Parietal Disruption Alters Audiovisual Binding in the Sound-Induced Flash Illusion

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Abstract

Selective attention and multisensory integration are fundamental to perception, but little is known about whether, or under what circumstances, these processes interact to shape conscious awareness. Here, we used transcranial magnetic stimulation (TMS) to investigate the causal role of attention-related brain networks in multisensory integration between visual and auditory stimuli in the sound-induced flash illusion. The flash illusion is a widely studied multisensory phenomenon in which a single flash of light is falsely perceived as multiple flashes in the presence of irrelevant sounds. We investigated the hypothesis that extrastriate regions involved in selective attention, specifically within the right parietal cortex, exert an influence on the multisensory integrative processes that cause the flash illusion. We found that disruption of the right angular gyrus, but not of the adjacent supramarginal gyrus or of a sensory control site, enhanced participants' veridical perception of the multisensory events, thereby reducing their susceptibility to the illusion. Our findings suggest that the same parietal networks that normally act to enhance perception of attended events also play a role in the binding of auditory and visual stimuli in the sound-induced flash illusion.

Keywords: angular gyrus; flash illusion; multisensory integration; selective attention; transcranial magnetic stimulation

1. Introduction

Perception is fundamentally shaped by the integration of information arising from the different senses. It is well established that compared with a unisensory event, inputs arising from multiple sensory modalities can enhance stimulus detection and reduce perceptual ambiguity, especially when the signal from one of the senses is weak (see for review, Calvert, 2001; Driver and Noesselt, 2008). Similarly, perception can be fundamentally altered by the cognitive processes of attention, which typically act to bias neural activity in favour of behaviourally relevant stimuli (e.g., Gilbert and Sigman, 2007; Knudsen, 2007). Although much recent research has been directed at describing the processes of both multisensory integration and attention, little is known about whether, or under what circumstances, these processes may interact to shape conscious awareness (Talsma et al., 2010). Here we used the widely studied 'sound-induced flash illusion' to investigate the contribution of a specific parietal node within the human attention network to multisensory integration.

The sound-induced flash illusion is a multisensory phenomenon involving a subjective change in the perception of an unambiguous visual stimulus. Specifically, when a single, briefly flashed visual stimulus is accompanied by two or more irrelevant sounds, the single flash of light is often falsely perceived as multiple flashes (Shams et al., 2000). This flash illusion can be induced by a variety of auditory stimuli, but only occurs when the irrelevant sounds fall within a critical window of around 100 ms (Shams et al., 2000, 2002); a touch-induced flash illusion has also been reported (Violentyev et al., 2005; Wozny et al., 2008). Numerous studies have shown that the flash illusion is not explicable as a simple response bias (e.g., McCormick and Mamassian, 2008; Mishra et al., 2007; Rosenthal et al., 2009; Watkins et al., 2006), or by participants incorrectly judging the number of sounds rather than the number of flashes (e.g.,Shams et al., 2002). Indeed, the illusory flash has even been shown to have measurable behavioural (Fiedler et al., 2011; McCormick and Mamassian, 2008) and neural (Mishra et al., 2008; Mishra et al., 2007; Watkins et al., 2007; Watkins et al., 2006) characteristics.

Various brain imaging studies have shown that illusory flash perception is associated with activity in early cortical visual areas (Mishra et al., 2008; Mishra et al., 2007; Watkins et al., 2007; Watkins et al., 2006). Moreover, using transcranial direct current stimulation (tDCS) Bolognini et al. (2004) have shown that occipital and temporal regions are causally involved in the illusion. The sound-induced flash illusion, however, appears to involve more than just the obligatory binding of auditory and visual stimuli. This hypothesis is supported by the observation that illusory flash perception is typically only reported on a proportion of trials (e.g., Shams et al., 2002), suggesting that stimulus characteristics alone do not determine the illusory percept. In this context it has been reported that cueing attention to stimulus events in the (normally) irrelevant modality alters perception of the flash illusion (Werkhoven et al., 2009). Similarly, the amplitude of neural event-related potentials, which had previously been shown to correlate with the frequency of illusory flash reporting (Mishra et al., 2007), has been shown to be amplified when the relevant stimulus is attended to (Mishra et al., 2009). These effects suggest that mechanisms of selective attention may be involved in generating – or at least modulating – the flash illusion. Such effects are likely to arise from activity within parietal cortex, which is known to play a critical role in attentional control (Gottlieb, 2007; Kanwisher and Wojciulik, 2000).

Previous studies that have used transcranial magnetic stimulation (TMS) to temporarily disrupt parietal cortex have shown that the right angular gyrus (AG) and supramarginal gyrus (SMG) play a critical role in various aspects of selective attention (Cattaneo et al., 2009; Chambers et al., 2006; Gobel et al., 2001; Hilgetag et al., 2001; Schenkluhn et al., 2008; Zenon et al., 2009). In particular, these parietal regions are important for shifting attention to unisensory stimuli both within and between the senses (Chambers et al., 2007; Chambers et al., 2004a), suggesting that they may also play a role in the perception of stimuli arising simultaneously from multiple sensory modalities. Thus, if selective attention is involved in generating the flash illusion, then TMS disruption of these parietal regions is likely to alter illusory perception.

