

Evoked Multisensory Cortical Representations During Unisensory Stimulation

Rina Blomberg

Linköping University

24 June 2013

ISRN: LIU-IDA/KOGVET-G--13/021--SE

Abstract

The primary aim of this study was to establish whether redintegrative effects can be revealed under conditions with complex sensory stimulation. Specifically, would the cortical activity involved in the single-trial, passive encoding of a movie, be reactivated when subsequently exposed to a unisensory component of that movie, e.g. an audio- or visual-only segment? High-density electrical neuroimaging analysis in the frequency domain was used to assist this aim. The statistical comparisons revealed a greater number of oscillating neuronal regions across all frequency bands in participants who received audiovisual stimulation prior to unisensory exposure (compared to participants who experienced the same unisensory stimulus without prior audiovisual stimulation). This difference between groups was significant in the alpha2 (right frontal lobe) and gamma (right frontal, sub-lobar and temporal lobes) frequencies during audio-only stimulation. This enhanced cortical activity during unisensory stimulation suggests that participants were retrieving associated memory traces from their prior multisensory experience, although specific redintegrative effects could not be confirmed.

Keywords: multisensory, unisensory, redintegration, episodic, retrieval, film, EEG, eLORETA

Evoked Multisensory Cortical Representations

During Unisensory Stimulation

The environment provides us with constant multisensory stimulation and the brain is seemingly able to integrate this complex flow of information without effort. A considerable amount of human and animal research has been dedicated to understanding the effects of multisensory integration upon cognition. Through such research, it has become increasingly clear that the integration of information from several sensory modalities can both enhance and facilitate processes such as: object recognition (Lehmann & Murray, 2005), reaction time (Gingras, Rowland, & Stein, 2009), sensory estimation and localisation (McDonald, Teder-Sälejärvi, & Hillyard, 2000; Frassinetti, Bolognini, & Làdavas, 2002), perceptual learning (Shams & Seitz, 2008) and memory (Thompson & Paivio, 1994; Murray, et al., 2004; Murray, Foxe, & Wylie, 2005); although there remains some doubt as to the necessary conditions (e.g. ethological validity, semantic, spatial and temporal congruency) for such effects to occur (Thelen, Cappe, & Murray, 2012).

Of particular interest for this study are findings indicating that brain regions involved in encoding of a multisensory experience are also involved during its subsequent active retrieval (Calvert, et al., 1997; Nyberg, Habib, McIntosh, & Tulving, 2000; Gottfried, Smith, Rugg, & Dolan, 2004) and also, that exposure to an associated unisensory component can trigger multisensory cortical representations even when the prior multisensory experience was of a single-trial nature (Murray, et al., 2004; Murray, Foxe, & Wylie, 2005; Shams, Wozny, Kim, & Seitz, 2011). These particular findings are suggestive of a classical notion from cognitive psychology known as redintegration (Hamilton, 1859) and in essence refers to the relationship between a whole and any one of its constituent parts (Tulving & Madigan, 1975). Since the

term's introduction, redintegration has been used with varying definitions in cognitive science. Horowitz and Prytulak (1969) for example, referred to redintegrative memory as being the probable likelihood of recalling a whole "brain state" given the recollection of a part (Tulving & Madigan, 1975) and in research investigating working memory the term is also used to refer to the use of long term memory to facilitate recall (Hulme, et al., 1997; Baddeley, 2007).

To avoid confusion, the term redintegration in this study refers to when a constituent part from a consolidated memory is sufficient enough to reactivate the entire encoded representation (Shams & Seitz, 2008; Thelen, Cappe, & Murray, 2012). Thus, if a multisensory experience involves both visual and auditory processing, then subsequent exposure to solely the visual component of that experience should result in both visual and auditory cortical activity. This particular notion of redintegration is similar to Teyler's and DiScenna's (1986; 2007) hippocampal memory indexing theory, which states that when given a partial cue of a memory representation, cortical activity spreads to the hippocampus which in turn reactivates the entire unified episodic memory representation (the associated spatiotemporal pattern of activity) in the cortex. Thelen et al. (2012) extend the definition of redintegration further by implying that "pure" redintegrative effects require that the reactivated cortical activity be both useful and necessary for memory performance. Redintegration according to this extended definition is not investigated in this study.

To the best of my knowledge, the research revealing redintegrative effects of multisensory experiences in humans has employed conventional experimental paradigms with non-naturalistic sensory stimuli such as pure tones, line drawings, somatosensory vibrations or artificial semantic pairings (e.g. words with complex sound-effects: "DOG" + barking sound). Such constrained stimulus conditions are designed to issue maximal control over as many

variables as possible whilst isolating any other potentially confounding factors. In contrast, Hasson et. al. (2004; 2009) argue that characteristics of cortical activity associated with multisensory perception can be best understood by probing with more naturalistic stimuli such as movies. Movies are rich, complex sensory stimulation that resemble multisensory experiences from our daily lives more closely than the conventional stimuli typically used in laboratory settings. Furthermore, like many perceived events from our natural surroundings, movies are passively encoded into memory - they do not require explicit encoding (Furman, Dorfman, Hasson, Davachi, & Dudai, 2007; Hasson, Malach, & Heeger, 2009).

