Improving the efficiency of multisensory integration in older adults: Audio-Visual temporal discrimination training reduces susceptibility to the sound-induced flash illusion

Article *in* Neuropsychologia · August 2014

Impact Factor: 3.3 · DOI: 10.1016/j.neuropsychologia.2014.06.027

6 authors, including:


Annalisa Setti
University College Cork
40 PUBLICATIONS **162** CITATIONS
SEE PROFILE


John Stapleton
Trinity College Dublin
6 PUBLICATIONS **15** CITATIONS
SEE PROFILE


Fiona N Newell
Trinity College Dublin
119 PUBLICATIONS **2,543** CITATIONS
SEE PROFILE

Improving the efficiency of multisensory integration in older adults: audio-visual temporal discrimination training reduces susceptibility to the sound-induced flash illusion

Authors: Annalisa Setti[a,b], asetti@tcd.ie, John Stapleton[a], stapletj@tcd.ie , Daniel Leahy[c], daniel.leahy@trilcentre.org, Walsh, Cathal, cathal.walsh@tcd.ie[d], RoseAnne Kenny[e,f], rkenny@tcd.ie, Fiona N. Newell[a], Fiona.Newell@tcd.ie

[a] School of Psychology and Institute of Neuroscience, Trinity College Dublin, Ireland; [b]School of Applied Psychology, University College Cork; [c] School of Computer Science and Informatics; University College Dublin, Ireland; [d]School of Computer Science and Statistics, Trinity College Dublin; [e]School of Medicine, Trinity College Dublin, Ireland; [f] St. James Hospital, Dublin, Ireland

Corresponding author:
Fiona N. Newell, Fiona.Newell@tcd.ie
Institute of Neuroscience,
Lloyd Building
Trinity College Dublin
Dublin 2, Ireland
Tel. +353-01-896-3914
Fax. +353-1-896 3183

Abstract: From language to motor control, efficient integration of information from different sensory modalities is necessary for maintaining a coherent interaction with the environment. While a number of training studies have focused on training perceptual and cognitive function, only very few are specifically targeted at improving multisensory processing. Discrimination of temporal order or coincidence is a criterion used by the brain to determine whether cross-modal stimuli should be integrated or not. In this study we trained older adults to judge the temporal order of visual and auditory stimuli. We then tested whether the training had an effect in reducing susceptibility to a multisensory illusion, the sound induced flash illusion. Improvement in the temporal order judgement task was associated with a reduction in susceptibility to the illusion, particularly at longer Stimulus Onset Asynchronies, in line with a more efficient multisensory processing profile. The present findings set the ground for more broad training programs aimed at improving older adults' cognitive performance in domains in which efficient temporal integration across the senses is required.

Words: 170

Keywords: Multisensory perception; audio-visual perception; temporal order judgement; cross modal illusions; ageing

1. Introduction

The possibility to capitalise on brain plasticity to train the brain through behavioural training programs represents an exciting perspective to support independent living in older age (Greenwood & Parasuraman, 2010). A relatively recent and yet large body of work has been dedicated to identifying effective training programs and to testing their validity in different populations, with mixed results (Green & Bavelier, 2008; Kraft, 2012; Kramer & Willis, 2002; Noack, Lövdén, Schmiedek, & Lindenberger, 2009). Brain training programs have shown that it is possible to obtain improvement in cognition (e.g. attention, memory, reasoning, language, etc.) in older age although the benefits do not always extend to non-trained tasks (Ball, et al., 2002; Ball, Edwards, & Ross, 2007; Ball, Edwards, Ross, & McGwin, 2010; Edwards, et al., 2005; Edwards, Ruva, O'Brien, Haley, & Lister, 2013; Mahncke, et al., 2006; Mozolic, Hayaska, & Laurienti, 2010; Mozolic, Long, Morgan, Rawley-Payne, & Laurienti, 2011; Smith, et al., 2009; Szelag & Skolimowskaa, 2012; Willis, et al., 2006).

To maximise the effectiveness of training programs, such as their impact on non-trained skills and, ultimately, their positive contribution to daily living, it is necessary to identify which specific cognitive processes can be trained. Moreover, it is pertinent to establish how (i.e. under which conditions) they can be trained (Bavelier & Davidson, 2013). One of these processes is multisensory integration, where integration of stimuli from different senses allows the brain to capitalise on the richness of our sensory environment for the purpose of more efficient cognitive functioning. Temporal coincidence is one of the criteria (together with spatial coincidence) used by the brain to establish whether integration should occur, producing multisensory perception, or not, as is evident for example in perceiving body ownership, or audio-visual speech (Calvert, Spence, & Stein, 2004).

The present study aims to train temporal discrimination processing in older adults. Specifically, it aims to improve their ability to discriminate the temporal order of inputs across two different modalities, vision and audition, and to show that this improvement generalises to a related, but not trained, multisensory integration task.

Temporal processing across different senses represents a challenge for the brain as different sensory inputs have different transmission velocities (e.g., from the source, light reaches the sensory receptors faster than sound) and different neural transduction rates (e.g. from the sensory receptors, sound reaches the brain faster than light) (Vroomen & Keetels, 2010). The minimum time interval necessary for the human brain to establish whether a visual input or a sound occurred first or whether they were coincident is thought to be under 100 ms in young adults (Zampini, Guest, Shore, & Spence, 2005; Zampini, Shore, & Spence, 2003a). When one input reaches the sensory receptors it ‘opens’ a window of opportunity whereby stimuli from other senses can be merged with this input to generate a multisensory experience. This window remains open only for a few milliseconds, after which any other sensory input will be perceived as independent and not merged into a multisensory percept (Colonius & Diederich, 2004, 2011; Pöppel, 1997). The temporal window of integration is the maximum temporal delay between the onset of two stimuli (e.g. a sound and a visual object or event) that the brain tolerates for the purpose of multisensory integration (Burr and Alais, 2006). This window is adaptive in that it varies across different sensory combinations, stimulus complexity and familiarity (e.g. Maier, Di Luca & Noppeney, 2011). As we age, however, the temporal discrimination thresholds become higher (Humes, Busey, Craig, & Kewley-Port, 2009) and the temporal window of integration becomes larger (Diederich, Colonius, & Schomburg, 2008) possibly in order to partially compensate for age-related decline in sensory acuity in peripheral sensory organs (Owsley, 2011) or for the general cognitive slowing characterising late adulthood (Salthouse, 1996, 2009). This implies that perception in older adults becomes more susceptible to multisensory integration. As a consequence perception becomes more efficient when multisensory stimuli are available and provide congruent information (Laurienti, Burdette, Maldjian, & Wallace, 2006; Peiffer, Mozolic, Hugenschmidt, & Laurienti, 2007). However, perception in older adults can also become more exposed to interference effects from sensory stimuli that are not task relevant (Poliakoff, Ashworth, Lowe, & Spence, 2006).

Multisensory illusions have often been used to study susceptibility to multisensory integration (Shams, Kamitani, & Shimojo, 2000). One relatively recently discovered but already widely studied illusion is the Sound-Induced Flash Illusion (SIFI) (Shams, et al., 2000). This illusion occurs when a single visual stimulus (e.g. a dot flashed on the screen) is presented with two brief sounds (e.g. two beeps), and the single visual stimulus is perceived as two stimuli (2 flashes when there is, in fact, only 1) as a consequence of the visual and the auditory stimuli being merged into a unified multisensory percept. Susceptibility to the illusion has well established neural correlates (Bolognini, Rossetti, Casati, Mancini, & Vallar, 2011; de Haas, Kanai, Jalkanen, & Rees, 2012; Mishra, Martinez, Sejnowski, & Hillyard, 2007; Shams, Kamitani, Thompson, & Shimojo, 2001) and is considered as a plausible indicator of the integrity of temporal multisensory integration processing (Foss-Feig, et al., 2010; Kwakye, Foss-Feig, Cascio, Stone, & Wallace, 2011). This integrity could be compromised in older adults and especially in older adults who have a history of falls, who present a much higher susceptibility to the illusion than younger adults over a more extended temporal window (Setti, Burke, Kenny, & Newell, 2011).

The temporal discrimination threshold across vision and audition plays a large part in determining whether a person will or will not perceive the illusion (Stevenson, Zemtsov, & Wallace, 2012). Importantly, it has been shown that training can reduce this temporal window of integration (Powers, Hillock, & Wallace, 2009). Accordingly, in the present study we hypothesized that if the older brain remains plastic (Dinse, 2006a; Dinse, et al., 2006b), particularly the sensory regions of the brain, we would obtain a refinement of older adult's ability to perform temporal discrimination by training their temporal order judgement (TOJ) skills (Hypothesis 1). We also hypothesised that older participants would be susceptible to the SIFI as previously shown (Hypothesis 2) and that the reduction of their perceptual threshold would be associated with a reduction in susceptibility to the SIFI (Hypothesis 3). Finally we hypothesised that the size of the temporal window of integration after training would be associated with individual susceptibility to the SIFI illusion (Hypothesis 4).