The only neurodisruption study that has addressed this issue to date found no effect of parietal stimulation on the flash illusion (Bolognini et al., 2011). In that study, participants were presented with various flash/sound combinations and were required to report the number of flashes perceived. They found that tDCS of the right parietal cortex did not alter illusory flash perception (Bolognini et al., 2011). Although this might be taken to suggest that parietal cortex is not involved in the flash illusion, it is possible that placement of the electrodes over P4 (which sits roughly above the intraparietal sulcus) and the contralateral supraorbital area induced current flow that failed to perturb activity within the inferior parietal lobule, which includes the AG and SMG. It is also possible that due to the low spatial resolution of tDCS (Stagg and Nitsche, 2011; Zaghi et al., 2010), widespread cortical disruption was induced that affected several parietal subregions, each of which plays a distinct – and potentially opposing – role in attention and multisensory integration (Chambers et al., 2004a; Chambers et al., 2004b; Gobel et al., 2001). Here, we use MRI-guided TMS to investigate the unique contributions of two distinct subregions within the inferior parietal lobule, the AG and SMG, in the sound-induced flash illusion. Based on previous studies of the critical role of the AG in regulating selective attention (e.g., Cattaneo et al., 2009; Chambers et al., 2004a; Gobel et al., 2001; Muggleton et al., 2008; Zenon et al., 2009), we predicted that disruption of this area would decrease the influence of attentional control mechanisms on the binding of visual and auditory information, thereby leading to a change in illusory flash perception.

2. Materials and Methods

All participants had normal or corrected to normal vision and no known hearing deficits. Experimental protocols were approved by a relevant University of Queensland human ethics committee and fully informed written consent was obtained from each participant.

2.1 Behavioural experiment

An initial behavioural experiment was conducted in which the basic task for participants was to report the number of visual flashes they perceived on a computer display while ignoring any irrelevant sounds. Data from 27 participants (15 male) were included in the analysis; data from a further six participants (two male) were not included because they performed at chance-level in identifying a single flash in the absence of sounds (< 29.2% correct). Visual stimuli were presented on a 21' CRT monitor (1024 x 768 resolution; 100 Hz refresh) with a black background in a dimly lit room. The visual stimulus consisted of a white disc of 2° diameter presented 8° to the left or right of a central fixation cross for 20 ms. We did not expect a difference in the flash illusion for visual stimuli presented to the left or right of fixation (Innes-Brown and Crewther, 2009), but included these positions to allow for investigation of any lateralised effects of right hemisphere TMS in the main experiment. Auditory stimuli were presented bilaterally from desktop speakers (Creative Gigaworks T20) located on either side of the monitor. The sound stimulus was a ramped 3500 Hz pure tone presented for 8 ms at an intensity of approximately 80 dB SPL (measured at the ear). Stimulus presentation was controlled by a PC running Matlab and the Cogent toolbox (LON at the Wellcome Department of Imaging Neuroscience, UK).

Four different stimulus types were used, as depicted in Fig. 1A. In two conditions participants were presented with either one flash or two flashes without any sounds. The stimulus onset asynchrony (SOA) in the two-flash condition was 70 ms, which was based on pilot testing that revealed that although the discrimination was difficult, most individuals could correctly identify two flashes on the majority of trials with this SOA. In the other two conditions a single flash accompanied a pair of tones, with the tones separated by an SOA of either 70 ms or 160 ms (Fig. 1A). Because the flash illusion only occurs when the irrelevant sounds fall within a window of approximately 100 ms (Shams et al., 2002), it was expected that in the 70 ms SOA condition participants would report the illusion of multiple flashes (the 'illusion condition') on a proportion of trials. The 160 ms SOA condition was not expected to induce a flash illusion (the 'illusion control' condition), and was included to examine if participants incorrectly reported the number of tones rather than the number of flashes (Shams et al., 2002). In both cases the flash and first tone were synchronized. In each of the four conditions the flashes occurred randomly on the left or right of fixation in equal proportions.

Insert Figure 1 approximately here

Participants sat 60 cm from the monitor with their head in a custom frame comprising a chinrest and forehead brace. The participants' task was to maintain central fixation and report the number of flashes they perceived on each trial, ignoring any irrelevant sounds. Because it is possible that participants could perceive more than two flashes on a given trial, responses were made via a button press with the left hand to indicate 'one flash' and the right hand to indicate that 'more than one flash' was perceived. No time pressure was placed upon participants, and their responses were not timed. The stimuli were presented in two blocks, each comprising 12 randomized trials of every condition (192 trials in total). A short rest break was offered between the blocks, and the inter-trial interval was jittered between 1 - 1.5 sec. A short practice (10 trials) preceded the task proper.

2.2 TMS Experiment

Following the initial behavioural investigation, participants went on to complete the TMS experiment if their performance in the illusion condition of the behavioural experiment was not at ceiling or floor level. This screening ensured that both TMS-induced increases and decreases in illusion perception could be detected. Twelve participants from the initial behavioural experiment met these criteria; eight were male and all were right handed (mean age 26 years; range 20-39). The behavioural task for the TMS experiment was identical to that described for the behavioural experiment, with the addition that remote, infrared eye-tracking was undertaken during the task (Eyelink 1000, SR Research, Ontario, Canada). The random presentation of visual stimuli to the left or right of centre encouraged central fixation, and the eye tracking data were used to discard trials from the analysis in which blinks occurred or where fixation deviated from centre by more than 2°. Eye tracking data were not available for two participants (one of whom wore glasses, and another due to technical reasons in one of the sessions), but online monitoring confirmed that these participants maintained fixation. For the remaining participants, eye-trace data resulted in the removal of an average of only 2.3% (SD = 3.5%) of trials.