The primary aim in this study was to establish whether redintegrative effects can be revealed under conditions with complex sensory stimulation. Specifically, would the cortical activity involved in the single-trial, passive encoding of a movie, be reactivated when subsequently exposed to a unisensory component of that movie (e.g. an audio or visual only segment)? Because an advanced background in neuroanatomy and neurophysiology is required for making a priori hypotheses regarding expected cortical responses during specific stimulus presentation (Cannon, 2012), this study made no a priori assumptions as to the localisation of cortical activity involved during complex audiovisual and subsequent audio-only and visual-only processing. Instead, low-resolution electromagnetic tomography (Pascual-Marqui, 2007; Pascual-Marqui, 2009; Pascual-Marqui, et al., 2011) was used to determine the following hypothesis:

If the cortical responses to a complex, audiovisual, sensory experience are reactivated during subsequent exposure to a unisensory component of that experience (i.e. audio only or visual only), then, comparisons with participants who experience the same unisensory stimulus without prior audiovisual exposure should reveal statistically significant differences. The difference

should involve: a) a larger number of synchronously oscillating neuronal regions for participants who received audiovisual stimulation; and b) the same oscillatory networks most active during audiovisual stimulation. This implies: a) the activation of associated memory traces not found in participants without audiovisual stimulation; and b) redintegrative effects.

Method

Participants

26 adults (14 females, $M_{age} = 28.4 \pm 9.7$) volunteered for the study. All but three of the subjects were right-handed and two participants reported having a past neurological/psychiatric diagnosis. All had normal or corrected-to-normal vision and no diagnosed hearing problems. Participants were divided randomly into two equal groups (A & B).

Upon examination of the recorded EEG data, two participants from group B, one of which was left handed, had to be eliminated from further analysis due to too much movement. Using source localisation analysis (see Data Analysis for more details) in the frequency domain, alpha activity (8 – 12 Hz) for the two participants who reported a past neurological/psychiatric diagnosis was compared with four other blindly selected participants. Of these two participants, one of them did not show comparably sufficient alpha attenuation in the posterior regions during eyes-open conditions (Cannon, 2012). This participant (group A) was therefore removed from further analysis. For the remaining two left handed participants, the alpha activity recorded during audiovisual film-viewing was statistically compared to two blindly selected right handed participants; no significant differences in alpha asymmetry were found (Galin, Ornstein, Herron, & Johnstone, 1982).

In order to keep the number of participants in each group equal, a new, clinically healthy, right handed volunteer was recruited and placed in group B. This gave a total of 24 participants

with twelve in each group (Group A: 4 females, $M_{age} = 29.8 \pm 11$; Group B: 8 females, $M_{age} = 27.4 \pm 8$).

Stimulus

The selected stimulus for this study was an unedited, eight-minute extract from the Swedish short film: *Mitt liv som en trailer*; by Andreas Öhman (Folkets Bio, 2009). This particular movie was chosen because of its "film-within-a-film" story line, whereby the protagonist attempts to sum up her life in the form of a movie trailer. A total of four trailers (circa 45 s each) were included in this eight-minute film extract, and because one session of the experiment required participants to be subjected to unisensory epochs (scenes consisting of audio-only or visual-only information), the trailers defined these unisensory epochs in a way that did not disturb the general flow and plot of the movie. The trailers employed common movie-trailer clichés pertaining to different genres, consisting of dynamic "shots" together with enhanced emotional effects (e.g. music, narration, reverberation, slow motion, colour filtering) and also contained very little dialog between characters. These aspects were beneficial to this study because the scenes were most likely familiar, easily identifiable concepts, facilitating a passive perceptual experience and providing a strong contrast between the unisensory epochs (i.e. the trailers) and the rest of the film which consisted mostly of dialogue between characters who looked straight into "the barrel" of the camera when talking.

None of the participants reported having seen the film prior to the experiment, although one participant from group A mentioned that the film was vaguely familiar but could not state with absolute certainty as to having watched it before.

Experiment Design and Procedure

Participants were seated in a comfortable chair in a shielded, sound-proof room and were

requested to limit eye and head movements as much as possible. The stimulus was presented using E-prime software (Psychology Software Tools, Inc., 2012, v. 2.0.8.73) on a 15 *in* monitor from which participants sat circa 60 *cm*. Sound was distributed via two (left, right) multimedia desktop speakers (response bandwidth: 80-20000 *Hz*) positioned on either side of the monitor. The volume was kept at a constant level for all subjects (loudest effect was music: 70-80 *dB*). Participants were shown the filmclip two times; one viewing session consisted only of multisensory (audiovisual) stimulation, the other contained epochs, roughly 45 *s* each, of unisensory: audio-only and visual-only stimulation. During the audio-only epochs, participants were told to keep their eyes on the stimulus screen which was black except for a white, centred fixation point.

For group A, the experiment began with a 60 *s* recording of silent, eyes-closed resting activity followed by an eight-minute multisensory film session. Then, another 60 *s* recording of resting EEG was recorded before viewing the unisensory film session. Finally, the experiment concluded with another 60 *s* recording of resting activity. Total EEG recording time was circa 20 *m*. The experiment design for group B was the same as group A except that the viewing sessions: multisensory versus unisensory; were presented to participants in opposite order (Figure 1).

EEG Procedures

Data Acquisition. Continuous cortical activity was recorded from the surface of the skull using dense array electroencephalography (Electrical Geodesics, Inc., 2013) from 128 scalp electrodes (impedances < 50 *k* Ω ; vertex reference; 250 *Hz* sampling rate; online bandpass filter 0.1–200 *Hz*). Dense array EEG uses more electrodes than in conventional EEG to directly measure the electrical fields generated by neuronal activity and includes four facial electrodes for monitoring ocular movements. This dense array of electrodes provides the researcher with a

relatively high spatial resolution for determining source localisation.

