

# The origin of the audiovisual bounce inducing effect: A TMS study

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## ARTICLE INFO

### Article history:

Received 21 December 2011  
Received in revised form 20 February 2012  
Accepted 27 February 2012  
Available online 6 March 2012

### Keywords:

Crossmodal perception  
Multimodal perception  
Audiovisual perception  
TMS  
Posterior parietal cortex

## ABSTRACT

The audiovisual bounce inducing effect (ABE) is a bouncing percept induced by the presence of a sound at the moment of two moving objects intercepting in a motion display otherwise perceived as streaming. The origin of the ABE is still debated: the effect could arise from the subtraction of attentional resources caused by the sound (needed to favor the perception of streaming), and/or from the cross-modal integration (binding) of visual and auditory information: indeed bouncing-like sounds are best in inducing the ABE. The neural mechanism responsible for the ABE is still unknown. Here, by using offline TMS, we investigated the role of the posterior parietal cortex (PPC), thought to be involved in both attentional and binding processes, in the generation of the ABE.

Results show that disrupting the functional integrity of the right (but not the left) PPC has the effect of weakening the binding of cross-modal information, which reduces the magnitude of the ABE. Indeed, if the effect of parietal stimulation was merely to disrupt attention, we would expect an increase (not a decrease) of bouncing percepts.

The present study not only shows the involvement of the right PPC in the ABE, but also support the notion that cross-modal binding (and not attention) is at the origin of the ABE.

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## 1. Introduction

The audiovisual bounce inducing effect (ABE, Sekuler, Sekuler, & Lau, 1997) is one of the most compelling examples of interaction between audition and vision. It can be observed by comparing the post coincidence trajectories of two moving objects. The objects are perceived as bouncing off each other or as streaming through each other according to whether a sound is presented (or not) when the objects overlap during the motion (Grassi & Casco, 2009, 2010, 2012; Grove & Sakurai, 2009; Kawabe & Miura, 2006; Kawachi & Gyoba, 2006; Remijn, Ito, & Nakajima, 2004; Sekuler et al., 1997; Watanabe & Shimojo, 2001; Zhou, Wong & Sekuler, 2007). The ABE is based on a motion display originally proposed by Metzger (1934). Metzger's display shows two identical objects (e.g., two discs) that move along the azimuth with uniform rectilinear motion and opposite directions: discs start their motion, overlap and stop at the other disc's starting point. This simple, two-dimensional display is a complex inverse optics problem for the visual system (Marr, 1982). The display is equally representative of two different events in the real, three-dimensional world. In both events the two objects are placed at different depths so that the retinal images of both have identical size. In one event, the objects start their motion, overlap (i.e., one object occludes the other), then stream past one another

(respectively, trajectories A–B, C–D in Fig. 1). In the other possible event, in contrast, after the occlusion, the objects reverse their motion and return to their original starting position (respectively, trajectories A–D, C–B in Fig. 1). In brief, the motion of the discs is bistable because both the streaming and bouncing (i.e., coming back) percept are compatible with the visual stimulus.

The origin of the ABE is still debated. One possibility is that the origin of the effect is attentional. When looking at the silent display, attention integrates the discs' local motion signals at overlap, favoring the perception of streaming (Kawabe & Miura, 2006; Watanabe & Shimojo, 1998, 2005). In audiovisual displays, the sound is presented when the integration process is occurring, i.e., when the discs overlap. Therefore, the sound subtracts part of the attentional resources that are necessary for the execution of the integration process. However, note that a perfect simultaneity between discs' overlap and sound is not necessary to induce the bounce response: sounds are effective in a temporal interval of  $\pm 150$  ms around the discs' overlap (e.g., Sekuler et al., 1997). Recent results, however, suggest that the attentional component alone cannot account for the explanation of the whole effect: the lack of attention is not sufficient for a compelling ABE (Grassi & Casco, 2009, 2010). In fact, the ABE is larger when the amplitude content of the sound (or its frequency content) is congruent with that of a real impact sound (Grassi & Casco, 2009, 2010). Therefore, Grassi and Casco (2009, 2010) argued that the ABE had also a non-attentional origin. The authors suggested that the ABE could be explained in terms of a response bias or, alternatively, that visual and auditory