Prior to participants' first TMS session a T1-weighted, high resolution (0.9 mm isotropic) structural MRI was acquired using a Siemens 3T Magnetom Trio or 4T Bruker Medspec imager (Centre for Advanced Imaging, The University of Queensland). Scans were processed with the neuro-navigation software ASA-Lab (ANT, The Netherlands) and used to anatomically locate the brain sites of interest in the right hemisphere. As shown for one participant in Fig. 1B, the AG was defined as the region directly adjacent to the dorsolateral projection of the superior temporal sulcus, which bifurcates the AG in both hemispheres (see Chambers et al., 2004a). The SMG was defined as the region adjacent to the dorsolateral projection of the lateral sulcus, posterior to the post-central sulcus and anterior to the superior temporal sulcus. The primary somatosensory cortex (SI) was chosen as a control site, due to its proximity to the AG and SMG, and because it was not expected to be involved in the flash illusion. TMS of SI was expected to produce similar TMS-related artefacts (noise and tactile sensations) to the critical AG and SMG sites, but was not expected to affect the flash illusion. The SI site was defined as the region lying between the central sulcus and post-central sulcus, posterior to but approximately along the midline of the superior frontal sulcus. Each cortical site was targeted with TMS using a Polaris-based infrared frameless stereotaxic system and Visor software (ANT, The Netherlands). For the purpose of reporting the stimulation sites Talairach co-ordinates were generated using the ASA-Lab software and mean coordinates are presenting in Fig. 1B.

The three brain sites were targeted with TMS in different sessions (counterbalanced across participants), separated by at least 24 hours. TMS was delivered using a Magstim Super Rapid-2 stimulator and 70 mm air-cooled figure-of-eight coil (Magstim, UK). Stimulus intensity was set at 100% of each participant's resting motor threshold, which was defined as the minimum TMS intensity required to induce a motor evoked potential in the abductor pollicis brevis of at least 50 μV in at least five out of ten pulses. The mean TMS intensity used across participants was 57% machine output (range 47-70%). For all sites the coil handle was oriented toward the vertex and the coil was held in place using a tripod and articulated clamp. A temple-guard was used in addition to the custom chinrest to help keep participants' head still during the delivery of TMS. Pulses were delivered at a rate of 1 Hz for 20 minutes, which has the effect of decreasing neural responses in the targeted area for at least 15 minutes following the cessation of stimulation (Chen et al., 1997). Importantly, across all sessions the behavioural task was completed within this timeframe of TMS effects (mean 11 min 26 sec; range 586-782 sec). Prior to delivering the TMS a short practice of the behavioural task was completed (10 trials). There were no adverse reactions to the TMS.

2.3 Auditory Control Experiment

To rule out any possibility that TMS over parietal cortex altered auditory perception, and that this in turn might have influenced the audiovisual illusion in the main experiment, we conducted an additional control experiment with the aim of examining the effect of AG stimulation on the perception of unisensory auditory events. Six participants (four male), all of whom had previously completed the main TMS study, took part in the auditory control. The multisensory stimuli were the same as those used in the main experiment, consisting of a single flash of light with two tones that had an SOA of either 70 or 160 ms (the 'illusion' and 'illusion control' conditions in the TMS experiment; see Fig. 1A). In the other two conditions sounds were presented without any concurrent visual stimuli, consisting of either a single tone or two tones with 70 ms SOA. The participant's task was to report the number of sounds perceived ('one' or 'more than one') while maintaining central fixation and ignoring any irrelevant flashes (fixation was verified online using infrared eye tracking). Stimulus characteristics, presentation and timing were identical to those used in the main experiment, with a total of 48 trials presented in each condition. For the multisensory trials, flashes occurred randomly on the left or right of fixation (in equal proportions), but flash side was not a factor of interest. Participants completed the auditory detection task before and immediately after TMS, with the post-TMS blocks completed within 638 sec of TMS cessation. The procedure used for TMS was the same as that used in the main TMS experiment (intensity range 55-71% machine output). There were no adverse reactions to TMS.

2.4 Statistical Analysis

Differences in accuracy were analysed using a repeated measures analysis of variance (ANOVA). For the initial behavioural experiment, two ANOVAs were undertaken. For the no-sound conditions an ANOVA with the factors of Flash (one, two) and flash Side (left, right) was conducted. For the sound conditions, an ANOVA with the factors Tone SOA (70 ms, 160 ms) and flash Side was used. In the TMS experiment, separate ANOVAs were also performed for the sound and no-sound conditions. For the no-sound conditions, an ANOVA with the factors TMS Site (SI, AG, SMG), Flash (one, two) and flash Side (left, right) was used. The sound condition was analysed using an ANOVA with the factors Tone SOA, TMS Site and flash Side. Analysis of simple main effects was undertaken using two-tailed t-tests, and stated p-values have been corrected for multiple comparisons using the Bonferroni method.

In the main TMS experiment, to further investigate whether any changes in accuracy following TMS were due to an increase in perceptual sensitivity rather than to response bias, analyses based on signal detection theory were also undertaken. Sensitivity (*d'*) and response bias (λ_{centre} or *c*) were defined as d' = [z(hits) – z(false alarms)] and c = -0.5*[z(hits) + z(false alarms)], where z(p) is the inverse of the cumulative normal distribution (MacMillan and Creelman, 2004). In line with previous studies (e.g., Rosenthal et al., 2009; Violentyev et al., 2005; Watkins et al., 2006), double flashes were treated as the target, such that the correct detection of two flashes in the two-flash condition was considered a 'hit', whereas the correct detection of a single flash in the one-flash condition was a 'correct rejection'. 'False alarms' therefore corresponded to single flash trials in which more than one flash was reported (i.e., an illusory flash). Instances of p = 1 were approximated as 1 - 1/N, where N is the number of trials. Because *d'* reflects how well two flashes are discriminated, decreased levels of illusory perception were expected to be associated with higher levels of sensitivity (increased *d'* values). The *d'* and *c* estimates were submitted to separate repeated measures ANOVA with the factors of TMS Site and flash Side. These ANOVAs were followed up with planned comparisons between the AG and the other two TMS sites using paired, two-tailed t-tests and the Bonferroni correction. Across all ANOVAs the sphericity assumption was only violated in one (non-significant) interaction. Behavioural data are plotted using within-subjects (normalized) s.e.m. (Cousineau, 2005).