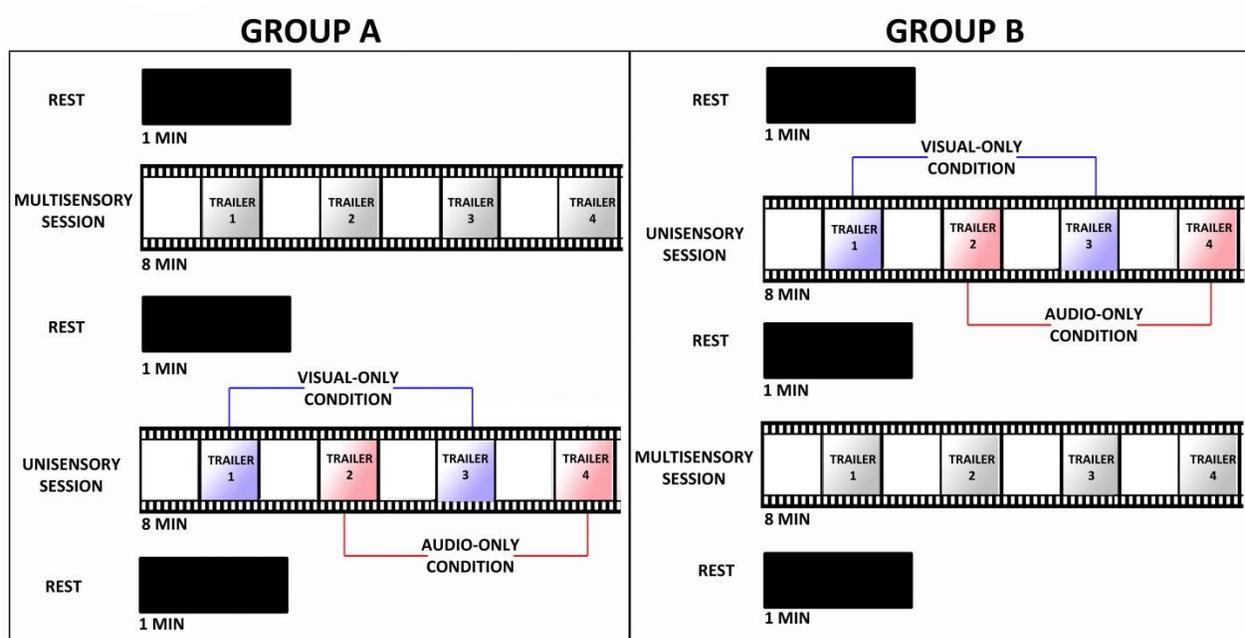


Figure 1. Graphical overview of experiment design and conditions. Total EEG recording time is circa 20 m. The 45 s (circa) trailers within the film defined the critical stimulus epochs. In the multisensory session all four epochs (grey) were shown with full audiovisual stimulation and formed the audiovisual condition. In the unisensory session trailers 1 and 3 (blue) made up the visual-only condition and trailers 2 and 4 (red) made up the audio-only condition. Recordings from these three stimulus conditions (audiovisual, visual-only and audio-only) were used for analysis. Scenes between each trailer (white) consisted mostly of character-dialogue and were shown with full audiovisual stimulation in both viewing sessions.

Data Preprocessing. Prior to frequency-domain analysis the data was preprocessed using Net Station (v. 4.4.2) EEG software (Electrical Geodesics, Inc., 2013). First, the EEG data was digitally filtered offline with a 1 - 45 Hz bandpass filter. Next, physiological artefacts (eye blinks $\geq 150 \mu v$ with a moving average of 120 ms and eye movements $\geq 100 \mu v$) and bad channels ($\geq 200 \mu v$ for more than 20 % of recording) were detected using Net Station's semi-automated artefact detection algorithm on the continuous data. Bad channel recordings were automatically replaced with data interpolated from the remaining channels. The data was then

rereferenced to the average reference and down sampled to the international 10-5 channel montage (Oostenveld & Praamstra, 2001; Jurcak, Tsuzuki, & Ippaita, 2007) resulting in 112 electrode coordinates (Appendix I). Finally the continuous data was segmented into the three critical stimulus conditions: audio-only, visual-only and audiovisual (Figure 1). Non-overlapping, three-second epochs (500 sample points) from manually verified artefact-free regions were extracted from each data segment for frequency-domain analysis. All epoch selection was done blindly. Because the number of artefact-free regions varied per participant, the total number of extracted epochs per participant and condition also varied (see Appendix II for more details).

Data Analysis. Data was analysed in the frequency-domain using the exact low resolution brain electromagnetic tomography (eLORETA) software module (Pascual-Marqui, 2007; Pascual-Marqui, 2009; Pascual-Marqui, et al., 2011). The eLORETA module is a discrete, three-dimensionally distributed, linear, weighted minimum norm inverse solution. Despite the presence of measurement and structured biological noise in the data, eLORETA provides the researcher with nonbiased, zero error, source localisation, although with low spatial resolution due to the fact that neighbouring neuronal sources are highly correlated (Pascual-Marqui, et al., 2011).

The epoched data for each participant was averaged to one cross-spectrum per stimulus condition (frequency resolution: 0.2 Hz). The cross-spectrum is a representation of frequency-transformed EEG data that contains all the phase and amplitude relationships among electrodes but remains constant to changes of phase applied simultaneously to all electrodes (Koenig & Pascual-Marqui, 2009). Averaging across epochs preserves the constant signal and gradually cancels the random noise. Because different EEG frequencies reflect different cognitive

functions (Allen, 2008), the data was digitally filtered into eight different frequency bands: δ (1.5 – 6 Hz), θ (6 – 8 Hz), $\alpha 1$ (8 – 10 Hz), $\alpha 2$ (10 – 12 Hz), $\beta 1$ (12 – 18 Hz), $\beta 2$ (18 – 21 Hz), $\beta 3$ (21 – 30 Hz) γ (30 – 45 Hz).