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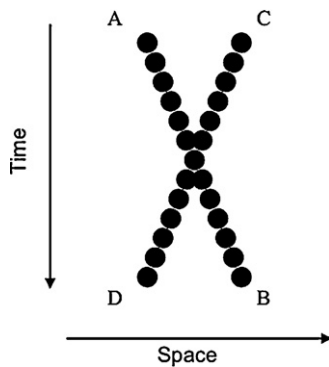


**Fig. 1.** Two-dimensional representation of the Metzger's motion display. The objects' motion is grouped as A–B and C–D with silent displays and as A–C, C–D if a sound is played when the discs overlap. In our experiments, the discs' actual motion was horizontal.

signal could be integrated in the multimodal percept in a way that is maximally consistent across both modalities (e.g., Ernst & Banks, 2002; Grassi & Casco, 2012). For example, because the sound is the acoustical consequence of the impact between solid objects (Sekuler et al., 1997), it is likely to be attributed to the discs' impact as suggested by the “unity assumption” hypothesis (e.g., Vatakis & Spence, 2007; Welch & Warren, 1980). Consequently, the discs motion is perceived as bouncing.

### 1.1. Where does the ABE originate in the brain?

A correlational fMRI study (Bushara et al., 2003) showed that the ABE is associated with higher activity in multimodal areas but lower activity in unimodal areas, suggesting the presence of competitive interactions between multimodal and unimodal areas. The ABE would arise when multimodal areas prevail in the competition. In particular, the sites more active in bouncing than in streaming percepts were a group of subcortical structures (such as the left insula, the superior colliculus, the posterior cerebellar vermis and the right thalamus), two frontal areas (the dorsolateral prefrontal cortex and the medial frontal gyrus), and the left PPC. Other imaging studies where a multimodal visual–auditory object recognition task was used, found partially different activation sites. For example, Beauchamp, Lee, Argall, and Martin (2004) found that the response of the posterior temporal sulcus and middle temporal gyrus, the ventral temporal cortex, and in particular the dorsolateral prefrontal cortex was larger to audiovisual stimulation than to auditory-only or visual-only stimulation. Molholm, Ritter, Javitt, and Foxe (2004), with a similar task and a high-density electrical mapping study, found that the N1 component evoked by multisensory integration of visual–auditory stimuli was likely to be generated by the lateral occipito-temporal cortices, suggesting that auditory inputs were modulating processing in visual regions.

However, these activations could either result from the higher saliency of the multimodal stimulus, or be the consequence of multimodal integration. In any case, the observed activations do not necessarily coincide with the sites where the integration process occurs.

Given the prominent role of the right PPC in both visuo-spatial attention (Ashbridge, Walsh & Cowey, 1997; Heinen et al., 2011; Mort et al., 2003) and cross-modalities spatial attention (Chambers, Payne & Mattingley, 2007) here, we investigated the role of the right PPC in the generation of the ABE.

The causal role of the PPC was investigated by means of the “virtual lesion” technique, applied either to the left or to the right PPC. The virtual lesion was obtained with offline 1-Hz TMS, a method that temporarily suppresses the functional

integrity of the stimulated area over a period of several minutes post-stimulation (Battelli, Alvarez, Carlson & Pascual-Leone, 2009; Boroojerdi, Prager, Muellbacher & Cohen, 2000; Chen et al., 1997). Behavioral, electrophysiological and neuroimaging studies converge in suggesting that the specific neural mechanism of functional suppression by 1-Hz TMS seems to rely on a decrease of cortical excitability. Behaviorally, 1-Hz TMS produces a decrease in motor evoked potentials – MEPs – following the stimulation of the motor cortex (Brignani, Manganotti, Rossini & Miniussi, 2008; Chen et al., 1997). Electrophysiological studies showed that 1-Hz TMS produced a long-lasting decrease in early VEP component amplitudes (Fumal et al., 2003); moreover, 1-Hz TMS reduced the visual-induced alpha wave desynchronization (Thut et al., 2003) and, conversely, produced an increase in the synchronization of EEG activity, in particular of the power and cortico-cortical coherence of the alpha band (Brignani et al., 2008; Strens et al., 2002), which has been related to an idling state (Mulholland, 1995; Pfurtscheller, Stancak & Neuper, 1996), or to an inhibitory control of neuronal activity (Brignani et al., 2008; Hummel, Andres, Altenmüller, Dichgans & Gerloff, 2002; Pfurtscheller & Andrew, 1999; Suffczynski, Pjin, Pfurtscheller & Lopes da Silva, 1999). Most neuroimaging studies have reported TMS-induced increases in local activity beneath the coil (Eisenegger, Treyer, Fehr & Knoch, 2008; Ferrarelli et al., 2004; Fox et al., 1997; Knoch et al., 2006; Siebner et al., 2001) supporting the idea of an active inhibitory mechanism produced by 1-Hz TMS.