2. Method

2.1. Participants

Thirty-four older participants took part in the present study. All participants were recruited through the Technology Research for Independent Living (TRIL) clinic located in St. James' Hospital (Dublin). Twenty-four participants (11 male) were recruited for the 'training group' and 10 participants (4 male) were recruited for the 'control group'. All participants underwent a comprehensive health assessment in the TRIL clinic; the characteristics of the two groups of participants relevant to this study are reported in Table 1(a). Participants were then tested either in their own home or in Trinity College Dublin for the main study, according to their own preference. The experiment was approved by the St. James Hospital Ethics Committee and by the School of Psychology Research Ethics Committee, Trinity College Dublin and conformed to the Declaration of Helsinki. All participants provided informed, written consent prior to taking part in the experiment.

Table 1

2.2. Apparatus and stimuli

All tasks were presented on a DELL XPS M1530 laptop computer (screen resolution of 1280x720, refraction rate of 60Hz). Participants were seated in front of the computer screen (approximate distance of 70 cm). An external keyboard was used when a key press was required to respond (i.e. during the training and control tasks).

The visual stimulus used in all tasks (i.e. the sound-induced flash illusion task, the TOJ training task and control tasks) comprised of a white disk with a diameter subtending a visual angle of 1.5 degrees and a luminance of 31.54fl, which was presented against a black background for 12 ms. The auditory stimulus comprised of a 'beep' which was a 10 ms long (1 ms ramp) sound burst of 3500 Hz presented at 79dB. Sounds were delivered through loudspeakers positioned at the left and right sides of the monitor at the same height as the fixation cross. Additional stimuli used in the 'control' task comprised of an orange-coloured visual disc (diameter of 1.5 degrees visual angle and a luminance of 31.54fl), and two auditory 'beeps' of low (100Hz) and high (250Hz) pitch.

2.3. Procedure

The study was divided into 5 separate testing sessions over 5 consecutive days. For each participant, the 5 sessions occurred in the same environment and at approximately the same time each day. In all cases the participants were tested in a dimly lit room and the experimenter took particular care to ensure that no reflections appeared on the screen and the environment was quiet (participants were also asked to switch off their phone during the study).

In session 1 all participants were tested on the SIFI task and then performed either the TOJ task described in detail below or the control task, also described below, depending on the group to which they belonged. In sessions 2 to 4 only the TOJ training or the control task were performed. In session 5 the TOJ training (or the control task) was followed by the SIFI task (re-test). The first and last sessions had duration of between 45 and 60 minutes for each participant, whereas the remaining sessions lasted approximately 30 minutes.

Susceptibility to the SIFI

The SIFI task (presented in session 1 and 5) comprised of three different types of trials randomly intermixed: those in which the illusion could occur, audio-visual (AV) congruent trials, or uni-sensory trials. For the illusory trials, a single visual flash was accompanied by 2 beeps. Varying stimulus onset asynchronies (SOA) of either 30, 70, 110, 150, 190, 230 or 270 ms were used, one beep always coincided with the presentation of the flash and the other beep could either precede or follow the bimodal stimulus pair (50% of times each). For the AV congruent trials 2 flashes were presented with 2 beeps, and the same SOAs were used as in the illusory trials. The unisensory trials comprised of a single beep only, a single flash only, 2 flashes only (with an SOA of 70ms) or 2 beeps only. Whenever 2 beeps were presented, these were presented with the same SOAs utilised for the illusory condition. Each trial was repeated 4 times, yielding a total of 156 trials (56 illusory trials [4 repetitions by 7 SOAs by 2 sequences per SOA, with either the beep presented after or before the AV stimuli]; 56 congruent 2 flashes/2 beeps trials [8 repetitions by 7 SOAs to balance with illusory trials]; 4 congruent 1 flash/1 beep trials; 32 unisensory beep-only trials [4 unisensory 1 beep trials and 4 repetitions of 2 beep trials by 7 SOAs]; 4 unisensory 1 flash trials and 4 unisensory 2 flashes trials). Participants were required to verbally report to the experimenter how many flashes they saw, while ignoring the beeps. It was emphasized that the flashes were the stimuli to count. When only beeps were presented participants were asked to report the number of beeps if they could but emphasis was put on the task being 'counting the flashes'. The experimenter recorded the number provided by the participant by pressing the corresponding key on the keyboard. The task was self-paced throughout.

TOJ training task

For the TOJ training task participants were presented with an auditory beep and a visual flash and they were required to indicate whether the beep or the flash had been presented first (2-alternative-forced choice task). For this task, a staircase procedure was adopted to maximise the chance of effective training for each participant. The staircase modulated the stimulus onset asynchrony (SOA) between the presentation of the visual and auditory stimuli. The initial SOA was fixed at 350 ms to ensure that the majority of participants would be able to easily perform the task and become familiarized with the task protocol (however higher SOAs could be reached in the case of an error). The SOA decreased in steps of 40 ms subsequent to 3 correct responses for one given SOA and it increased by 40 ms after 1 incorrect response at any one given SOA. The 40 ms step size was chosen to yield timings which were compatible with the SOAs used in the SIFI task. The procedure automatically ended after 30 reversals. The minimum SOA which could be reached was 30 ms. Across all trials, there was a 50% probability of the beep appearing first (or the flash first) for each SOA. After each trial the participant received feedback on his/her performance ('Correct Response' or 'Incorrect Response'). Within each session, there were 3 testing blocks of trials and participants could take a self-timed break after each block. The number of trials per block varied depending on the participant's performance on the staircase procedure (i.e. when 30 reversals were reached).

Control task

The control task also comprised of a cross-modal discrimination of auditory 'beep' and visual 'flash' stimuli and was constructed to be as similar as possible to the training task while not including either the staircase procedure or feedback on performance. We adopted a similar task previously described by Powers et al. (2009) with one main difference: here participants were asked to respond to either a visual or an auditory target instead of a visual only target. This choice was to ensure that the participant's attention was divided between modalities as it was for participants in the temporal order judgement training task. If difficulty in switching between modalities is crucial in determining older adults' temporal order judgment performance, it was necessary to include this component in the control task to assess the effectiveness of the training procedure (see e.g. Andrés, Parmentier, and Escera 2006). In the current task, participants were presented with a cross-modal trial consisting of a single flash and a single beep, randomly presented over SOAs varying between 30 and 590 ms with fixed 40 ms intervals (30 – 70 – 110 – 150 ms etc.). The visual stimulus (white flash) was paired with a low pitch sound (100Hz) in 90% of the trials, otherwise either a high pitch tone (250Hz) or an orange-coloured visual flash appeared (the use of the orange flash was necessary to avoid selective attention to the auditory stimuli only). Participants were required to press a key ('z') when the white flash appeared with the low pitch sound and to press another key ('m') when either the high pitch sound or the orange flash appeared (which never co-occurred in the same trial). Each session consisted of three blocks of 140 trials and participants could take a self-timed break between blocks.

2.4. Data analysis

Hypothesis 1 (Improvement in the TOJ training task): for each participant, the median SOA in session 1 was derived per block. We then used the median SOA obtained in session 1 to conduct a median split of the data in session 1 and session 5: this allowed us to determine the number of trials in which each participant correctly judged the temporal order of the stimuli with SOAs below or above this median (in each block). These frequencies (3, one per block) were analysed for each participant by means of a one-way, by items, Analysis of Variance (ANOVA) (session 1 or 5). Participants who presented a significant decrease in the frequency of correct trials below the median from session 1 to session 5 were considered to have improved in the TOJ training task. In order to establish whether improvement (or lack of it) could depend on individual characteristics we also performed a series of t-tests for independent samples on the relevant variables (age, vision, MMSE, baseline SOA) between the training and the control group. The frequency of correct responses below the median was used as criterion for improvement because it is less conservative than using the difference in SOA when the staircase converges and, moreover, it allows us to take account of the response variability across the 30 trials that older adults may show.

Hypothesis 2 (Susceptibility to the SIFI illusion): to test whether each group (training-improved; training-no improvement; control group) showed overall susceptibility to the illusion, a 2-way ANOVA was conducted to compare the proportion of correct responses in the unisensory condition (1 flash) with those in the multisensory condition (1 flash/ 2 beeps mean across all SOAs) (within-subjects factor), across the three groups (training-improved; training-no improvement; control group) (between-subjects factor). The proportion of correct responses was used as the dependent variable. Responses to each of the two SIFI testing sessions were analysed separately.

