458	0.268
No Beeps	2.016	0.367
3 Flashes	2.564	0.421
1 Beep	2.317	0.576
2 Beeps	2.435	0.346
3 Beeps	2.823	0.142

No Beeps	2.68	0.335
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Chapter 1 Continued

Younger	Mean	SD
No Attentional Control	1.974	0.675
1 Flash	1.283	0.371
1 Beep	1.094	0.098
2 Beeps	1.415	0.258
3 Beeps	1.551	0.560
No Beeps	1.073	0.114
2 Flashes	2.043	0.491
1 Beep	1.63	0.490
2 Beeps	2.073	0.307
3 Beeps	2.42	0.410
No Beeps	2.05	0.432
3 Flashes	2.595	0.351
1 Beep	2.416	0.453
2 Beeps	2.436	0.306
3 Beeps	2.816	0.189
No Beeps	2.71	0.252
Visual Go/No-Go Condition	1.963	0.625
1 Flash	1.339	0.391
1 Beep	1.126	0.180
2 Beeps	1.491	0.342
3 Beeps	1.613	0.510
No Beeps	1.124	0.189
2 Flashes	2.038	0.452
1 Beep	1.640	0.433
2 Beeps	2.064	0.210
3 Beeps	2.408	0.375
No Beeps	2.039	0.421
3 Flashes	2.514	0.345
1 Beep	2.378	0.432
2 Beeps	2.376	0.299
3 Beeps	2.721	0.227
No Beeps	2.580	0.298

Chapter 2

Sound-Induced Flash Illusion

Older	Mean	SD
70% Visual Threshold	1.508	0.367
70% Auditory Threshold	1.491	0.388
1 Flash	1.162	0.189
1 Beep	1.115	0.115
2 Beeps	1.21	0.240
2 Flashes	1.82	0.214
1 Beep	1.725	0.245
2 Beeps	1.915	0.131
82% Auditory Threshold	1.505	0.359
1 Flash	1.205	0.187
1 Beep	1.125	0.111
2 Beeps	1.285	0.217
2 Flashes	1.805	0.201
1 Beep	1.745	0.253
2 Beeps	1.865	0.117
94% Auditory Threshold	1.517	0.353
1 Flash	1.242	0.221
1 Beep	1.12	0.135
2 Beeps	1.365	0.228
2 Flashes	1.792	0.218
1 Beep	1.695	0.238
2 Beeps	1.89	0.150
No Beeps	1.532	0.393
1 Flash	1.21	0.280
2 Flashes	1.855	0.130
82% Visual Threshold	1.505	0.371
70% Auditory Threshold	1.498	0.361
1 Flash	1.21	0.222
1 Beep	1.11	0.114
2 Beeps	1.31	0.262
2 Flashes	1.787	0.207
1 Beep	1.71	0.254
2 Beeps	1.865	0.113

Chapter 2 Continued

Older	Mean	SD
82% Auditory Threshold	1.506	0.377
1 Flash	1.192	0.226
1 Beep	1.09	0.084
2 Beeps	1.295	0.278
2 Flashes	1.82	0.185
1 Beep	1.77	0.226
2 Beeps	1.87	0.127
94% Auditory Threshold	1.515	0.378
1 Flash	1.222	0.226
1 Beep	1.085	0.100
2 Beeps	1.36	0.237
2 Flashes	1.807	0.248
1 Beep	1.675	0.290
2 Beeps	1.94	0.084
No Beeps	1.497	0.390
1 Flash	1.175	0.271
2 Flashes	1.82	0.133
94% Visual Threshold	1.499	0.366
70% Auditory Threshold	1.491	0.363
1 Flash	1.185	0.173
1 Beep	1.115	0.137
2 Beeps	1.255	0.183
2 Flashes	1.797	0.207
1 Beep	1.715	0.238
2 Beeps	1.88	0.137
82% Auditory Threshold	1.492	0.368
1 Flash	1.185	0.209
1 Beep	1.125	0.095
2 Beeps	1.245	0.275
2 Flashes	1.8	0.188
1 Beep	1.725	0.227
2 Beeps	1.875	0.103

Chapter 2 Continued

Older	Mean	SD
94% Auditory Threshold	1.497	0.376
1 Flash	1.22	0.246
1 Beep	1.075	0.088
2 Beeps	1.365	0.271
2 Flashes	1.775	0.260
1 Beep	1.645	0.305
2 Beeps	1.905	0.111
No Beeps	1.532	0.372
1 Flash	1.215	0.246
2 Flashes	1.85	0.088