Each cross-spectrum (per participant and stimulus condition) was used to compute the corresponding three dimensional (3D) cortical distribution of the electric neuronal generators for each frequency band (eLORETA). The solution space was restricted to the cortical grey matter, corresponding to 6239 voxels at $5 \times 5 \times 5$ mm spatial resolution.

Source Localisation. In order to determine the cortical oscillations involved in audiovisual processing, the eLORETA was averaged across participants for the audiovisual condition. The resulting current source density (CSD) values were mapped onto the Montreal Neurologic Institute average MRI brain (MNI152) realistic head model (Mazziotta, et al., 2001) and a 3D Colin cortex (Dickson, Drury, & Van Essen, 2001).

The statistical difference in source localisation of cortical oscillations between groups in each frequency band, was assessed by voxel-by-voxel independent sample F -ratio tests, based upon eLORETA log-transformed current density power. Cortical voxels showing significant differences were identified by a nonparametric randomisation/permutation procedure that compares the mean source power of each voxel and the distribution of the permuted values (Holmes, Blair, Watson, & Ford, 1996; Nichols & Holmes, 2002). This randomization/permutation procedure has been proven to be effective in controlling for Type I errors in neuroimaging studies (Nichols & Holmes, 2002). A total of 5000 permutations were used to determine the critical probability threshold values for the actually observed log F -ratios with correction for multiple comparisons across all voxels and all frequencies. Both single voxel statistics as well as cluster statistics were computed in this process (Holmes, Blair, Watson, &

Ford, 1996). Results of the statistical analysis were mapped onto the MNI152 brain and 3D Colin cortex. The use of statistical nonparametric maps applied to LORETA images has been validated in a number of studies (Anderer, Pascual-Marqui, Semlitsch, & Saletu, 1998; Pascual-Marqui, et al, 2001; Flor-Henry, Lind, & Koles, 2004).

Results

Audiovisual Condition

Group A. Table 1 outlines the predominantly active brain structures (top 40 % of log10 averaged eLORETA values) for group A's audiovisual experience in each frequency band. Electric neuronal activity was found in the parietal lobes (BA: 7, 5) for the delta ($CSD_{max} = 3.80 \pm 3.66$), theta ($CSD_{max} = 3.78 \pm 3.85$), alpha1 ($CSD_{max} = 3.79 \pm 3.94$) and alpha2 ($CSD_{max} = 3.78 \pm 4.14$) frequency bands. Lower beta oscillations (beta1: $CSD_{max} = 4.15 \pm 4.29$; beta2: $CSD_{max} = 3.77 \pm 3.92$) were observed in the temporal lobes (BA: 20, 21, 38, 37), most strongly in the left hemisphere, and frontal lobes (BA: 11). Current density maxima in the upper-beta ($CSD_{max} = 4.21 \pm 4.32$) and gamma ($CSD_{max} = 4.36 \pm 4.43$) bands were found in both the parietal lobes (BA: 7) and temporal lobes (BA: 20, 21, 36, 37, 38, 19). The temporal lobe activity was strongest in the left hemisphere for the gamma range.

Group B. Table 2 outlines the predominantly active brain structures (top 40 % of log10 averaged eLORETA values) for group B's audiovisual experience in each frequency band. Electric neuronal activity was found in the parietal lobes (BA: 7, 5) for the delta ($CSD_{max} = 3.73 \pm 3.36$), theta ($CSD_{max} = 3.51 \pm 3.06$), alpha1 ($CSD_{max} = 3.49 \pm 3.04$) and alpha2 ($CSD_{max} = 3.43 \pm 3.00$) frequency bands. Lower beta oscillations (beta1: $CSD_{max} = 3.82 \pm 3.49$; beta2: $CSD_{max} = 3.41 \pm 3.04$) were observed in the temporal lobes (BA: 20, 21, 38, 37), most strongly in the left hemisphere, and frontal lobes (BA: 11). Current density maxima in the

upper-beta (CSDmax = 3.81 ± 3.41) and gamma (CSDmax = 4.04 ± 3.76) bands were found in both the parietal lobes (BA: 7) and temporal lobes (BA: 20, 21, 36, 37, 38, 19). The temporal lobe activity was strongest in the left hemisphere for the gamma range.

Group A = Group B. An independent statistical comparison between groups revealed no significant differences for the audiovisual condition. Figure 2 shows how similar the cortical responses in both groups were across all frequency bands for this condition.

Table 1

Top 40 % of active brain structures during the audiovisual condition for group A. Log10 current source density maxima (CSDmax) correspond to the first, listed structure in each frequency band.