Hypothesis 3 (Group differences in susceptibility to the illusion): prior to testing differences in susceptibility to the illusion, we tested whether performance on the unisensory or congruent conditions may differentiate the groups. We conducted a 3-way ANOVA across performance to the unisensory conditions, with the following factors: 3 (group: training-improved; training-no improvement; control group) by 2 (session: session 1 or session 5) by 3 (unisensory condition: 1 flash; 2 flashes; 1 beep). Then we conducted a 3-way ANOVA on performance to the unisensory beeps with the following factors: 3 (group: training-improved; training-no improvement; control group) by 7 (SOAs) by 2 (session: session 1 or session 5). Accuracy of perception in the congruent condition (2 flashes/2 beeps) was assessed with a 3 way ANOVA, 3 (group: training-improved; training-no improvement; control group) by 7 (SOAs) by 2 (session: session 1 vs. session 5). Finally we tested our main hypothesis on group differences in their susceptibility to the illusion from session 1 to session 5 with a 3-

way ANOVA on the proportion of correct responses in the illusion condition, with group (training-improved; training-no improvement; control group), test session (session 1 or session 5) and SOA (7) as factors and the overall mean number of correct responses to the AV congruent 2 flashes/2 beeps (for session 1 and 5) condition as covariates.

We also calculated d' to test whether the sensitivity in correctly detecting 2 unisensory flashes or 2 flashes when presented with 2 beeps increased following training, i.e. from session 1 to session 5. For the detection of the unisensory flashes, sensitivity was expressed by d' [*z*(hits) – *z*(false alarms)], where hits are 2 flashes correctly identified (presented with no beeps) and false alarms are single flashes incorrectly identified as 2 flashes (presented with no beeps) and *z* is the inverse cumulative normal. For the detection of 2 flashes when presented with 2 beeps, hits were defined as 2 flashes (with 2 beeps) correctly identified and false alarms were single flashes incorrectly identified as 2 flashes when presented with 2 beeps and *z* is the inverse cumulative normal. The d' for each SOA was calculated separately. We also calculated the criterion bias β with the following formula $\beta = \mathrm{Exp}(-0.5 * d' * (z(\text{hits})^2 + z(\text{false alarms})^2)$ for each SOA separately (Green & Swets, 1966).

Hypothesis 4 (Relationship between the size of the temporal window in session 5 and susceptibility to the SIFI): We calculated the average SOA over the final 10 reversals for each of the 3 testing blocks in both the first (day 1) and last (day 5) training sessions. We entered the SOA values from the final training session as a predictor in a linear regression model, with the proportion of correct responses to the SIFI task presented after the final training session as the dependent variable. We introduced the average SOA across 10 reversals in the first training session as a covariate as well as susceptibility to the illusion in session 1 to account for individual differences. To control for performance in the unisensory and congruent conditions we also introduced, as covariates, responses to the 1 flash, 2 flashes, 2 beeps and 2 flashes/ 2 beeps conditions (from session 5). This analysis was conducted separately for each of the SOAs tested in the SIFI trials (from 30 ms to 270 ms).

3. Results

All participants completed the tasks (either training or control task and SIFI illusion task). The analyses of performance in the SIFI task are conducted on the proportion of correct responses unless otherwise specified.

Hypothesis 1 (Improvement in the TOJ training task)

According to the analysis on the frequency of correct responses which were below or above the median SOA in session 1 and 5, we found that 18 of the 24 participants significantly improved their performance between the first and last training session. For the participants who improved, their mean frequency of correct trials below the median in session 1 was 38.41 (st. dev. = 10.16) and in session 5 was 81.48 (st. dev. =18.36). For the participants who did not improve, their mean performance in session 1 was 32.8 (st. dev.= 9.3) whereas in session 5 it was 57.58 (st. dev = 13.38).

Participants who did not improve or who improved did not significantly differ in terms of their baseline characteristics (see Table 1(b)). No pattern was apparent in the participants' responses in relation to whether the participant was tested in the home or the laboratory.

Hypothesis 2 (Susceptibility to the SIFI illusion)

Susceptibility to the illusion was defined as significantly fewer correct responses to the illusory than the unisensory conditions (Shams, et al., 2000). Table 2 reports the proportion of correct responses in each condition across groups. The 2-way ANOVA conducted on the unisensory flash or illusory 1 flash/2beeps conditions in session 1 revealed a significantly lower proportion of correct responses to the illusory than the unisensory condition [F(1,31)=32.5, p<0.001] and no significant group effect in the overall susceptibility to the illusion [F(2,31)=0.11, p=0.9]. The interaction between group and condition did not reach significance. The same pattern was found in session 5, with a significant effect of condition [F(1,31)=39.17, p<0.001] but not of group [F(2,31)=2.49, p=0.1]. Again, the interaction did not reach significance.

[Table 2]

Hypothesis 3 (Group differences in susceptibility to the illusion)

The 3-way ANOVA conducted on responses to the unisensory conditions, 1 flash, 2 flashes and 1 beep, resulted in no effects of group [F(2,31)=1.04, p=0.36] or session [F(1,31)=0.86, p=0.77], while the main effect of condition was significant [F(2,31)=20.26, p<.001]. There were fewer correct responses made to the 2-flashes condition than either the 1 flash or 1 beep conditions (post hoc, Fisher LSD ps < .001). None of the interactions reached significance. The 3-way ANOVA (group; session; SOA) on responses to the unisensory 2 beeps condition revealed no significant group difference [F(2,31)=2.2, p=0.13], no effect of session [F(1,31)=1.95, p=.17] and a significant effect of SOA [F(6,186)=13.49, p<.001]: there was a greater number of correct responses to longer SOAs (>70 ms) than shorter SOAs (30 and 70 ms) (post hoc, Fisher LSD ps < .05). Again, none of the interactions were significant. In the 3-way ANOVA (group; session; SOA) on responses to the congruent condition, 2 flashes\2 beeps, there was a trend towards a main effect of group [F(2,31)=2.92, p=.07]: participants who did not improve during the training had a lower overall proportion of correct responses than the other participant groups, as can be observed in Table 2. There was no effect of session [F(1,31)=0.31, p=.58], but an effect of SOA was found [F(6,186)=24.17, p<0.001], whereby trials with longer SOAs (>70 ms) were responded to more correctly than those with shorter SOAs (30 and 70 ms) (post hoc, Fisher LSD ps < .01). None of the interactions were significant.

To test our main hypothesis that susceptibility to the SIFI was modulated by the training performance, and whether SOA modulated this difference, we then investigated whether there were differences in susceptibility to the SIFI illusion in session 1 relative to session 5 in the three groups of participants. A 3-way ANOVA (group; session; SOA) on the proportion of correct responses in the illusion condition revealed no effect of group [F(2,29) = 1.11, $\eta_p^2 = 0.07$, p=0.34] or SOA [F(6,174) = 1.21, $\eta_p^2 = 0.07$, p=0.04]. As expected, there was a main effect of test session [F(1,29) = 4.44 $\eta_p^2 = 0.13$, p<0.05]. The covariate 2 flash/2 beeps in session 5 was significant [F(1,29) = 4.97, $\eta_p^2 = 0.15$, p<0.05]. The covariate also interacted with performance across the sessions [F(1,29) = 7.53, $\eta_p^2 = 0.21$, p<0.05]. More importantly to our aims there was a significant interaction between group and test session [F(2,29) = 5.45, $\eta_p^2 = 0.27$, p<0.01]. The effect size for the interaction is $\eta_p^2 = 0.27$ considered i.e. a large effect.

A post hoc Fisher LSD analysis of the interaction showed that the only group presenting a reliable increase in the proportion of correct responses (i.e. reduced susceptibility) in session 5 relative to session 1 was the successfully trained participants [p<0.05], while no difference was found either in the unsuccessfully trained [p=0.09] or the control group [p=0.93]. No other interactions with group were significant.

In order to understand the effect of training better, for each SOA we ran separate 2-way ANOVAs with group (training-improved; training-no improvement during training) and session (session 1 or session 5) as factors to test for significant group by session interactions for each of the different SOAs (see Table 2). Significant interactions were found for the SOAs of 270 ms [F(1,22)=11.01, p<0.01] and 190 ms [F(1,22)=5.82, p=0.02] only, but not for shorter SOAs. Post-hoc analysis of the interaction at 270ms revealed that susceptibility to the SIFI was lower in session 5 than in session 1 in the group who successfully trained on the TOJ task but not the group who failed to improve [post hoc LSD p <0.01]. However post-hoc tests on the interaction at 190 ms failed to reveal any significant pairwise comparisons (a trend only for the group who improved was found p=0.087).