3 Results

3.1 The sound-induced flash illusion

Mean responses for identifying flashes in the absence of sounds are presented in Fig. 2A. In the absence of tones participants were highly accurate in identifying flashes, with no difference between flashes presented to the left or right of fixation (Side: $F_{1,26} = 1.77$, $p = .195$; Flash x Side: $F_{1,26} = 0.21$, $p = .653$), but a weak trend toward slightly superior performance in the one flash condition (Flash: $F_{1,26} = 3.43$, $p = .075$). In contrast, as shown in Fig. 2B, in the presence of irrelevant sounds accuracy for identifying one flash was reduced to less than 25% correct in the illusion condition. That is, participants reported perceiving multiple flashes on more than 75% of trials when in fact only one flash had been presented. Importantly, this illusory effect cannot be explained by participants simply counting tones instead of flashes, as accuracy in the other two-tone (illusion-control) condition remained significantly higher (Tone SOA: $F_{1,26} = 86.18$, $p < .001$). It can also be seen from Fig. 2B that for both sound conditions there was a trend toward higher accuracy when flashes were presented on the left side of the display than on the right side (Side: $F_{1,26} = 4.06$, $p = .054$; Tone SOA x Side: $F_{1,26} = 0.65$, $p = .427$).

Insert Figure 2 approximately here

To summarize, the initial behavioural experiment replicated previous findings (e.g., Shams et al., 2002) by showing a robust illusory flash effect when a single visual stimulus was presented concurrently with a pair of tones separated by 70 ms. As expected, the illusory effect did not occur when a single visual stimulus was presented with a pair of tones separated by 160 ms (the illusion-control condition). We can thus rule out that the illusory flash effect arose because participants simply counted the tones.

3.2 The effect of parietal disruption on the sound-induced flash illusion

Mean accuracy for identifying flashes in the absence of sounds following TMS is presented in Fig. 3A. Accuracy was uniformly high, and did not differ between the one- and two-flash conditions (Flash: $F_{1,11} = 0.34$, $p = .572$). Importantly, there was no difference in accuracy across the TMS sites (Site: $F_{2,22} = 0.88$, $p = .429$), or for left versus right flashes (Side: $F_{1,11} = 1.35$, $p = .270$; all interactions $p > .28$). These results suggest that parietal TMS does not affect veridical perception of brief, suprathreshold visual stimuli when these are presented in isolation (i.e., without any concurrent auditory events). By contrast, in the multisensory conditions shown in Fig. 3B, whereas accuracy in the illusion-control condition remained high, accuracy in the illusion condition was significantly reduced (Tone SOA: $F_{1,11} = 147.22$, $p < .001$). These effects are consistent with those of the initial behavioural experiment in showing that the illusion is robust and is not simply a result of participants counting tones. There was no difference in accuracy for visual stimuli presented on the left or right of the display (Side: $F_{1,11} = 0.97$, $p = .347$).

Insert Figure 3 approximately here

Critically, TMS of the different brain sites induced a change in accuracy (Site: $F_{2,22} = 9.08$, $p < .01$) that varied across the sound conditions (Site x Tone SOA: $F_{2,22} = 11.57$, $p < .001$; all other interactions $p > .32$). There was no difference in accuracy across TMS sites for the illusion-control condition ($F_{2,22} = 0.74$, $p = .489$), but there was a highly significant difference across sites for the illusion condition ($F_{2,22} = 11.81$, $p < .001$). Follow-up analysis revealed that in the illusion condition, TMS of AG resulted in a significant increase in accuracy for detecting flashes relative to TMS of SI ($t_{11} = 3.743$, $p < .05$) or SMG ($t_{11} = 3.826$, $p < .01$; SMG versus SI: $t_{11} = 0.097$, $p = 1$). Specifically, TMS of the AG caused an increase in accuracy in the illusion-inducing condition – consistent with reduced susceptibility to the flash illusion – of around 50% relative to the baseline level.

To further explore whether the observed reduction in the flash illusion following TMS of the AG is attributable to a change in perceptual sensitivity, additional analyses based on signal detection theory were undertaken. Mean sensitivity (d') values for the three TMS sites are presented in Fig. 4A, which shows that sensitivity varied across the TMS sites (Site: $F_{2,22} = 9.07$, $p < .01$; Side: $F_{1,11} = 0.06$, $p = .811$; Site x Side: $F_{2,22} = 0.19$, $p = .831$). Specifically, following TMS of the AG there was a 68% increase in sensitivity compared with TMS of SI, and a 44% increase in sensitivity compared with TMS of the SMG; both these effects were statistically reliable (AG versus SI: $t_{11} = 3.833$, $p < .01$; AG versus SMG: $t_{11} = 2.692$, $p < .05$). As shown in Fig. 4B, independent of this increase in sensitivity there was also an increase in mean criterion following stimulation of the AG (Site: $F_{2,22} = 7.21$, $p < .01$; Side: $F_{1,11} = 0.06$, $p = .814$; Site x Side: $F_{2,22} = 1.50$, $p = .245$). This shift in c toward more unbiased values following stimulation of the AG was significant compared to the SMG site ($t_{11} = 3.388$, $p < .05$), but only marginal compared to SI ($t_{11} = 2.426$, $p < .067$). Importantly, these additional analyses show that the change in illusory perception following TMS of the AG is due to a real change in sensitivity for detecting flashes, and is not merely due to a change in response bias.