In the current experiment, participants evaluated Metzger's display in three different conditions: after a virtual lesion of the left PPC, after a virtual lesion of the right PPC or without any virtual lesion (NO TMS, control condition). In particular, we investigated whether the disruption of the right PPC with TMS (and the consequent decrease of attentional processing) could weaken the integration of discs' local motion signals at overlap thus increasing the perception of bouncing (Kawabe & Miura, 2006; Watanabe & Shimojo, 1998, 2005). In alternative, if the role of the right PPC was to bind not just simple features within a single domain (Ashbridge et al., 1997; Ellison, Lane & Schenk, 2007; Ellison, Schindler, Pattison, & Milner, 2004; Friedman-Hill, Robertson, & Treisman, 1995; Koivisto & Silvanto, 2011; Muggleton, Cowey & Walsh, 2008), but also multimodal visual–auditory information that causes the ABE, we may expect that the disruption of the right PPC would weaken the visual–auditory integration thus reducing the perception of bouncing (e.g., Grassi & Casco, 2009, 2010). In addition, the role of the left PPC was also investigated, due to its activation in both the ABE (Bushara et al., 2003) and other tasks involving visual–auditory integration (Joassin et al., 2011).

## 2. Material and methods

### 2.1. Subjects

Twelve subjects (4 females) with normal or corrected to normal vision and reported normal hearing participated in the experiment. They were all naive as to the purpose of this study. All subjects understood the information given about TMS and gave written informed consent according to the Declaration of Helsinki. This study was approved by the Local Ethics Committee.

### 2.2. Apparatus

We implemented the behavioral experiment in Matlab (Mathworks®) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The software was running on a Pentium IV computer connected to a NEC Multisync FP950 monitor (100 Hz refresh rate). Sounds had a sample rate of 44.1 kHz and 16 bit resolution. The output of the soundcard (M-AUDIO Fast Track Pro) was passed to two M-AUDIO Studiophile AV 30 amplified speakers. The speakers were placed at the left/right of the monitor's sides and the speakers' drivers were aligned with the monitor's horizontal midline so that the combined sound wave originated from a direction coinciding with the monitor's center. The experiment was conducted in a dark and silent (below 35 dBA at the listener's ear) room. During the experiments, the sounds' peak pressure at the listener's ear was 95 dBA.

### 2.3. Stimuli

Subjects evaluated two audiovisual displays: the silent version of Metzger's display (Metzger, 1934) and a version of Metzger's display accompanied with a sound. The motion display was the same in all conditions. Two black discs ( $0.41^\circ$  visual angle) moved within a white ( $67.0 \text{ cd/m}^2$ ) square ( $6.19^\circ$ ) placed in the center of a black ( $0.09 \text{ cd/m}^2$ ) background. The background and white square were continuously present during the experiment. The discs' motion started at the beginning of each trial from the left/right extremities of the square's horizontal axis. Discs moved horizontally with uniform rectilinear motion ( $2.07^\circ/\text{s}$ ) from two opposite positions in space: they overlapped partially, then completely, and finally continued their motion and stopped at the other disc's starting point. The discs' motion lasted 1.4 s. The discs disappeared after the motion.