A further analysis utilising Signal Detection Theory explored the change in sensitivity across sessions (see Section 2.4 for details of the formula used to calculate d'). In the multisensory conditions the d' for each SOA was calculated separately. According to our hypotheses the d' for the unisensory condition should not be modulated by training, while the d' for the multisensory flashes detection should.

Sensitivity in detecting 2 unisensory flashes: A 3 way ANOVA with group (training-improved; training-no improvement; control), session (session 1 or session 5) and SOA (30, 70, 110, 150, 190, 230, 270 ms) as variables performed on the *d'* scores across participants showed no main effect of group [F(2,31)=0.13, p=0.88] or session [F(1,31)=0.001, p=0.98], while there was an effect of SOA [F(6,186)=6.56, p<0.001] and no evidence of an interaction between the factors. Therefore there was no benefit of training on the detection of the unisensory stimuli, which is to be expected considering both the high proportion of correct responses in these trials and the fact that training specifically targeted multisensory processing. Participants' response criterion (β) was also calculated and entered into a 3-way ANOVA with group (training-improved; training-no improvement; control), session (session 1 or session 5) and SOA (30, 70, 110, 150, 190, 230, 270 ms) as variables. There was no main effect of group [F(2,31)=0.09, p=0.91], session [F(1,31)=0.18, p=0.68] or SOA [F(6,186)=1.82, p=0.09], and there was no evidence for an interaction between the factors.

Sensitivity in detecting 2 (veridical) flashes with 2 beeps: A 3-way ANOVA with group (training-improved; training-no improvement; control), session (session 1 or session 5) and SOA (30, 70, 110, 150, 190, 230, 270 ms) on d' performance to the AV congruent trials showed a significant main effect of SOA [F(6,186)=24.70, p<0.001], no main effect of group [F(2,31)=0.5, p=0.61], and no main effect of session [F(1,31)=0.76, p=0.39]. There was a significant group by session interaction [F(2,31)=3.8, p<0.05] which is shown in Figure 1. Post hoc analysis (Fisher LSD) revealed that the improvement in *d'* scores between session 1 and session 5 for participants who successfully trained in the TOJ task approached significance [p=0.055], with higher sensitivity after training (*d'*=1.5) than before training (d'=1.1). In contrast, performance failed to improve from session 1 to session 5 for each of the other two participant groups. This indicates that sensitivity in perceiving 2 real flashes improved in session 5 particularly in the group of participants who successfully trained on the TOJ task. Participants' response criterion β was also calculated and entered in a 3-way ANOVA with group (training-improved; training-no improvement; control), session (session 1 or session 5) and SOA (30, 70, 110, 150, 190, 230, 270 ms) as variables. No main effects of group [F(2,31)=0.69, p=0.5]; session [F(1,31)=0.82, p=0.37 or SOA [F(6,186)=0.7, p=0.65] was found, nor did any of the interactions reach significance (group by session interaction was not significant [F(2,31)=1.1, p=0.34], training-improved session 1 β=1.54; session 5 β=2.60; training-no improvement session 1 β=2.97; session 5 β=3.12; control group session 1 β=2.04; session 5 β=3.04).

[Figure 1]

Hypothesis 4. Relationship between size of the temporal window and SIFI (trained participants only).

The results reported by Stevenson et al. (2012) based on younger adults suggest that the size of the temporal window, as assessed in the TOJ task, could be related to susceptibility to the SIFI illusion. Moreover, it has been recently shown that a larger AV temporal discrimination threshold is associated with higher susceptibility to the Temporal Ventriloquist Effect in an older population (de Boer-Schellekens & Vroomen, 2013). Here we performed the following analyses to show that the relationship between the size of the temporal window, and susceptibility to the SIFI illusion, generalises to an older population. By calculating the average SOA at which the staircase converged (i.e. the average SOA over the final 10 reversals for each of the 3 testing blocks) we obtained an indication of the average size of the temporal window of integration for each participant (as shown in Figure 2).

[Figure 2]

The correlations between the size of the temporal window and susceptibility to the SIFI are shown in Figure 3 for each of the SOAs. The SOAs (size of the window) in session 1 and session 5 significantly correlated with the proportion of correct responses in the SIFI task before and after training (all p <.05). When the correlation between the size of the window and the susceptibility to the SIFI was calculated separately for each SOA used in the SIFI, as expected, accuracy in the two shorted SOAs (30ms and 70ms) was not correlated with the window size, while it was for all other SOAs (Figure 3). This indicates a relationship between the temporal discrimination abilities in the TOJ task (training task) and the susceptibility to the illusion in our older group of participants, and is consistent with Stevenson et al.'s findings based on younger adults (2012). In keeping with these results, a correlation was found between participants' d' score (to the 2 flashes/2 beeps conditions) in session 5 and the temporal window of integration in session 5 (r= -.44, p< .05) but not the temporal window of integration in session 1 (r=-1.7, p= 0.43).

[Figure 3]

We then hypothesised that the size of the temporal window in training session 5 would predict susceptibility to the illusion post-training better than the size of the temporal window in training session 1, as the window was modified by training. The results of these analyses for each SOA are shown in Table 3. We found that susceptibility to the SIFI illusion at SOAs of 110 ms, 190 ms, 230 ms and 270 ms was predicted by the size of the temporal window at the end of training (i.e. session 5). For the SOA of 70 ms in the SIFI trials the predictor was significant but the model was not, whereas for 30 ms SOA neither the model nor the predictor were significant. The SOA in the first training session was not a significant covariate for any of the SOAs. This suggests that the size of the temporal window after the 5 days of training is predictive of susceptibility to the sound induced flash illusion. Moreover, susceptibility to the illusion prior to training was predictive of susceptibility following training with a positive association for all SOAs. No other covariates were consistently significant predictors across the SOAs.

Table 3

4. Discussion

Effective training of perceptual abilities in older adults can potentially have an impact on a number of cognitive functions, considering the close relationship between efficient perception and cognitive outcomes in older age (Lindenberger & Ghisletta, 2009). It is clear from a growing body of literature that older adults process sensory stimuli differently from their younger counterparts even when the task requirements are very simple (De Sanctis, et al., 2008). When presented with incoming inputs from different modalities, perceptual performance in older adults typically suggests enhanced multisensory interactions (Mozolic, Hugenschmidt, Peiffer, & Laurienti, 2012) as shown by the higher susceptibility to the sound-induced flash illusion in older than in younger adults (Setti, et al., 2011). This relative increase in susceptibility to the SIFI is related to the extended temporal window of integration found in older individuals (Diederich, et al., 2008) and to a possible disadvantage in temporal discrimination at longer audio-visual SOAs in older compared to younger adults (Setti, et al., 2011 but see Fiacconi, Harvey, Sekuler, & Bennett, 2013) . The specific aim of the present study was to investigate whether targeted training in older adults, designed to refine temporal discrimination abilities across audio and visual modalities, would subsequently be linked to a reduction in susceptibility to the SIFI.

The main results can be summarised as follows: (1) older adults maintain plasticity in their audio-visual perceptual discrimination abilities since audio-visual temporal discrimination training effectively ameliorates temporal discrimination performance in the majority of individuals. (2) The beneficial effect of more refined temporal discrimination abilities is associated with a decreased susceptibility to the SIFI, indicating that temporal discrimination training has effects that can impact other perceptual processes that are not directly trained. (3) The effect is not due to the mere exposure to the stimuli in a cross-modal discrimination task since there was no evidence for a change in susceptibility to the illusion in the participants assigned to the control task. (4) The size of the temporal window of integration following training was predictive of subsequent susceptibility to the illusion. These findings strongly indicate that there is a link between the training of temporal discrimination abilities and more efficient multisensory integration in older adults.

Two limitations of the study should be acknowledged; the relatively small sample size and the short duration of the training. The sample size, while smaller than other multisensory training studies with older adults (e.g. Mozolic et al. 2011) was sufficient to show training effects for the majority, but not all, of the participants. As to the training duration, while we cannot exclude the possibility that a larger number of participants could improve their TOJ performance with a longer training period we found that based on the literature on similar procedures (see Powers et al., 2009) 5 days was a sufficient amount of time to obtain a perceptual improvement without incurring a reduction in participant numbers (due to drop outs from a lengthy training protocol). The possibility that a longer training may have produced positive effects for a larger number of participants does not weaken the present results that training effects can be obtained in older adults which, in turn, benefit multisensory integration.