Frequency	CSDmax	Hemisphere	Lobe	Structure	Brodmann area
Gamma	4.36	R	Parietal Lobe	Precuneus, Superior Parietal Lobule, Postcentral Gyrus	7
		L	Parietal Lobe	Postcentral Gyrus, Precuneus, Superior Parietal Lobule	7
		L	Temporal Lobe	Inferior Temporal Gyrus	20, 37
				Fusiform Gyrus Middle Temporal Gyrus	20, 37, 36, 19 21
Beta3	4.21	R	Parietal Lobe	Precuneus, Superior Parietal Lobule, Postcentral Gyrus	7
		L	Parietal Lobe	Postcentral Gyrus, Precuneus, Superior Parietal Lobule	7
		R	Temporal Lobe	Middle Temporal Gyrus	21
				Inferior Temporal Gyrus, Fusiform Gyrus	20
				Superior Temporal Gyrus, Middle Temporal Gyrus	38
		L	Temporal Lobe	Inferior Temporal Gyrus, Fusiform Gyrus	20
				Middle Temporal Gyrus	21
				Superior Temporal Gyrus	38
Beta2	3.78	L	Temporal Lobe	Inferior Temporal Gyrus, Fusiform Gyrus	20, 37
				Middle Temporal Gyrus	21
				Superior Temporal Gyrus	38
		R	Temporal Lobe	Middle Temporal Gyrus	21
				Frontal Lobe	Superior Temporal Gyrus
		L	Frontal Lobe	Orbital Gyrus, Rectal Gyrus	11
				Orbital Gyrus, Rectal Gyrus	11
Beta1	4.15	L	Temporal Lobe	Inferior Temporal Gyrus, Fusiform Gyrus	20, 37
				Middle Temporal Gyrus	21
				Superior Temporal Gyrus	38
		R	Temporal Lobe	Fusiform Gyrus, Inferior Temporal Gyrus	20
				Middle Temporal Gyrus	21, 38
		R	Frontal Lobe	Superior Temporal Gyrus	38
				Orbital Gyrus, Rectal Gyrus	11
		L	Frontal Lobe	Rectal Gyrus	11
Alpha2	3.91	R	Parietal Lobe	Precuneus, Postcentral Gyrus, Superior Parietal Lobule	7
		L	Parietal Lobe	Postcentral Gyrus, Precuneus, Superior Parietal Lobule	7
Alpha1	3.79	R	Parietal Lobe	Precuneus, Postcentral Gyrus, Superior Parietal Lobule	7
		L	Parietal Lobe	Postcentral Gyrus, Precuneus, Superior Parietal Lobule	7
Theta	3.78	R	Parietal Lobe	Postcentral Gyrus, Precuneus, Superior Parietal Lobule	7
		L	Parietal Lobe	Postcentral Gyrus	7
Delta	3.68	R	Parietal Lobe	Postcentral Gyrus	7, 5
				Precuneus, Superior Parietal Lobule	7

	L	Parietal Lobe	Postcentral Gyrus	7, 5
	R	Frontal Lobe	Paracentral Lobule	5

Table 2

Top 40 % of active brain structures during the audiovisual condition for group B. Log10 current source density maxima (CSDmax) correspond to the first, listed structure in each frequency band.

Frequency	CSDmax	Hemisphere	Lobe	Structure	Brodmann area
Gamma	4.04	R	Parietal Lobe	Precuneus, Superior Parietal Lobule, Postcentral Gyrus	7
		L	Parietal Lobe	Postcentral Gyrus, Precuneus, Superior Parietal Lobule	7
		L	Temporal Lobe	Inferior Temporal Gyrus Fusiform Gyrus	20 20, 37
Beta3	3.81	R	Parietal Lobe	Precuneus, Superior Parietal Lobule, Postcentral Gyrus	7
		L	Parietal Lobe	Postcentral Gyrus, Precuneus, Superior Parietal Lobule	7
		R	Temporal Lobe	Middle Temporal Gyrus	21
				Inferior Temporal Gyrus, Fusiform Gyrus	20
				Superior Temporal Gyrus, Middle Temporal Gyrus	38
		L	Temporal Lobe	Middle Temporal Gyrus Inferior Temporal Gyrus	21 20
Beta2	3.41	L	Temporal Lobe	Inferior Temporal Gyrus	20
				Fusiform Gyrus	20, 37
				Middle Temporal Gyrus	21
				Superior Temporal Gyrus	38
		R	Temporal Lobe	Inferior Temporal Gyrus, Middle Temporal Gyrus	37
				Middle Temporal Gyrus	21
				Superior Temporal Gyrus	38
				Orbital Gyrus, Rectal Gyrus	11
L	Frontal Lobe	Rectal Gyrus, Orbital Gyrus	11		
Beta1	3.82	L	Temporal Lobe	Inferior Temporal Gyrus, Fusiform Gyrus	20, 37
				Middle Temporal Gyrus	21
				Superior Temporal Gyrus	38
				Middle Temporal Gyrus	21, 38
		R	Temporal Lobe	Superior Temporal Gyrus	38
				Inferior Temporal Gyrus, Fusiform Gyrus	20
				Orbital Gyrus, Rectal Gyrus	11
				Rectal Gyrus	11
Alpha2	3.43	R	Parietal Lobe	Precuneus, Superior Parietal Lobule, Postcentral Gyrus	7
		L	Parietal Lobe	Postcentral Gyrus, Precuneus, Superior Parietal Lobule	7
Alpha1	3.49	R	Parietal Lobe	Precuneus, Superior Parietal Lobule, Postcentral Gyrus	7
		L	Parietal Lobe	Postcentral Gyrus, Precuneus, Superior Parietal Lobule	7
Theta	3.51	R	Parietal Lobe	Postcentral Gyrus, Superior Parietal Lobule, Precuneus	7
		L	Parietal Lobe	Postcentral Gyrus	7
Delta	3.73	R	Parietal Lobe	Postcentral Gyrus	7, 5
				Superior Parietal Lobule, Precuneus	7
		L	Parietal Lobe	Postcentral Gyrus	7, 5
R	Frontal Lobe	Paracentral Lobule	5		