Younger	Mean	SD
70% Visual Threshold	1.500	0.391
70% Auditory Threshold	1.502	0.416
1 Flash	1.158	0.242
1 Beep	1.116	0.174
2 Beeps	1.2	0.297
2 Flashes	1.845	0.220
1 Beep	1.762	0.280
2 Beeps	1.929	0.089
82% Auditory Threshold	1.510	0.379
1 Flash	1.210	0.230
1 Beep	1.083	0.068
2 Beeps	1.337	0.266
2 Flashes	1.810	0.229
1 Beep	1.725	0.272
2 Beeps	1.895	0.142

Chapter 2 Continued

Younger	Mean	SD
94% Auditory Threshold	1.514	0.378
1 Flash	1.229	0.239
1 Beep	1.095	0.128
2 Beeps	1.362	0.255
2 Flashes	1.8	0.254
1 Beep	1.65	0.286
2 Beeps	1.95	0.067
No Beeps	1.45	0.411
1 Flash	1.079	0.072
2 Flashes	1.820	0.222
82% Visual Threshold	1.497	0.389
70% Auditory Threshold	1.495	0.385
1 Flash	1.183	0.201
1 Beep	1.116	0.083
2 Beeps	1.25	0.261
2 Flashes	1.808	0.243
1 Beep	1.725	0.306
2 Beeps	1.891	0.124
82% Auditory Threshold	1.522	0.379
1 Flash	1.212	0.223
1 Beep	1.129	0.105
2 Beeps	1.295	0.279
2 Flashes	1.833	0.209
1 Beep	1.75	0.251
2 Beeps	1.916	0.117
94% Auditory Threshold	1.483	0.409
1 Flash	1.154	0.220
1 Beep	1.05	0.060
2 Beeps	1.258	0.272
2 Flashes	1.812	0.260
1 Beep	1.704	0.315
2 Beeps	1.920	0.132
No Beeps	1.481	0.394
1 Flash	1.120	0.125
2 Flashes	1.841	0.160

Chapter 2 Continued

Younger	Mean	SD
94% Visual Threshold	1.489	0.395
70% Auditory Threshold	1.484	0.398
1 Flash	1.162	0.212
1 Beep	1.108	0.106
2 Beeps	1.216	0.277
2 Flashes	1.806	0.250
1 Beep	1.725	0.299
2 Beeps	1.887	0.165
82% Auditory Threshold	1.489	0.397
1 Flash	1.183	0.229
1 Beep	1.095	0.107
2 Beeps	1.270	0.285
2 Flashes	1.795	0.273
1 Beep	1.666	0.331
2 Beeps	1.925	0.101
94% Auditory Threshold	1.505	0.393
1 Flash	1.2	0.231
1 Beep	1.1	0.126
2 Beeps	1.3	0.272
2 Flashes	1.810	0.260
1 Beep	1.679	0.308
2 Beeps	1.941	0.097
No Beeps	1.470	0.412
1 Flash	1.116	0.119
2 Flashes	1.825	0.260

Chapter 2 Continued

Flash-Induced Beep Illusion

Older	Mean	SD
70% Auditory Threshold	1.310064935	0.308505774
1 Beep	1.114285714	0.120267559
70% Visual Threshold	1.106818182	0.103849083
1 Flash	1.081818182	0.084477001
2 Flashes	1.131818182	0.118896441
82% Visual Threshold	1.120454545	0.115118046
1 Flash	1.095454545	0.110576999
2 Flashes	1.145454545	0.119278132
94% Visual Threshold	1.143181818	0.157582521
1 Flash	1.081818182	0.090201794
2 Flashes	1.204545455	0.189016594
No Flashes	1.059090909	0.043693145
2 Beeps	1.505844156	0.315391781
70% Visual Threshold	1.463636364	0.322631228
1 Flash	1.468181818	0.322701664
2 Flashes	1.459090909	0.338244129
82% Visual Threshold	1.495454545	0.300756622
1 Flash	1.454545455	0.311812881
2 Flashes	1.536363636	0.29840485
94% Visual Threshold	1.579545455	0.30615087
1 Flash	1.531818182	0.336357494
2 Flashes	1.627272727	0.280502795
No Flashes	1.463636364	0.364067926
82% Auditory Threshold	1.381493506	0.315293789
1 Beep	1.135064935	0.124357542
70% Visual Threshold	1.115909091	0.10621896
1 Flash	1.095454545	0.061051394
2 Flashes	1.136363636	0.13800527
82% Visual Threshold	1.131818182	0.109702471
1 Flash	1.086363636	0.077752521
2 Flashes	1.177272727	0.121168553