Several issues remain open: firstly, due to the nature of our task we cannot determine if the training effects hold for both the flash-first (visual stimulus preceding the auditory stimulus) and beep-first (auditory stimulus preceding the visual stimulus) conditions or whether they are specific to the flash first as previously reported in younger adults (Stevenson, et al., 2012). Secondly, while we did find an overall training effect in susceptibility to the SIFI in the trained participants, (with no significant interaction found when susceptibility to the SIFI in session 1 and session 5 was analysed separately for each SOA), this significant improvement appeared to be specific to the longest SOA of 270 ms. This could be due to the fact that most participants maintained a relatively large temporal discrimination threshold, albeit decreased by the training. While all successfully trained participants successfully reduced their average audio-visual temporal discrimination threshold (average SOA over 10 reversals) to lower than 270 ms by session 5 (5 participants had windows higher than 270 in session 1), thresholds of less than100 ms, which are typical of younger adults (Zampini, et al., 2003a; Zampini, Shore, & Spence, 2003b), are found in only 4 of the older participants. Therefore it is plausible to argue that when the illusory trials in the SIFI task are presented with SOAs lower than 270 ms, for some participants the discrimination is still near-threshold, which may have led to a less clear-cut result in terms of the benefit of the training at shorter SOAs. Nonetheless the size of the window in training session 5 was the only significant predictor of susceptibility to the illusion after training for SOAs of 110 ms and higher (apart from the initial susceptibility to the SIFI pre-training, which is indicative of individual differences). The size of the window in training session 1 was not an independent predictor of susceptibility to the illusion following training. Thirdly, 25% of our participants failed to improve on the TOJ task with training, according to our criteria. It is not clear why these participants did not benefit from the training procedure as much as the other participants: we found no difference across groups in terms of age, cognitive ability or sensory acuity, which may underpin individual differences in rates of training or perceptual learning (see e.g. Astle, Levi, & McGraw, 2013)). However, we acknowledge that the small sample size of the group who failed to train may preclude us from identifying the underlying cause. One possible reason may lie in their history of experiencing falls: during debriefing, 5 of the 6 participants who did not improve their performance with training reported a history of at least one fall requiring medical attention, while only 6 out the 18 in the group who improved their performance in the TOJ task had a history of falls (3 out of 10 had a history of falls in the control group). The potential beneficial effects of this training program on the incidence of falls in older adults and the relationship between improvement in the training and susceptibility to falls will need to be addressed in future research (see Setti et al., 2011). Finally we observed a relatively high variability in responses across participants, with some older adults having large temporal windows of integration in the TOJ task and others with temporal windows which were similar to those found in younger adults (see also Fiacconi et al., 2013; Stevenson, 2012). This variability in cross-modal AV perception across individuals has been found in other studies (e.g. Mishra & Gazzaley, 2013). However, whether these differences are due to attentional or purely perceptual effects, and their implication for other cognitive tasks, remains to be elucidated.

In the present study we extended both Powers et al. (2009) and Stevenson et al. (2012) findings to a population of older adults and demonstrate the link between the modulation of the temporal window by training and susceptibility to the SIFI. Training may reduce activity in the Superior Temporal cortex as found in an audio-visual discrimination training study conducted with younger adults (Powers, Hevey, & Wallace, 2012). The Superior Temporal cortex, as well as visual and auditory cortices, is involved in the perception of the SIFI (Bolognini, et al., 2011; Watkins, Shams, Tanaka, Haynes, & Rees, 2006). Indeed Bolognini et al. (2011) found that an induced increase in the excitability of the superior temporal cortex was associated with higher susceptibility to the illusion, while the opposite was true for reduced excitability. This would suggest that functional changes involving the multisensory areas in the Superior Temporal cortex and its interaction with visual and auditory cortices could underlie the association between the TOJ task and susceptibility to the SIFI found in older adults' performance in the present work.

Another possibility is that temporal discrimination training operates by increasing the threshold needed for an illusory percept to reach awareness as a consequence of the individual being better able to discriminate the veridical flash as a single perceptual event (Bhattacharya, Shams, & Shimojo, 2002). In fact visual training has been recently shown to modulate the audio-visual temporal window of integration *via* increased visual discrimination (Stevenson, Wilson, Power, Wallace, 2013). It is possible that TOJ training may increase discriminability of auditory and visual percepts in a similar manner.

A final possibility may lie in the role played by attention. Kamke et al. (2012) found that when TMS is applied over the parietal cortex, in particular the right angular gyrus (AG), this induces an increase in the number of correct responses made to the SIFI illusory condition. The AG is part of a ventral network associated with stimulus driven shifting of attention within and between the senses (Corbetta & Shulman, 2002). It is possible that cross-modal temporal discrimination training could act on this network by refining the participant's ability to process the task-relevant flash as an independent percept from the task irrelevant beeps. Participants may be better able to attend to vision whilst ignoring the beep sounds, therefore diminishing the effect of audition on the perceived flash especially at longer SOAs. The TOJ task which requires a rapid shift in attention between the two modalities, may have improved older adults' ability to focus attention on the flash instead of dividing attention between the two modalities. Considering that older adults tend to be highly susceptible to audio-visual integration in divided attention conditions but maintain some ability to focus attention on one modality (Hugenschmidt, Mozolic, & Laurienti, 2009; Hugenschmidt, Peiffer, McCoy, Hayasaka, & Laurienti, 2009), shifting the attentional setting to a more focused state could have led to the decreased susceptibility to the SIFI recorded here. The role of attention in this case does not indicate a bias in responding but a contribution of attentional networks to the detection of relevant stimuli in the environment (Kamke, et al., 2012). Interestingly a recent study has shown that shifting attention towards vision or audition by means of a go/no-go task modulates susceptibility to the illusion in older (and in younger) adults (DeLoss, Pierce, & Andersen, 2013).

The neural underpinnings of the effect of training and the subsequent impact of training on susceptibility to the SIFI in the older population will need to be explored further. However considering the evidence for brain plasticity in older adults based on perceptual tasks across different modalities (Dinse, 2006a) one could expect that temporal discrimination across the senses can be trained in other modalities and produce beneficial effects on cognition (Pöppel, 1997).

In sum, the results of the present study suggest that susceptibility to the sound induced flash illusion in older adults can be modified by temporal discrimination training. The processes described above, such as the narrowing of the temporal window, or attentional modulation, are plausible candidates to account for explaining these effects. The finding that multisensory perception in older adults is amenable to training and that this training generalises to other tasks, suggests possibilities for rehabilitating optimal multisensory function as we age with a positive impact on a number of cognitive and functional abilities including falls (Setti et al., 2011). It is interesting to note that this training was conducted in the homes of the majority of the older adults tested. This is relevant in the context of allowing older people to avail of interventions that do not require access to services and can be carried out in older peoples’ own homes. A feasibility study is currently on-going to assess whether the TOJ task can be self-administered at home through the use of mobile (e.g. tablet) technology.

Acknowledgements

We would like to thank Kate E. Burke for her help with testing the participants and Cathal Walsh for his support with the data analyses. This research was completed with the support of the EU-FP7 VERVE project (grant no. 288914) and as part of a wider programme of research within the TRIL Centre, (Technology Research for Independent Living). The TRIL Centre is a multidisciplinary research centre, bringing together researchers from TCD, UCD, NUIG and Intel, funded by Intel, IDA Ireland and GE Healthcare. http://www.trilcentre.org

References

Andrés, P., Parmentier, F. B. R., & Escera, C. (2006). The effect of age on involuntary capture of attention by irrelevant sounds: A test of the frontal hypothesis of aging. *Neuropsychologia, 44*, 2564-2568.

Astle, A. T., Li, R. W., Webb, B. S., Levi, D. M., & McGraw, P. V. (2013). A Weber-like law for perceptual learning. *Scientific Reports, 3,* 1158.

Ball, K., Berch, D. B., Helmers, K. F., Jobe, J. B., Leveck, M. D., Marsiske, M., Morris, J. N., Rebok, G. W., Smith, D. M., Tennstedt, S. L., Unverzagt, F. W., Willis, S. L., & for the, A. S. G. (2002). Effects of Cognitive Training Interventions With Older Adults: A Randomized Controlled Trial. *Journal of the American Medical Association, 288,* 2271-2281.

Ball, K., Edwards, J. D., & Ross, L. A. (2007). The Impact of Speed of Processing Training on Cognitive and Everyday Functions. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 62,* 19-31.

Ball, K. K., Edwards, J. D., Ross, L. A., & McGwin, G., Jr. (2010). Cognitive training decreases motor vehicle collision involvement of older drivers. *Journal of the American Geriatrics Society, 58,* 2107-2113.

Bavelier, D., & Davidson, R. J. (2013). Brain training: Games to do you good. *Nature, 494,* 425-426.