Insert Figure 4 approximately here

3.3 Effect of AG stimulation on unisensory auditory perception

The results of the main TMS experiment suggest that the effect of AG stimulation on the sound-induced flash illusion is not due to a change in unisensory *visual* perception. It remains possible, however, that a change in unisensory *auditory* perception could underlie the effect. Specifically, if TMS of the AG resulted in two tones (with 70 ms SOA) being perceived as a single tone, a concomitant reduction in illusory perception would ensue. To investigate whether AG stimulation altered unisensory auditory perception, a control experiment was conducted using a subgroup of the participants who had completed the main TMS experiment. This group had shown a substantial reduction in susceptibility to the flash illusion following TMS of the AG compared to both the SI (55% reduction) and SMG (67% reduction) sites. Data for the unisensory auditory control experiment are presented in Fig. 5, which shows that accuracy was uniformly high in all conditions. Critically, accuracy for detecting both one and two tones was not reduced following TMS. In particular, in the two-tone condition with 70 ms SOA and no flash, no errors were made either before or after TMS. Similarly, in the condition in which one flash was paired with two tones that had an SOA of 70 ms – the illusion condition in the main experiment – detection accuracy was perfect before and after

TMS (note that because mean accuracy was 100% in these conditions, inferential statistical analysis is not possible). These data show that stimulation of the AG did not alter observers' ability to discriminate the sound stimuli that were used to generate the flash illusion in the main experiment. The effect of AG stimulation on the flash illusion in the main experiment therefore cannot be attributed to disruption of unisensory auditory perception.

Insert Figure 5 approximately here

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4. Discussion

The sound induced flash illusion is a robust multisensory phenomenon that is associated with neural activity in visual cortex (Watkins et al., 2007; Watkins et al., 2006) and is resistant to feedback training (Rosenthal et al., 2009). Illusory flash perception, however, only occurs on a proportion of trials (e.g., Shams et al., 2002) and is sensitive to manipulations of selective attention (Werkhoven et al., 2009), suggesting that top-down cognitive processes may be involved in the erroneous binding of visual and auditory signals. We investigated the role of attentional control regions within the inferior parietal lobule in the flash illusion. We showed that stimulation of the right AG, but not of the adjacent SMG or of a sensory control site, selectively improved veridical perception of visual events under conditions that normally produce a robust flash illusion. Analysis based on signal detection theory revealed that the decrease in illusory perception following TMS of the AG was associated not only with a shift in criterion toward less biased (more conservative) values, but also with a reliable increase in sensitivity for detecting visual events. These observations are consistent with a previous report showing that the flash illusion is associated with a decrease in sensitivity and a shift in criterion to less conservative values (McCormick and Mamassian, 2008). Critically, we were able to show that TMS did not alter perception of visual stimuli when they were presented in the absence of sounds, or when the visual events were accompanied by two sounds separated by a slightly longer SOA. Stimulation of the AG in a follow-up control experiment revealed that disruption of this parietal area also did not alter unisensory perception of the auditory stimuli. Together, these results suggest that the AG is involved in modulating the binding of visual and auditory stimuli in the sound-induced flash illusion.

4.1 Role of the parietal cortex in audiovisual integration

Although several neuroimaging studies have shown that multisensory integration is associated with activity in the inferior partial lobule (for a review, see Stein and Stanford, 2008), studies using neuro-disruption techniques have failed to demonstrate a causal role for this area (Bertini et al., 2010; Bolognini et al., 2009; Bolognini et al., 2010; Pourtois and de Gelder, 2002). It has even been suggested that the parietal cortex is not critically involved in the flash illusion (Bolognini et al., 2011), or in ventriloquism, a multisensory illusion in which a sound is mislocalised toward an irrelevant visual stimulus (Bertini et al., 2010). The discrepancy between those results and our findings may reflect experimental differences, such as the exact parietal region targeted with TMS, or the use of direct current stimulation to polarize a large expanse of cortex (Bolognini et al., 2011). They may also point to a divergence in the role of the parietal cortex in various aspects of multisensory integration (Driver and Noesselt, 2008). For example, the subtle spatial changes induced in ventriloquism might involve different mechanisms to those responsible for the phenomenological change in perception observed with the flash illusion (Bertini et al., 2010). Unlike the flash illusion, however, the ventriloquist illusion is not affected by manipulations of selective attention (Bertelson et al., 2000; Vroomen et al., 2001), even though attention can spread across modalities during ventriloquism (Busse et al., 2005). Therefore, the contrasting results may also be explained by the involvement of attentional mechanisms in generating the flash illusion.