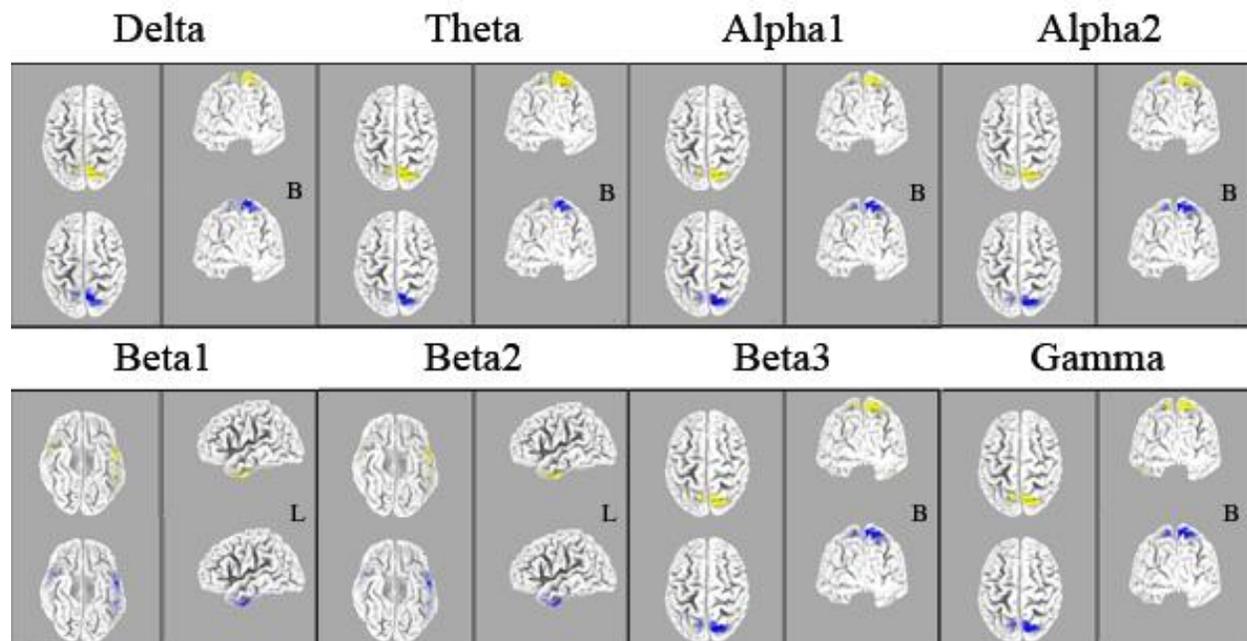


Figure 2. Top 40 % of eLORETA values for the audiovisual condition mapped onto Colin cortical surface. Yellow = group A; blue = group B; L = left; B = back.

Visual-only Condition

Results of the independent significant test for the visual-only condition revealed greater activity across all frequency bands for group A but this difference was not significant. Increased frontal lobe activity (BA: 47, 10, 9) was found in delta ($\log-F_{max} = 0.45$), theta ($\log-F_{max} = 0.36$), alpha1 ($\log-F_{max} = 0.28$) and alpha2 ($\log-F_{max} = 0.43$) frequency bands. Greater beta1 oscillations ($\log-F_{max} = 0.35$) were located in the left limbic lobe (BA: 31). Beta2 ($\log-F_{max} = 0.36$) and beta3 oscillations ($\log-F_{max} = 0.17$) were revealed in the left occipital lobe (BA: 17, 19). Increased gamma activity ($\log-F_{max} = 0.32$) was found in the right limbic lobe (BA: 36).

Audio-only Condition

Results of the independent significant test for the audio-only condition revealed greater activity across all frequency bands for group A. This difference was statistically significant ($p < .05$, corrected) in the alpha2 (Figure 3) and gamma frequencies (Figure 4). Alpha2 oscillations ($\log-F_{max} = 0.87$) were located in the right frontal lobe (BA: 10, 11) and gamma activity ($\log-F_{max} = 0.86$) was located in the right frontal lobe (BA: 9), sub-lobar (BA: 13) and temporal lobe (BA: 21). In addition to this significant activity, a number of active brain structures commonly involved in auditory processing and episodic memory (see Discussion for more details) were discovered in the theta and gamma frequencies just below the significance threshold ($\log-F = 0.84$); these structures together with the significant brain structures are outlined in Table 3.