Bhattacharya, J., Shams, L., & Shimojo, S. (2002). Sound-induced illusory flash perception: Role of gamma band responses. *Neuroreport, 13,* 1727-1730.

Bolognini, N., Rossetti, A., Casati, C., Mancini, F., & Vallar, G. (2011). Neuromodulation of multisensory perception: A tDCS study of the sound-induced flash illusion. *Neuropsychologia, 49*, 231-237.

Calvert, G. A., Spence, C., & Stein, B. E. (2004). The Handbook of Multisensory Processes. In. Boston: MIT.

Colonius, H., & Diederich, A. (2004). Multisensory interaction in saccadic reaction time: A time-window-of-integration model. *Journal of Cognitive Neuroscience, 16*, 1000-1009.

Colonius, H., & Diederich, A. (2011). Computing an optimal time window of audiovisual integration in focused attention tasks: illustrated by studies on effect of age and prior knowledge. *Experimental Brain Research, 212*, 327-337.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*, 201-215.

de Boer-Schellekens, L., & Vroomen, J. (2013). Multisensory integration compensates loss of sensitivity of visual temporal order in the elderly. *Experimental Brain Research, in press*.

de Haas, B., Kanai, R., Jalkanen, L., & Rees, G. (2012). Grey matter volume in early human visual cortex predicts proneness to the sound-induced flash illusion. *Proceedings of the Royal Society B: Biological Sciences, 279*, 4955-4961.

De Sanctis, P., Katz, R., Wylie, G. R., Sehatpour, P., Alexopoulos, G. S., & Foxe, J. J. (2008). Enhanced and bilateralized visual sensory processing in the ventral stream may be a feature of normal aging. *Neurobiology of Aging, 29*, 1576-1586.

DeLoss, D. J., Pierce, R. S., & Andersen, G. J. (2013). Multisensory Integration, aging, and the sound-induced flash illusion *Psychology and Aging, 28*(3), 802-812.

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

Dinse, H. R. (2006). Cortical reorganization in the aging brain. In A. R. Moller (Ed.), *Progress in Brain Research* (pp. 57-80). Amsterdam: Elsevier.

Dinse, H. R., Kleibel, N., Kalisch, T., Ragert, P., Wilimzig, C., & Tegenthoff, M. (2006). Tactile coactivation resets age-related decline of human tactile discrimination. *Ann Neurol 60*, 88–94.

Edwards, J. D., Wadley, V. G., Vance, D. E., Wood, K., Roenker, D. L., & Ball, K. K. (2005). The impact of speed of processing training on cognitive and everyday performance. *Aging & Mental Health, 9,* 262-271.

Edwards, J. D., Ruva, C. L., O'Brien, J. L., Haley, C. B., & Lister, J. J. (2013). An examination of mediators of the transfer of cognitive speed of processing training to everyday functional performance. *Psychology and Aging*, 28*(2)*, 314-321.

Fiacconi, C. M., Harvey, E. C., Sekuler, A. B., & Bennett, P. J. (2013). The influence of aging on audiovisual temporal order judgment. *Experimental Aging Research, 39,* 179-193.

Foss-Feig, J., Kwakye, L., Cascio, C., Burnette, C., Kadivar, H., Stone, W., & Wallace, M. (2010). An extended multisensory temporal binding window in autism spectrum disorders. *Experimental Brain Research, 203,* 381-389.

Green, C. S., & Bavelier, D. (2008). Exercising your brain: A review of human brain plasticity and training-induced learning. *Psychology and Aging, 23,* 692-701.

Green, D. M., & Swets, J. A. (1966). *Signal Detection Theory and Psychophysics*. New York: Wiley.

Greenwood, P. M., & Parasuraman, R. (2010). Neuronal and cognitive plasticity: A neurocognitive framework for ameliorating cognitive aging. *Frontiers in Aging Neuroscience, 2*.

Hugenschmidt, C. E., Mozolic, J., & Laurienti, P. J. (2009). Suppression of multisensory integration by modality-specific attention in aging. *Neuroreport, 20,* 349-353.

Hugenschmidt, C. E., Peiffer, A. M., McCoy, T., Hayasaka, S., & Laurienti, P. J. (2009). Preservation of crossmodal selective attention in healthy aging. *Experimental Brain Research, 198*, 273-285.

Humes, L. E., Busey, T. A., Craig, J. C., & Kewley-Port, D. (2009). The effects of age on sensory thresholds and temporal gap detection in hearing, vision, and touch. *Attention, Perception & Psychophysics, 71*, 860-871.

Kamke, M. R., Vieth, H. E., Cottrell, D., & Mattingley, J. B. (2012). Parietal disruption alters audiovisual binding in the sound-induced flash illusion. *NeuroImage, 62*(3),1334-1341.

Kraft, E. (2012). Cognitive function, physical activity, and aging: Possible biological links and implications for multimodal interventions. *Aging, Neuropsychology, and Cognition, 19*, 248-263.

Kramer, A. F., & Willis, S. L. (2002). Enhancing the Cognitive Vitality of Older Adults. *Current Directions in Psychological Science, 11*, 173-177.

Kwakye, L. D., Foss-Feig, J. H., Cascio, C. J., Stone, W. L., & Wallace, M. T. (2011). Altered auditory and multisensory temporal processing in autism spectrum disorders. *Frontiers in Integrative Neuroscience, 4*.

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

Lindenberger, U., & Ghisletta, P. (2009). Cognitive and sensory declines in old age: Gauging the evidence for a common cause. *Psychology and Aging, 24*, 1-16.

Mahncke, H. W., Connor, B. B., Appelman, J., Ahsanuddin, O. N., Hardy, J. L., Wood, R. A., Joyce, N. M., Boniske, T., Atkins, S. M., & Merzenich, M. M. (2006). Memory enhancement in healthy older adults using a brain plasticity-based training program:

A randomized, controlled study. *Proceedings of the National Academy of Sciences, 103*, 12523-12528.

Mishra, J., & Gazzaley, A. (2013). Preserved discrimination performance and neural processing during crossmodal attention in aging. *PLoS ONE, 8*, e81894.

Mishra, J., Martinez, A., Sejnowski, T. J., & Hillyard, S. A. (2007). Early cross-modal interactions in auditory and visual cortex underlie a sound-induced visual illusion. *Journal of Neuroscience, 27,* 4120-4131.

Mozolic, J. L., Hayaska, S., & Laurienti, P. J. (2010). A cognitive training intervention increases resting cerebral blood flow in healthy older adults. *Frontiers in Human Neuroscience, 4*.

Mozolic, J. L., Hugenschmidt, C. E., Peiffer, A. M., & Laurienti, P. J. (2012). Multisensory integration and ageing. In M. M. Murray & M. T. Wallace (Eds.), *The Neural Basis of Multisensory Processes*. Boca Raton (FL): CRC Press.

Mozolic, J. L., Long, A. B., Morgan, A. R., Rawley-Payne, M., & Laurienti, P. J. (2011). A cognitive training intervention improves modality-specific attention in a randomized controlled trial of healthy older adults. *Neurobiology of Aging, 32,* 655-668.

Noack, H., Lövdén, M., Schmiedek, F., & Lindenberger, U. (2009). Cognitive plasticity in adulthood and old age: Gauging the generality of cognitive intervention effects. *Restorative Neurology & Neuroscience, 27*, 435-453.

Owsley, C. (2011). Aging and vision. *Vision Research, 51*, 1610-1622.

Peiffer, A. M., Mozolic, J. L., Hugenschmidt, C. E., & Laurienti, P. J. (2007). Age-related multisensory enhancement in a simple audiovisual detection task. *Neuroreport, 18,* 1077-1081.

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

Pöppel, E. (1997). A hierarchical model of temporal perception. *Trends in Cognitive Sciences, 1*, 56-61.

Powers, A. R., III, Hevey, M. A., & Wallace, M. T. (2012). Neural Correlates of Multisensory Perceptual Learning. *Journal of Neuroscience, 32*, 6263-6274.

Powers, A. R., III, Hillock, A. R., & Wallace, M. T. (2009). Perceptual Training Narrows the Temporal Window of Multisensory Binding. *Journal of Neuroscience, 29*, 12265-12274.

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychol Rev, 103*, 403-428.

Salthouse, T. A. (2009). When does age-related cognitive decline begin? *Neurobiology of Aging, 30,* 507-514.

Setti, A., Burke, K. E., Kenny, R. A., & Newell, F. N. (2011). Is inefficient multisensory processing associated with falls in older people? *Experimental Brain Research, 209,* 375-384.

Setti, A., Finnigan, S., Sobolewski, R., McLaren, L., Robertson, I. H., Reilly, R. B., Anne Kenny, R., & Newell, F. N. (2011). Audiovisual temporal discrimination is less efficient with aging: an event-related potential study. *Neuroreport, 22,* 554-558.