Chapter 2 Continued

Older	Mean	SD
94% Visual Threshold	1.190909091	0.155560709
1 Flash	1.136363636	0.083937206
2 Flashes	1.245454545	0.192943704
No Flashes	1.068181818	0.071668428
2 Beeps	1.627922078	0.248216468
70% Visual Threshold	1.604545455	0.235487888
1 Flash	1.586363636	0.24196168
2 Flashes	1.622727273	0.239127201
82% Visual Threshold	1.638636364	0.256780348
1 Flash	1.590909091	0.28090762
2 Flashes	1.686363636	0.233549683
94% Visual Threshold	1.670454545	0.231793777
1 Flash	1.609090909	0.228930319
2 Flashes	1.731818182	0.228333886
No Flashes	1.568181818	0.301887998
94% Auditory Threshold	1.455194805	0.372246704
1 Beep	1.12987013	0.149617877
70% Visual Threshold	1.072727273	0.099674796
1 Flash	1.077272727	0.116969304
2 Flashes	1.068181818	0.084477001
82% Visual Threshold	1.179545455	0.16231883
1 Flash	1.118181818	0.125045446
2 Flashes	1.240909091	0.177226101
94% Visual Threshold	1.168181818	0.179646117
1 Flash	1.113636364	0.148477118
2 Flashes	1.222727273	0.197943977
No Flashes	1.068181818	0.078334945
2 Beeps	1.780519481	0.205220652
70% Visual Threshold	1.795454545	0.214869335
1 Flash	1.781818182	0.235873618
2 Flashes	1.809090909	0.202259959
82% Visual Threshold	1.784090909	0.194805375
1 Flash	1.745454545	0.226334427
2 Flashes	1.822727273	0.158687801

Chapter 2 Continued

Older	Mean	SD
94% Visual Threshold	1.779545455	0.19497197
1 Flash	1.763636364	0.220330331
2 Flashes	1.795454545	0.175291964
No Flashes	1.745454545	0.248449739

Younger	Mean	SD
70% Auditory Threshold	1.384340659	0.284720187
1 Beep	1.148351648	0.114855114
70% Visual Threshold	1.130769231	0.103030989
1 Flash	1.111538462	0.112089708
2 Flashes	1.15	0.093541435
82% Visual Threshold	1.153846154	0.131090104
1 Flash	1.138461538	0.093883452
2 Flashes	1.169230769	0.162709431
94% Visual Threshold	1.161538462	0.102281662
1 Flash	1.115384615	0.080064077
2 Flashes	1.207692308	0.103774904
No Flashes	1.146153846	0.134569589
2 Beeps	1.62032967	0.192927451
70% Visual Threshold	1.609615385	0.18655789
1 Flash	1.607692308	0.193483584
2 Flashes	1.611538462	0.187254112
82% Visual Threshold	1.619230769	0.193430568
1 Flash	1.588461538	0.217134603
2 Flashes	1.65	0.16955825
94% Visual Threshold	1.615384615	0.218983666
1 Flash	1.561538462	0.227443991
2 Flashes	1.669230769	0.204672972
No Flashes	1.653846154	0.165153386

Chapter 2 Continued

Younger	Mean	SD
82% Auditory Threshold	1.484065934	0.397879679
1 Beep	1.104945055	0.096048294
70% Visual Threshold	1.1	0.083666003
1 Flash	1.084615385	0.077418278
2 Flashes	1.115384615	0.089871703
82% Visual Threshold	1.088461538	0.091986621
1 Flash	1.069230769	0.094733093
2 Flashes	1.107692308	0.088614695
94% Visual Threshold	1.113461538	0.106355717
1 Flash	1.092307692	0.11336915
2 Flashes	1.134615385	0.098709623
No Flashes	1.130769231	0.109045979
2 Beeps	1.863186813	0.135981037
70% Visual Threshold	1.851923077	0.122049801
1 Flash	1.819230769	0.123387029
2 Flashes	1.884615385	0.116161912
82% Visual Threshold	1.880769231	0.133474284
1 Flash	1.85	0.170782513
2 Flashes	1.911538462	0.076794765
94% Visual Threshold	1.855769231	0.147191659
1 Flash	1.826923077	0.187766904
2 Flashes	1.884615385	0.089871703
No Flashes	1.865384615	0.155970905
94% Auditory Threshold	1.49532967	0.429335412
1 Beep	1.078021978	0.082397678
70% Visual Threshold	1.075	0.071063352
1 Flash	1.065384615	0.068873723
2 Flashes	1.084615385	0.074678799
82% Visual Threshold	1.067307692	0.059903769
1 Flash	1.05	0.045643546
2 Flashes	1.084615385	0.068873723