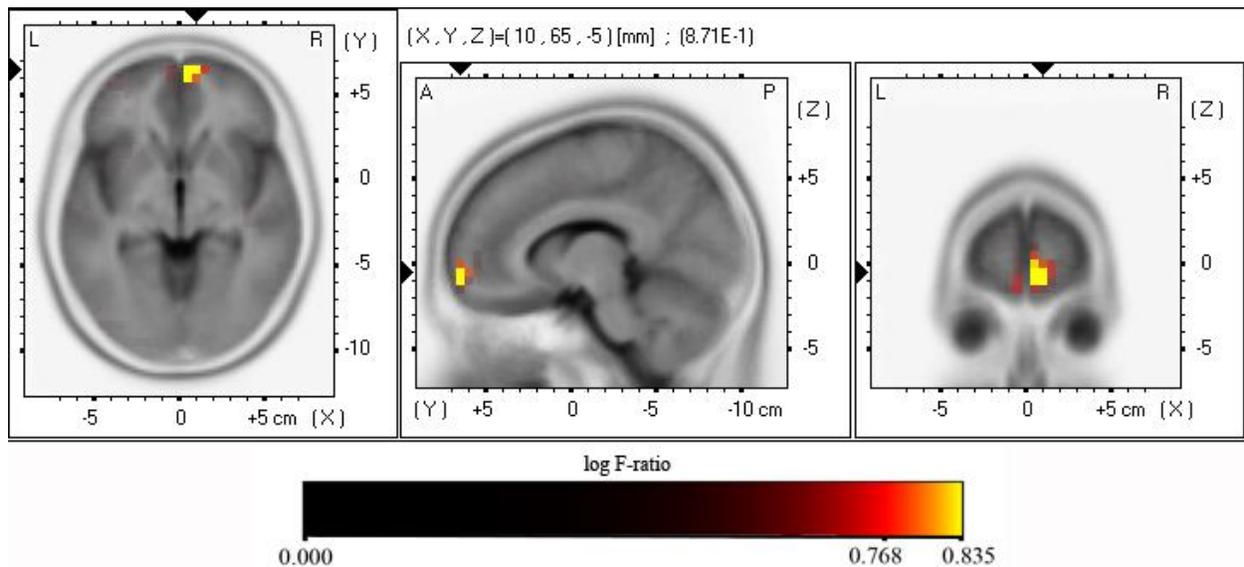


Figure 3. Statistical map of alpha2 oscillations (group A > B) for the audio-only condition. MNI-space coordinates indicated in the figure correspond to the voxel of highest significance (i.e. right superior frontal gyrus). L = left; R = right; A = anterior; P = posterior. The colour scale represents log F -ratio values (threshold: $\log-F = 0.835$, $p < .05$; $\log-F = 0.768$, $p < .1$).

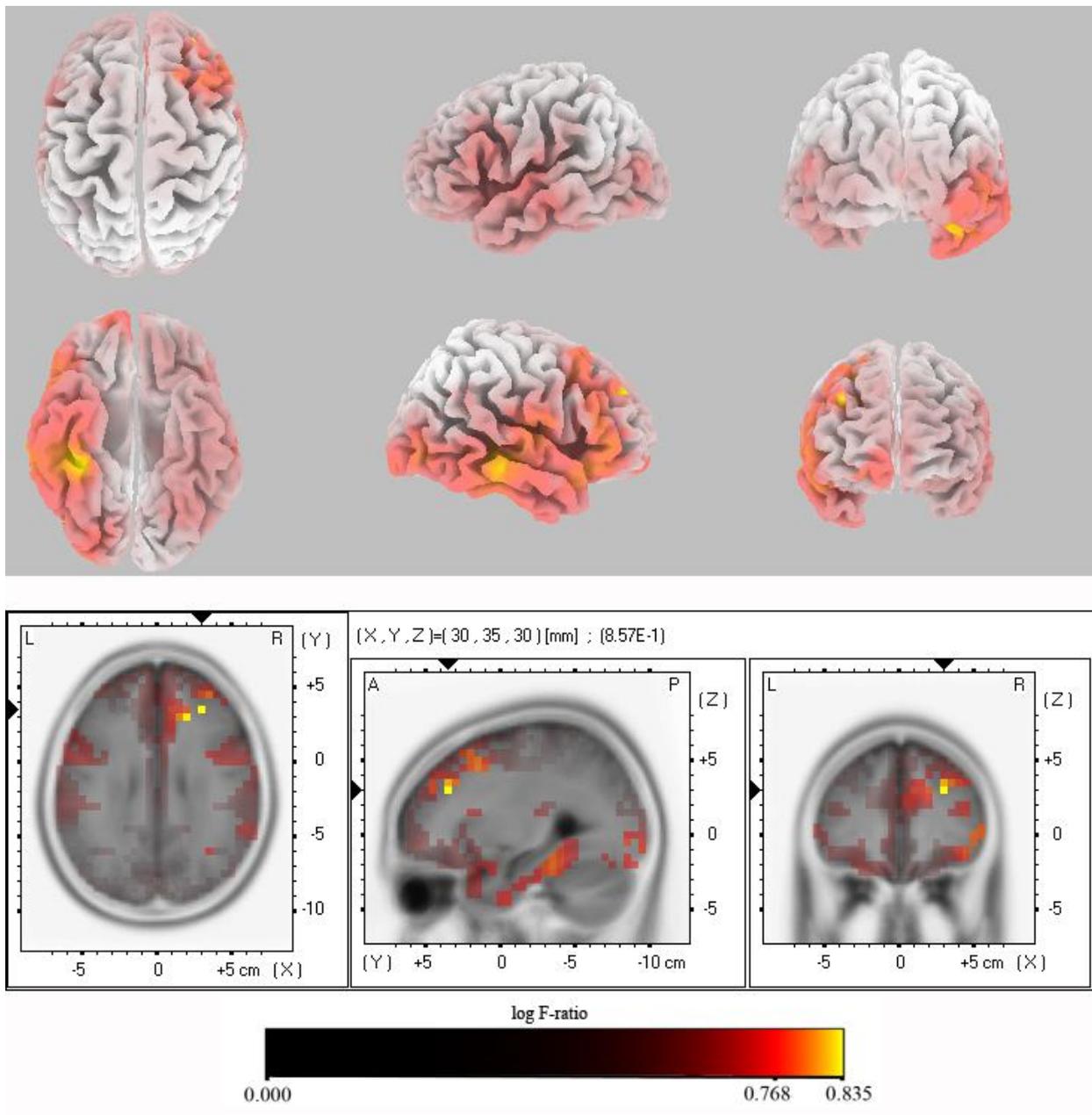


Figure 4. Statistical map of gamma oscillations (group A > B) for the audio-only condition. Results are projected onto the Colin cortical surface (top panel) and a brain MRI template (bottom panel). MNI-space coordinates indicated in the figure correspond to the voxel of highest significance (i.e. right middle frontal gyrus). L = left; R = right; A = anterior; P = posterior. The colour scale represents log F -ratio values (threshold: $\log-F = 0.835$, $p < .05$; $\log-F = 0.768$, $p < .1$).

Table 3

List of significant ($p < 0.05$) and predominantly active ($p < 0.1$) brain structures found in alpha2, gamma and theta frequency bands for the audio-only condition (group $A > B$). Maximum log-F values correspond to the first listed structure in each frequency band.