Shams, L., Kamitani, Y., & Shimojo, S. (2000). What you see is what you hear. *Nature, 408,* 788-788.

Shams, L., Kamitani, Y., Thompson, S., & Shimojo, S. (2001). Sound alters visual evoked potentials in humans. *Neuroreport, 12*, 3849-3852.

Smith, G. E., Housen, P., Yaffe, K., Ruff, R., Kennison, R. F., Mahncke, H. W., & Zelinski, E. M. (2009). A cognitive training program based on principles of brain plasticity: Results from the Improvement in Memory with Plasticity-based Adaptive Cognitive Training (IMPACT) Study. *Journal of the American Geriatrics Society, 57*, 594-603.

Stevenson, R. A., Wilson, M. M., Powers, A. R., & Wallace, M. T. (2013). The effects of visual training on multisensory temporal processing. *Experimental brain research, 225*(4), 479–89.

Stevenson, R. A., Zemtsov, R. K., & Wallace, M. T. (2012). Individual differences in the multisensory temporal binding window predict susceptibility to audiovisual illusions. *Journal of Experimental Psychology: Human Perception and Performance*.

Szelag, E., & Skolimowskaa, J. (2012). Cognitive function in elderly can be ameliorated by training in temporal information processing. *Restorative Neurology and Neuroscience, 30*, 419–434.

Vroomen, J., & Keetels, M. (2010). Perception of intersensory synchrony: A tutorial review. *Attention, Perception, & Psychophysics, 72*, 871-884.

Watkins, S., Shams, L., Tanaka, S., Haynes, J. D., & Rees, G. (2006). Sound alters activity in human V1 in association with illusory visual perception. *NeuroImage, 31*, 1247-1256.

Willis, S. L., Tennstedt, S. L., Marsiske, M., Ball, K., Elias, J., Koepke, K. M., Morris, J. N., Rebok, G. W., Unverzagt, F. W., Stoddard, A. M., Wright, E., & for the, A. S. G. (2006). Long-term effects of cognitive training on everyday functional outcomes in older adults. *JAMA, 296*, 2805-2814.

Zampini, M., Guest, S., Shore, D. I., & Spence, C. (2005). Audio-visual simultaneity judgments. *Percept Psychophys, 67*, 531-544.

Zampini, M., Shore, D. I., & Spence, C. (2003a). Audiovisual temporal order judgments. *Experimental Brain Research, 152*, 198-210.

Zampini, M., Shore, D. I., & Spence, C. (2003b). Multisensory temporal order judgments: the role of hemispheric redundancy. *International Journal of Psychophysiology*, *50*, 165-180.

Table 1. (a) Training and control group participants' characteristics; (b) Characteristics for the training group participants whose performance did or did not improve during training from session 1 to 5.

a)

	Training group **(n=24, 11 male)**	**Control group** **(n=10, 4 male)**	**P value**
Age	72.75 (61-86, SD = 6.3)	75.8 (70-83, SD = 4.4)	>0.1
Hearing (Hughson-Westlake test)	Normal^	Normal+	
Visual acuity (LogMar)/	0.005 (SD = 0.1)	0.036 LogMar (SD = 0.08)	>0.4
Contrast sensitivity (Pelli-Robson chart)	1.77 (SD=0.13)	1.68 (SD = 0.22)	>0.2
Mini Mental State Examination	28.2 (SD = 1.2)	28 (SD = 1.32)	>0.8

b)

	Training group: participants who did improve	**Training group: participants who did not improve**	**P value**
Age	71.88 (SD= 5.12)	75.33 (SD= 9)	>0.2
Hearing (Hughson-Westlake test)	Normal	Normal	
Visual acuity (LogMar)/	0.002 (SD= 0.12)	0.013 (SD= 0.11)	>0.8
Contrast sensitivity (Pelli-Robson chart)	1.78 (SD=0.13)	1.72 (SD=0.16)	>0.3
Mini Mental State Examination	27 (SD= 1.72)	29 (SD= 1.04)	>0.1
Median SOA in session 1	290 (SD=134.6)	231 (SD=60.8)	>0.5

^2 participants with hearing loss in one ear only; 2 no audiometric test;
+1 participant with hearing loss in one ear only;

Table 2. Performance (proportion of correct responses) in session 1 and session 5 in the SIFI task, illusory and control conditions for each of the groups (the group who took part in the training task is split according to their improvement in the TOJ task). In the 1 flash/2 beeps condition a high proportion of correct responses corresponds to a low susceptibility to the SIFI illusion (and vice versa).

	Trained group (improve in TOJ)	**Trained group (no improvement in TOJ)**	**Control group (no training)**
Session1	**Mean(st.dev.)**	**Mean(st.dev)**	**Mean(st.dev.)**
1 flash/2 beeps			
30ms	0.51(0.36)	0.52(0.31)	0.39(0.40)
70ms	0.43(0.35)	0.48(0.40)	0.38(0.28)
110ms	0.43(0.40)	0.56(0.21)	0.44(0.38)
150ms	0.50(0.39)	0.65(0.12)	0.43(0.38)
190ms	0.47(0.38)	0.69(0.27)	0.48(0.38)
230ms	0.50(0.43)	0.71(0.29)	0.49(0.34)
270ms	0.50(0.40)	0.75(0.32)	0.54(0.37)
1 flash	0.92(0.15)	0.79(0.29)	0.88(0.21)
2 flashes	0.58(0.34)	0.54(0.25)	0.63(0.21)
1 beep	0.93(0.24)	0.88(0.31)	0.90(0.17)
2 beeps^	0.89(0.15)	0.83(0.26)	0.88(0.21)
2 fl\2b^	0.80(0.19)	0.64(0.22)	0.79(0.23)
Session5	**Mean(st.dev.)**	**Mean(st.dev.)**	**Mean(st.dev.)**
1 flash/2 beeps			
30ms	0.53(0.36)	0.33(0.33)	0.40(0.37)
70ms	0.50(0.35)	0.27(0.24)	0.25(0.28)
110ms	0.55(0.37)	0.46(0.32)	0.46(0.31)
150ms	0.59(0.35)	0.52(0.34)	0.43(0.33)
190ms	0.57(0.37)	0.52(0.29)	0.45(0.35)
230ms	0.61(0.36)	0.69(0.30)	0.49(0.34)
270ms	0.63(0.33)	0.56(0.38)	0.61(0.41)
1 flash	0.92(0.21)	0.67(0.38)	0.73(0.36)
2 flashes	0.63(0.31)	0.63(0.26)	0.60(0.27)
1 beep	0.91(0.21)	0.70(0.41)	0.80(0.31)
2 beeps^	0.88(0.14)	0.69(0.37)	0.87(0.13)
2 fl\2b^	0.77(0.16)	0.63(0.14)	0.78(0.14)

^ Average of all SOAs (30 to 270ms)

Table 3. Linear regression beta coefficients for each separate SOA, calculated by averaging the SOAs for the last 10 reversals for each participant. The susceptibility to the illusion post-training is the dependent variable, the TOJ SOA post-training over the last 10 reversals is the predictor variable. The model is adjusted for the TOJ SOA pre-training over the last 10 reversals and the unisensory performance in the 1 flash, 2 flashes, 2 beeps and the congruent condition 2 flashes/ 2 beeps. Performance in the SIFI trials in session 1 is also introduced as covariate.

SOA (ms) in SIFI task

	270		**230**		**190**		**110**		**70**		**30**	
Predictors	**beta^**	**p**	**beta**	**p**	**beta**	**p**	**beta**	**p**	**beta**	**p**	**beta**	**p**
average 10 rev. Day1	-0.14	0.33	-0.02	0.92	-0.08	0.65	0.23	0.27	0.22	0.42	0.13	0.59
average 10rev. Day5	**-0.31**	**0.04**	**-0.37**	**0.04**	**-0.50**	**0.01**	**-0.88**	**0.00**	**-0.64**	**0.02**	**-0.17**	**0.51**
1 flash	0.26	0.14	0.14	0.52	0.29	0.17	0.67	0.00	0.10	0.71	0.01	0.97
2 flashes	-0.32	0.03	-0.25	0.12	-0.06	0.68	-0.31	0.07	-0.44	0.08	-0.35	0.13
1 beep	-0.34	0.09	-0.45	0.10	-0.22	0.43	-0.60	0.02	-0.45	0.13	-0.36	0.22
2 beeps+	-0.03	0.82	0.14	0.45	-0.03	0.86	0.08	0.62	0.19	0.46	0.23	0.37
2 flashes/2 beeps+	0.28	0.07	0.07	0.71	-0.14	0.43	-0.28	0.17	-0.06	0.82	-0.07	0.77
1 flash/2 beeps (day 1)+	0.77	0.00	0.82	0.00	0.61	0.00	0.99	0.00	0.76	0.02	0.75	0.01
adjusted R^2	0.74		0.65			0.61		0.60		0.25		0.22
F, p (model)	F=9.14, p<0.001		F=6.29, p<0.001		F=5.6, p<0.01		F=5.36, p<0.01		F=1.98, p=0.12		F=1.83, p=0.15	

+ The relevant SOA was used for each model

^ Negative coefficients indicate that the higher the proportion of correct responses in the SIFI task (i.e. fewer illusions) the smaller the size of the temporal window after training (i.e. a shorter SOA in the TOJ training task).