The sound used for the displays accompanied by sound was a harmonic complex tone obtained by adding ten sinusoids, with frequencies corresponding to harmonics 1–10, of a 250 Hz fundamental. All sinusoids had identical phase and amplitude. The tone's duration was 100 ms and the tone's envelope was damped in sound pressure level over the tone's duration. The damping was obtained modulating the amplitude of the tone with an exponential ramp (100 ms long) that decreased of 40 dB over the sound's duration. The resulting amplitude modulated tone was gated on and off with two 5 ms raised cosine ramps. The tone was switched on when the discs touched each other. In sound absent displays a 'sound' was also played. However, the amplitude of this sound was null. This was done so that the timing and quality of the audiovisual displays would not be different from those of the silent displays (because of the call of the sound card).

### 2.4. Procedure

Subjects performed the experiment in three separate sessions. Each session corresponded to a different TMS condition: NO TMS, TMS over the right PPC and TMS over the left PPC. The order of the sessions was counterbalanced across subjects. Each session consisted in a block of thirty random trials where Metzger's display was presented with (15 trials) or without the accompanying sound (15 trials). Subjects viewed the display binocularly from a distance of 1.20 m. At the end of each trial the subject was asked to report whether discs appeared to be streaming or bouncing.

### 2.5. Transcranial magnetic stimulation: individual intensity setting

TMS was delivered via a Magstim Super-Rapid stimulator (Magstim Company Ltd., Spring Gardens, Wales, UK) and a 70 mm figure-of-eight coil. TMS intensity was set for each subject proportionally to the individual motor threshold (MT). MT was defined as the minimum stimulator output (single pulse mode) that evoked a visually detectable twitch in the index finger-to thumb opposition of the hand contralateral to the stimulated motor cortex. The method of limits (one descending and one ascending run) was used to find the MT. The motor cortex was localized as the site, laying at approximately 3 cm to the right of Cz, which produced the largest twitch in the index finger-to thumb opposition of the hand contralateral to the stimulated motor cortex, when stimulated with single pulses at 70% of maximum stimulator output.

### 2.6. Transcranial magnetic stimulation: localization of stimulation sites

Two stimulation sites were localized on the scalp of each single subject, corresponding to the right PPC and the left PPC.

The right PPC was identified by using the hunting procedure described in Ashbridge et al. (1997), which has been employed in several previous studies (e.g.: Campana, Walsh & Cowey, 2002; Ellison, Schindler et al., 2004; Rushworth, Ellison & Walsh, 2001). Subjects performed a conjunction search task in which they had to find a target (red bar oriented  $45^\circ$ ) among a group of distractors (green bars oriented  $45^\circ$  and red bars oriented  $135^\circ$ ). They were instructed to respond as fast and accurately as possible by pressing one of two alternative keys on a computer keyboard to the presence vs. absence of the target. Each session consisted of 10 trials (5 target present and 5 target absent trials), randomly presented. After a practice block of 40 trials to familiarize with stimuli and procedure, each subject performed 10 sessions, the first one without TMS, the remaining 9 with rTMS at 10 Hz for 500 ms, starting at stimulus onset. The intensity of the stimulation was set at the 110% of MT. A  $3 \text{ cm} \times 3 \text{ cm}$  grid was applied with the central square on the position of the scalp, located 9 cm anterior and 6 cm to the right respect to theinion. This point roughly corresponds to P4 of the international 10–20 system. In each TMS session, single pulse TMS was applied to one of the nine marked sites of the grid (the order was randomized between subjects). The right PPC site used for the subsequent experimental sessions was defined as the site where TMS caused the greater drop in performance, increasing the mean RTs of at least 50 ms in the conjunction search task compared with the other eight stimulation sites of the grid. Previous studies showed that this procedure accurately pinpoints the position of the posterior part of the PPC, specifically the part corresponding to the right angular gyrus (Rushworth et al., 2001). The left PPC was defined as the point on the left hemisphere mirror-symmetric to the one localized in the right hemisphere.