Chapter 2 Continued

Younger	Mean	SD
94% Visual Threshold	1.1	0.106770783
1 Flash	1.065384615	0.068873723
2 Flashes	1.134615385	0.128102523
No Flashes	1.061538462	0.086971849
2 Beeps	1.912637363	0.108421351
70% Visual Threshold	1.9	0.121655251
1 Flash	1.880769231	0.157504579
2 Flashes	1.919230769	0.072279727
82% Visual Threshold	1.909615385	0.090575086
1 Flash	1.896153846	0.10095696
2 Flashes	1.923076923	0.080662322
94% Visual Threshold	1.932692308	0.090490118
1 Flash	1.938461538	0.098221362
2 Flashes	1.926923077	0.085672304
No Flashes	1.903846154	0.147847808

Chapter 3

Response Data

Older	Mean	SD
Center	1.358	0.479
1 Flash	1.263	0.440
No Beeps	1.054	0.226
1 Beep	1.025	0.156
2 Beeps	1.710	0.454
2 Flashes	1.453	0.498
No Beeps	1.3	0.458
1 Beep	1.177	0.382
2 Beeps	1.883	0.321
1m	1.419	0.493
1 Flash	1.360	0.480
1 Beep	1.047	0.213
2 Beeps	1.672	0.469
2 Flashes	1.479	0.499
1 Beep	1.118	0.323
2 Beeps	1.839	0.367
0.5m	1.425	0.494
1 Flash	1.355	0.478
1 Beep	1.039	0.195
2 Beeps	1.670	0.470
2 Flashes	1.494	0.500
1 Beep	1.15	0.357
2 Beeps	1.839	0.367

Chapter 3 Continued

Younger	Mean	SD
Center	1.409	0.491
1 Flash	1.303	0.459
No Beeps	1.138	0.345
1 Beep	1.032	0.178
2 Beeps	1.738	0.439
2 Flashes	1.515	0.499
No Beeps	1.465	0.499
1 Beep	1.207	0.406
2 Beeps	1.873	0.333
1m	1.455	0.498
1 Flash	1.385	0.486
1 Beep	1.028	0.167
2 Beeps	1.742	0.437
2 Flashes	1.525	0.499
1 Beep	1.159	0.366
2 Beeps	1.892	0.310
0.5m	1.460	0.498
1 Flash	1.381	0.486
1 Beep	1.038	0.192
2 Beeps	1.725	0.446
2 Flashes	1.539	0.498
1 Beep	1.217	0.412
2 Beeps	1.861	0.345

Chapter 3 Continued

Reaction Time Data

Older	Mean	SD
0.5m	0.942253021	1.099933282
1 Flash	0.976721563	1.1975752
1 Beep	0.876923125	0.933003561
2 Beeps	1.07652	1.407448102
2 Flashes	0.907784479	0.992170867
1 Beep	0.856776042	0.911057366
2 Beeps	0.958792917	1.06565523
1m	0.930673229	1.097037688
1 Flash	0.937759792	1.145181592
1 Beep	0.784137917	0.590015217
2 Beeps	1.091381667	1.49338668
2 Flashes	0.923586667	1.047232974
1 Beep	0.862942708	1.002703285
2 Beeps	0.984230625	1.087611486
Center	0.921127986	0.97321465
1 Flash	0.920567153	1.011161295
1 Beep	0.86095625	0.857738221
2 Beeps	1.029278542	1.336690492
No Beeps	0.871466667	0.728927052
2 Flashes	0.921688819	0.93407918
1 Beep	0.904310417	0.972587855
2 Beeps	0.938215417	0.973270499
No Beeps	0.922540625	0.852874611

Chapter 3 Continued

Younger	0.57059717	2.369585055
0.5m	0.671503317	3.066623437
1 Flash	0.710006058	3.108905017
1 Beep	0.469168077	1.014417491
2 Beeps	0.950844038	4.266606554
2 Flashes	0.633000577	3.024756454
1 Beep	0.521570385	0.986604011
2 Beeps	0.744430769	4.16144962
1m	0.574982933	2.915455107
1 Flash	0.541612885	1.975743261
1 Beep	0.434670962	0.785943722
2 Beeps	0.648554808	2.678436003
2 Flashes	0.608352981	3.619688811
1 Beep	0.666408654	5.02575922
2 Beeps	0.550297308	0.982104638
Center	0.500402564	1.076129381
1 Flash	0.486838846	1.028865647
1 Beep	0.383370385	0.484238653
2 Beeps	0.594777692	1.369544143
No Beeps	0.482368462	1.023335212
2 Flashes	0.513966282	1.121569883
1 Beep	0.537790769	1.18204628
2 Beeps	0.468734615	0.959889256
No Beeps	0.535373462	1.207023607