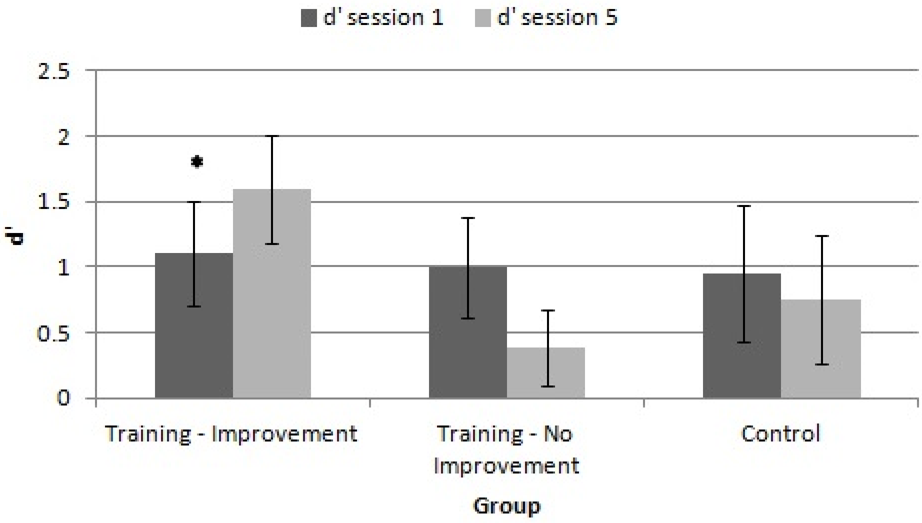

Figure 1. Sensitivity in detecting 2 flashes when presented with 2 beeps in session 1 and session 5 across groups. For the purpose of calculating d', the illusory response of '2 flashes' to the 1 flash/2 beeps stimuli was considered as the false alarm rate. (See text for more details on the d' formula).

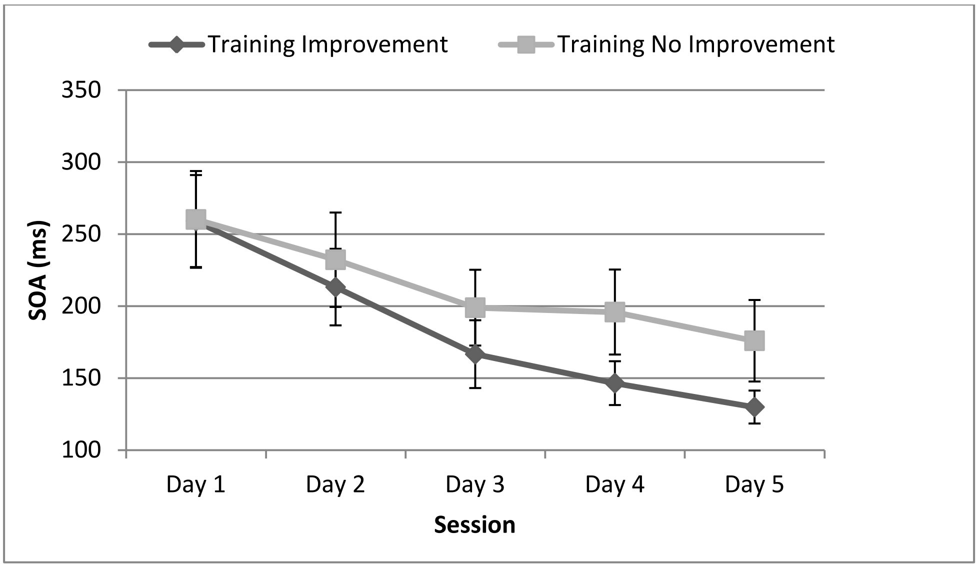

Figure 2. Average SOA at which the staircase converged in session 1 and session 5 in the two groups who underwent TOJ training.

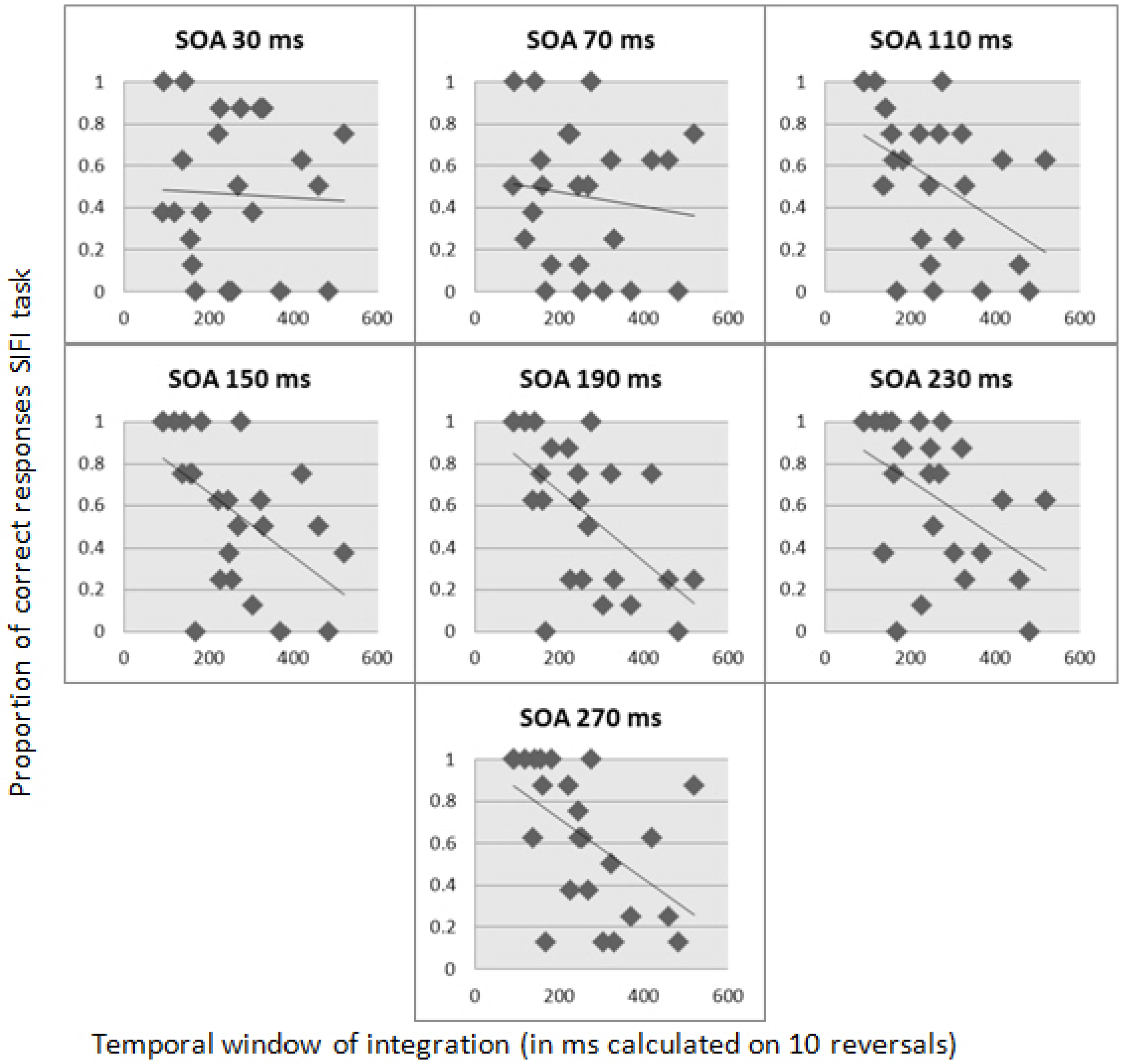

Figure 3. Correlation between the susceptibility to the SIFI (session 5) and the size of the temporal window of integration (session 5) at each stimulus onset asynchrony utilised in the SIFI task. Higher correlations were found with longer SOAs.