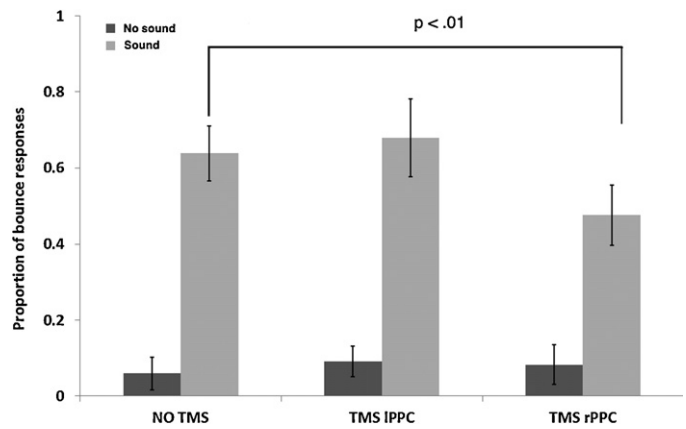


**Fig. 2.** Mean proportion of bounce responses for each condition of stimulation (No TMS, left parietal cortex, right posterior parietal cortex) vs. presence/absence of sound. Error bars are  $\pm 1$  standard error of the mean.

Before each session, except for the NO TMS session, the subject underwent 1-Hz offline TMS for 10 min at an intensity corresponding to 100% of MT. The suppressive effect of 1 Hz TMS outlasts the period of stimulation (Battelli et al., 2009; Boroojerdi et al., 2000; Chen et al., 1997), and the time required to perform the below-described psychophysical task (<5 min) is within that for which 1 Hz TMS has been shown to have lasting effects in parietal regions – namely: half as long as the time of stimulation (Battelli et al., 2009; Hilgetag, Theoret, & Pascual-Leone, 2001).

In order to avoid any possible influence of a previously stimulated site, a minimum of a three hours interval was required between two consecutive sessions.

## 3. Results

Subjects' responses were transformed into proportions of bounce responses. Proportions were subjected to a 3 (TMS condition) by 2 (sound condition) two-way ANOVA.<sup>1</sup> The ANOVA revealed a main effect of the sound condition ( $F_{1,11} = 50.15$ ,  $p < .0001$ ), showing that, in agreement with the previous literature, the proportion of bounce responses was larger with the sound ( $M = 0.60$ ,  $SD = \pm 0.24$ ) with respect to when no sound was presented ( $M = 0.08$ ,  $SD = \pm 0.14$ ). There was also a significant main effect of TMS condition ( $F_{2,22} = 3.93$ ,  $p < .05$ ), and a significant interaction TMS by sound condition ( $F_{2,22} = 4.52$ ,  $p < .05$ ). Simple contrasts showed that TMS over the right PPC reduced the proportion of bounce responses ( $M = 0.29$ ,  $SD = \pm 0.19$ ) with respect to the NO TMS condition ( $M = 0.40$ ,  $SD = \pm 0.16$ ) ( $F_{1,11} = 6.07$ ,  $p < .05$ ), whereas TMS over the left PPC did not ( $M = 0.39$ ,  $SD = \pm 0.20$ ) ( $F_{1,11} = 0.53$ ,  $p > .05$ ). Specifically, TMS over the right PPC reduced the proportion of bounce responses with respect to the NO TMS condition, but only when the sound was also presented ( $F_{1,11} = 9.47$ ,  $p < .01$ ) (see Fig. 2). Therefore, TMS over the right PPC seems to specifically affect the perception of bouncing induced by the sound, which is the ABE.

## 4. Discussion

In the current study we investigated where the ABE originates in the brain. In particular, we investigated the role of the left and right PPC in the change of perception due to the sound by inducing virtual lesions to participants via 1-Hz offline TMS. The results of the experiment confirm literature findings: participants returned a much larger proportion of bouncing responses when the sound was presented in comparison to when the sound was not presented.

<sup>1</sup> Proportions do not meet all the assumptions of the ANOVA. However, Monte Carlo simulations reveal that this statistical test is robust enough to be used with proportions with no evident effect on type-I error or in the magnitude of the effect size (Milligan, 1987; Pastore, 2010).

However, when TMS was delivered over the right PPC, the proportion of bounce responses in the sound condition dropped from 65% (in the NO TMS condition) to 48%, showing an involvement of the right PPC in generating the ABE. On the contrary, TMS over the left PPC did not have any effect in the way subjects responded to the various displays. This last result rules also out the possibility that any effect we could have obtained with TMS over the right PPC was due to a general increase in alertness. In contrast, we have proven a causal role of the right PPC in eliciting the ABE: when its functionality was disrupted by 1-Hz offline TMS, the proportion of bouncing percepts significantly decreased when the sound was also presented, but remained unchanged when the sound was not presented. This result demonstrates that the role of the right PPC is not limited to a general modulation of the proportion of bounce responses, but it is important for the integration process of the audio and visual signals that give rise to the ABE.