Previous research has shown that the right AG is involved in various aspects of visuo-spatial attention (Cattaneo et al., 2009; Muggleton et al., 2008) and in the control of shifts of attention within and between sensory modalities (Chambers et al., 2007; Chambers et al., 2004a). These observations are consistent with the idea that the right AG is part of a ventral frontoparietal attention network that serves an alerting function, drawing attention to salient sensory stimuli (Corbetta and Shulman, 2002). This system is well positioned to modulate the integration of multisensory stimuli, as it links ventral frontal, inferior parietal and temporal cortices. It has been proposed that the ventral attention system acts as a ‘circuit-breaker’ for a dorsal attention system, which is more concerned with the goal-directed selection of stimuli (Corbetta and Shulman, 2002). In the flash illusion, the ventral (stimulus-driven) attention network could provide a basis for the irrelevant auditory signals to interfere with processing of the task-relevant visual event, resulting in the erroneous binding (integration) of the auditory and visual stimuli. By targeting the AG with TMS, the circuit-breaker function of the ventral attention network is disrupted, suppressing the influence of the irrelevant auditory stimuli on neural processing of the relevant visual event.

In a previous study of the flash illusion it was shown that illusory perception was reduced under conditions in which both modalities (visual and tactile) were attended compared with conditions in which only one modality was attended (Werkhoven et al., 2009). These effects were taken to indicate that attentional mechanisms act to reduce bottom-up interference from the irrelevant modality. Our results, however, suggest that attentional mechanisms usually act to increase illusory perception, as suppression of attention-related networks resulted in more veridical perception. These differences can be explained by the fact that attending to both modalities (Werkhoven et al., 2009) would have engaged the dorsal (goal-directed) attentional network, whereas TMS over the AG disrupted the ventral (stimulus-driven) attentional network. On this account, the influence of attention on the multisensory flash illusion should depend on the interaction between top-down and stimulus-driven attentional mechanisms; this idea is consistent with the notion that these partially segregated attentional networks usually interact to shape (unisensory) visual perception (Corbetta and Shulman, 2002).

Although the results of our study are consistent with the notion that the AG influences the flash illusion through a ‘bottom-up’ (attentional alerting) function, we cannot exclude the possibility that this parietal area has an influence on the flash illusion that does not involve mechanisms of attention. One way in which this could occur is through modulation of cortical oscillations. It was recently demonstrated that the McGurk effect, another audio-visual illusion that is affected by manipulations of selective attention (Alsius et al., 2005; Alsius et al., 2007) and that also only occurs on a proportion of trials (e.g., Kilian-Hütten et al., 2011; Nath and Beauchamp, 2012), depends on the pre-stimulus state of cortical networks (Keil et al., 2012). Specifically, it was found that synchronisation across large-scale cortical networks predisposes individuals to illusory binding of audiovisual stimuli in the McGurk effect. Interestingly, mechanisms of attention can modify oscillatory activity (Buschman and Miller, 2007; Lakatos et al., 2009; Siegel et al., 2008), suggesting that fluctuations in attention may underlie trial-by-trial variability in illusory binding of audiovisual stimuli (see also, Hipp et al., 2011). Nonetheless, both the sound-induced flash illusion (Bhattacharya et al., 2002; Mishra et al., 2007) and the touch-induced flash illusion (Lange et al., 2011) have been associated with alterations in gamma-band activity in occipital areas. Thus, it is possible that TMS of the AG induced a state in which the critical cortical networks involved in generating the flash illusion were less disposed to illusory binding.

In this study we found a non-lateralised effect of right parietal TMS on visual perception, a result that is consistent with some previous studies that employed unisensory stimuli (Cattaneo et al., 2009; Chambers et al., 2004a). The effect of TMS on perception of the flash illusion was only found following stimulation of the AG, suggesting that the SMG is not a critical node in the attention network that influences multisensory integration. Our study is not the first to report a dissociation between the AG and SMG in attention (see, e.g., Chambers et al., 2004a; Chambers et al., 2004b; Gobel et al., 2001). It is likely that such differences in function are underpinned by variations in neural connectivity of the two areas. Recent neuroimaging has revealed that even within the AG there are different patterns of cortical and subcortical connectivity, with the anterior portion more closely associated with a ventral (alerting) attention system (Uddin et al., 2010). The AG also has different connectivity to that of the nearby intraparietal sulcus (Uddin et al., 2010), which was the region targeted by Bolognini et al. (2011) in their tDCS study of the flash illusion. In this context, it was recently reported that patients with acquired brain lesions that display visual extinction have lesions in the AG and superior temporal sulcus, but not the intraparietal sulcus or SMG (Chechlacz et al., 2012; see also, Petrides and Iversen, 1978). As well as demonstrating the functional segregation of attention networks within the parietal lobule, those results suggest that TMS of the AG might interfere with a network incorporating the superior temporal sulcus, which was previously shown to be involved in the flash illusion (Mishra et al., 2007; Watkins et al., 2006).

4.2 Conclusions

Previous research has shown that the flash illusion is sensitive to manipulations of selective attention and is typically only perceived on a proportion of trials, suggesting that the illusion involves more than just the obligatory binding of visual and auditory stimuli. Here, we have shown that disruption of the right AG, which is known to play a critical role in various aspects of attentional control, significantly reduces the consistency of the flash illusion. We have proposed that disruption of the AG alters a stimulus-driven attentional network, effectively attenuating the influence of irrelevant auditory stimuli on the processing of visual events, and reducing the likelihood that visual and auditory stimuli are erroneously integrated. An interesting question for future research is whether these effects extend to the fusion effect, in which two flashes of light are incorrectly perceived as one flash in the presence of a single sound (e.g., Andersen et al., 2004; but see, e.g., Innes-Brown and Crewther, 2009). Whatever the mechanism underlying the current results, we have shown for the first time that a critical node in the parietal attentional network is involved in the sound induced flash illusion and hence plays a causal role in multisensory integration.