It could be argued that the TMS effect over the right PPC could reflect the degradation of the stimulus representation via top-down modulation to early visual areas (Ruff et al., 2009; Silvanto, Muggleton, Lavie & Walsh, 2009), or because of its role in awareness (Koch, Oliveri, Torriero & Caltagirone, 2005). Indeed, 1-Hz TMS does not only suppresses excitability in the stimulated area, but also at distant sites directly connected with the site of stimulation (Gerschlagier, Siebner & Rothwell, 2001). However, even though 1-Hz TMS over the right PPC was able to suppress the cortical excitability of early visual or auditory cortices and therefore to degrade the processing of visual or auditory stimuli, it is unlikely that this might have produced a change in the proportion of streaming vs. bouncing percepts. In fact, it has been shown that if the experimenter uses stimuli that are difficult to perceive, such as below-threshold sounds (Dufour, Touzalin, Moessinger, Brochard & Despres, 2008) or low-contrast visual stimuli (Kawabe & Miura, 2006), subjects still experiences the ABE with no substantial changes in the proportion of streaming vs. bouncing responses. Moreover, the modulation of either early sensory cortices or right PPC with TMS on the representation or awareness of sensory stimuli only occurs with short-duration near-threshold stimuli (Boyer, Harrison, & Ro, 2005; Koch et al., 2005), whereas its occurrence is implausible with high-contrast and long-lasting sequences of stimuli as the ones we have used.

Previous imaging results (Bushara et al., 2003) showed a larger activation of subcortical and frontal areas, but also of the left PPC, in bouncing percepts with respect to streaming percepts when observing Metzger's display; yet, later studies trying to locate the sites of multimodal integration (Beauchamp, Lee, Argall, & Martin, 2004; Molholm et al., 2004) found different results, suggesting that the site of visual–auditory integration could be located in temporal or occipito-temporal regions.

In fact, the use of correlational methods cannot discriminate the neural substrates where the multimodal integration takes place, from those that are best activated by the output of the multimodal integration. Indeed, the activations found in these studies could result from the higher saliency of the multimodal stimulus with respect to the unimodal one, not necessarily the sites where the integration process occurs.

The right PPC has been invoked for its role on visuo-spatial attention (Ashbridge et al., 1997; Heinen et al., 2011; Mort et al., 2003), but also on feature binding (Ashbridge et al., 1997; Ellison, Lane et al., 2007; Ellison, Schindler et al., 2004; Friedman-Hill et al., 1995; Koivisto & Silvanto, 2012; Muggleton et al., 2008). Hypothesis on the mechanisms subserving the ABE include both visuo-spatial attention (Kawabe & Miura, 2006; Watanabe & Shimojo, 1998, 2005) and multimodal feature binding (Ernst & Banks, 2002; Grassi & Casco, 2009, 2010, 2012; Vatakis & Spence, 2007). In the first case, the sound would subtract part of the attentional resources necessary for integrating the discs' local motion signals at overlap,

i.e., those favoring the perception of streaming. As a result of this subtraction of attention, the discs are perceived more frequently as bouncing. In the second case, visual and auditory components would be integrated in a unitary percept that is consistent with both modalities and ecologically plausible (since the sound is the acoustical result of the impact between solid objects, it could be attributed to the discs' impact).

If TMS over the right PPC impaired visuo-spatial attention, making more difficult the integration of local motion signals at overlap and thus less likely the streaming percept, we would expect an increase of bouncing responses. On the other hand, if TMS over the right PPC impaired the multimodal integration, we would expect a decrease of bouncing responses. Our results clearly show that TMS over the right PPC produced a reduction of bouncing responses specifically when the sound was presented with Metzger's display, implying that the mechanism underlying the ABE is likely due to multimodal integration of visual and audio signals. Thus, the right PPC seems not to be involved only in binding different visual features in a unitary visual object, but also in integrating features of different modalities in a unitary multimodal object.

## Acknowledgment

Authors would like to thank Mattia Doro for his help in data collection.

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