Acknowledgements

This work was supported by a University of Queensland Postdoctoral Fellowship to MK. We would like to thank Dr David Lloyd for programming and technical assistance.

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Figure Legends

Fig. 1. Experimental stimuli, TMS sites in one participant and mean Talairach co-ordinates.

A, Stimuli used in both experiments. The stimulus consisted of either a single flash of light ('one flash' condition) or two flashes ('two flash' condition) presented without sounds, or a single flash of light presented with two tones that were separated by either 70 ms ('illusion' condition) or 160 ms ('illusion-control' condition). **B,** The three right parietal sites targeted with TMS are shown for one participant in the top panel: triangle = somatosensory cortex (SI), circle = angular gyrus (AG), square = supramarginal gyrus (SMG). In the bottom panels, the coronal and sagittal sections show the location of the AG (left panel) and SMG (right panel) for the same participant. The insert table shows mean (SD) Talairach co-ordinates for the three sites across all participants.

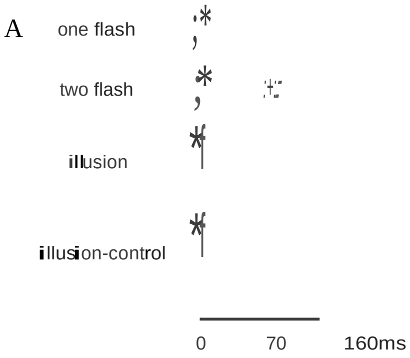
Fig. 2. Mean accuracy for detecting flashes in the initial behavioural experiment. **A,** Mean accuracy is shown for flashes presented to the left (black bars) and right (grey bars) of fixation in the absence of sounds. Accuracy is high in both the no-sound conditions. **B,** Mean accuracy for detecting flashes is shown for the two-tone conditions as a function of flash side. Significantly poorer accuracy in the illusion condition compared with the illusion-control condition shows that participants perceived the illusion of multiple flashes on most trials in which just a single flash was presented. Error bars indicate within-subjects s.e.m.

Fig. 3. Mean accuracy for detecting flashes following TMS. **A,** Accuracy is shown for the one- and two-flash conditions in the absence of sounds for visual stimuli presented to the left (black bars) and right (grey bars) of fixation for the three brain sites stimulated. Accuracy does not vary across the TMS sites. **B,** Accuracy for detecting flashes is shown for the two-tone conditions as a function of flash side and TMS site. Accuracy is lower in the illusion condition compared with the illusion-control condition, demonstrating a sound-induced flash illusion. Critically, compared with TMS of SI or SMG, TMS of AG increases accuracy for detecting flashes in the illusion condition, thereby reducing illusory perception. Error bars indicate within-subjects s.e.m.

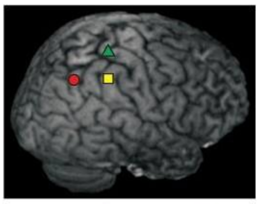
Fig. 4. Perceptual sensitivity (*d*') and response criterion (*c*) following TMS. Mean sensitivity and criterion values are shown for flashes presented to the left (black bars) and right (grey bars) of fixation for the different brain sites stimulated. **A,** TMS of the AG increased perceptual sensitivity compared with TMS of both the SI and SMG sites. **B,** TMS of the AG shifted the criterion to less biased (higher) values compared with TMS of the SMG site, but this effect was only marginal in comparison with SI. Error bars indicate within-subjects s.e.m.

Fig. 5. Mean accuracy for detecting tones in the auditory control experiment. Accuracy for detecting tones before (black bars) and after (grey bars) TMS of the AG is shown for the various auditory conditions. Accuracy was uniformly high in all conditions and was not reduced by TMS. Error bars indicate s.e.m.

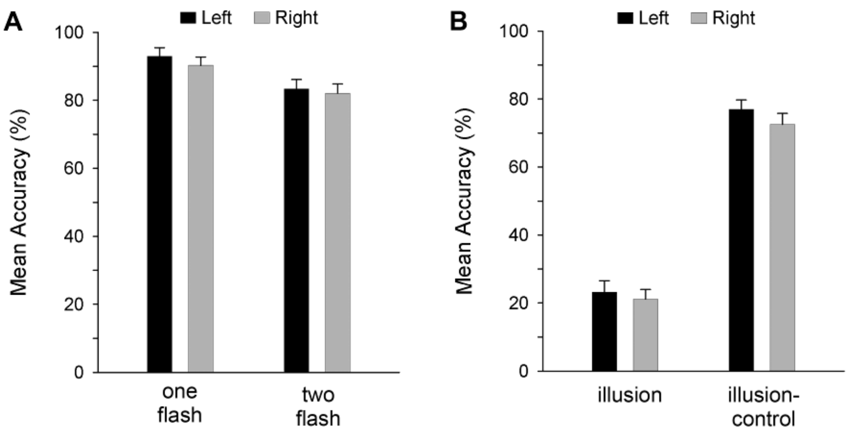
A

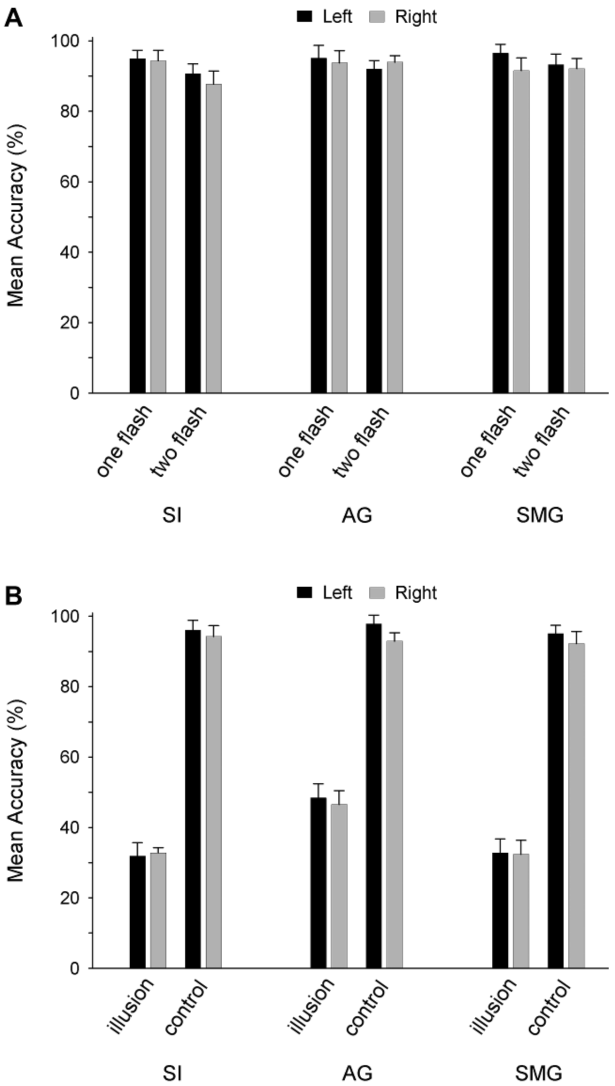


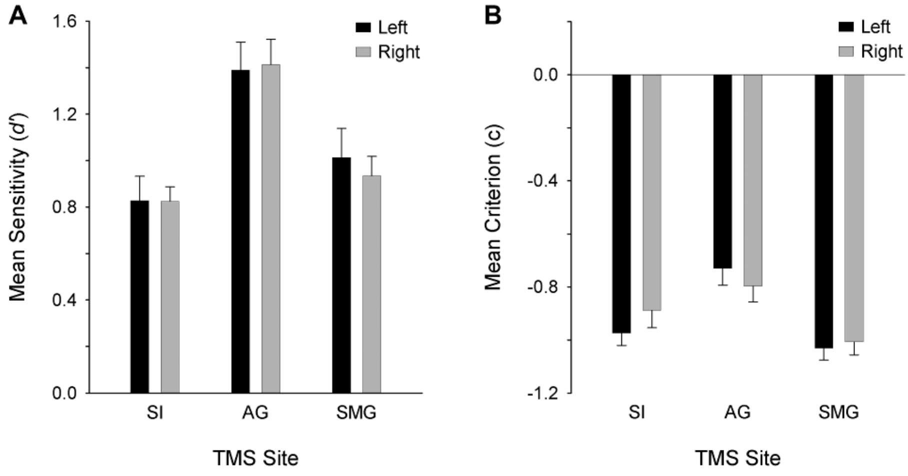
B



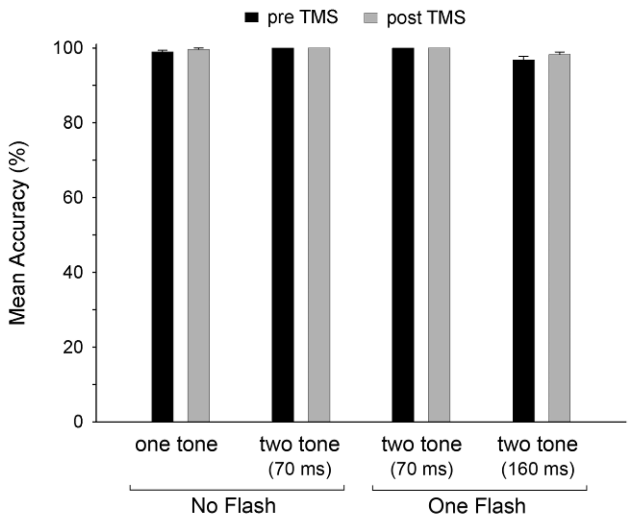
	Mean (SO) Talairach co-ordinates (mm)		
SI	34.0 (5.1)	-32.5 (8.0)	64.6 (2.6)
AG	43.9 (3.6)	.j)7.4 (6.4)	41.4 (5.4)
SMG	53.6 (3.5)	-41.6 (7.0)	47.3 (4.8)


A
Left
Right
Mean Accuracy (%)
100
80
60
40
20
0
one flash
two flash
B
Left
Right
Mean Accuracy (%)
100
80
60
40
20
0
illusion
illusion-control


A
Left
Right
Mean Accuracy (%)
100
80
60
40
20
0
one flash
two flash
one flash
two flash
one flash
two flash
SI
AG
SMG
B
Left
Right
Mean Accuracy (%)
100
80
60
40
20
0
illusion
control
illusion
control
illusion
control
SI
AG
SMG



A
1.6
1.2
0.8
0.4
0.0
Mean Sensitivity (d')
Left
Right
SI
AG
SMG
TMS Site
B
0.0
-0.4
-0.8
-1.2
Mean Criterion (c)
Left
Right
SI
AG
SMG
TMS Site


pre TMS
post TMS
Mean Accuracy (%)
100
80
60
40
20
0
one tone
two tone
(70 ms)
two tone
(70 ms)
two tone
(160 ms)
No Flash
One Flash