Frequency	p	\log_{Fmax}	Lobe	Structure	Brodmann area
Alpha2	0.05	0.87	R Frontal Lobe	Superior Frontal Gyrus	10, 11
Gamma	0.05	0.86	R Frontal Lobe	Middle Frontal Gyrus	9
				Superior Frontal Gyrus	9
			R Temporal Lobe	Superior Temporal Gyrus	22, 21
				Middle Temporal Gyrus	21
	0.1		R Sub-lobar	Insula	13
				R Temporal Lobe	Middle Temporal Gyrus
			R Temporal Lobe	Superior Temporal Gyrus	21, 22, 41, 13, 38
				Fusiform Gyrus	20, 37, 20, 36
				Inferior Temporal Gyrus	20, 19, 37
				Transverse Temporal Gyrus	42, 41
				Sub-Gyral	21, 20
				R Limbic Lobe	Parahippocampal Gyrus
			R Frontal Lobe	Anterior Cingulate	32
				Medial Frontal Gyrus	9, 32, 10
				Middle Frontal Gyrus	9, 8, 10, 47, 46
				Superior Frontal Gyrus	9, 8, 11, 10
				Inferior Frontal Gyrus	47, 46, 45, 13
				Precentral Gyrus	6, 4, 43, 9, 44
R Sub-lobar	Insula	13			
	Extra-Nuclear	13			
R Occipital Lobe	Middle Occipital Gyrus	19, 37, 18			
	Inferior Temporal Gyrus	37			
	Inferior Occipital Gyrus	18			
R Parietal Lobe	Postcentral Gyrus	43			
Theta	0.1		R Frontal Lobe	Inferior Frontal Gyrus	47
				Superior Frontal Gyrus	11

Discussion

This study investigated whether subsets of brain regions initially activated during the encoding of an audiovisual film experience are reactivated during subsequent exposure to a unisensory (audio-only or visual-only) version of that experience, i.e. redintegration. No a priori assumptions as to the localisation of cortical activity involved during complex audiovisual and subsequent audio-only and visual-only processing were made. Instead, exact, low-resolution electromagnetic tomography together with statistical nonparametric mapping in the frequency-

domain, was used to determine effects of redintegration. In order for redintegration to be apparent, two requisites had to be met:

1. That a significantly greater number of oscillating neuronal regions are found in participants who received audiovisual stimulation prior to unisensory exposure (compared to participants who experience the same unisensory stimulus without prior audiovisual stimulation) due to the activation of associated memory traces.
2. That the significantly active subsets of brain regions revealed in requisite one, are also actively involved in the encoding of the prior audiovisual film experience.

The statistical comparisons between groups revealed positive (group A > B) oscillations across all frequency bands for both the audio- and visual-only conditions, however, a significant difference was only revealed in the audio-only condition. The reason for this may simply be in the nature of the task itself. The visual-only condition presented participants with rich, dynamic stimulation that perhaps, for group A, did not require much retrieval of associated acoustic memories. Maybe the outcome would have been very different had there been more dialog in the visual-only stimulus, requiring participants to remember what had been said. Extensive dialogue however was deliberately avoided in both the visual- and audio-only conditions so as not to confine the stimulus to solely linguistic processing. Likewise, in the audio-only condition, participants may have found it easier to evoke the memories of the accompanying visual stimulus simply because they were so rich and vivid. The following subsections examine the evidence from the audio-only condition and speculate as to whether the cortical responses, revealed in this comparison between groups, sufficiently fulfil the two requisites for redintegration.

Upper Alpha Oscillations

Significantly enhanced alpha2 activity from group A was found in the right superior

frontal gyrus. The only difference between group A and group B was that group A had received, circa ten minutes prior, an audiovisual version of the same stimulus. Given this fact, it is difficult to determine from scientific literature regarding auditory, emotional and attentional processing, memory retrieval and executive control as to which cognitive process these right frontal alpha oscillations are likely involved in. Suggestions from two sources seem probable.

The first source argues that frontal alpha activity reflects the functional inhibition of task-irrelevant interference (i.e. executive control) (Park, et al., 2011). Here it is believed that the prefrontal cortex "filters" (see Shimamura, 2000) the sensory information by way of inhibitory control – a feature commonly associated with alpha oscillations (see: Knyazev, 2007; for a review). Perhaps then, this alpha activity is a reflection of participants attempting to maintain focus upon the auditory stimulus. Considering, however, that both group A and B were asked to focus upon the auditory stimulus this notion seems unlikely – although maybe prior multisensory processing has in some way enhanced task-related inhibitory/executive control.

Alternatively, the second source refers to findings pertaining to cognitive load during visual working memory processing. Matias Palva et. al (2010), found that frontoparietal alpha band activity was positively correlated with an increasing visual working memory load. This frontoparietal network (which manifested bilaterally), had strong connections to the cingulate gyrus, insula and occipitotemporal cortex. In this study, only strong, right frontoparietal oscillations were observed in the alpha band, but gamma oscillations were revealed in the cingulate gyrus, insula and occipitotemporal cortex. A cross frequency connectivity analysis may provide more insight into the behaviour of this alpha activity, thus future research should investigate this notion further.

Right Hemispheric Activity

The statistical difference between group A and B for the audio-only condition was found only in the right hemisphere. Given the enhanced emotional content embedded in the stimulus, this right hemispheric activity may likely be the result of emotional prosody processing (Gazzaniga, Ivry, & Mangun, 2009). Wildgruber et al. (2006) presented a model of emotional prosody that involves three successive stages of processing: 1) the extraction of suprasegmental acoustic information predominantly subserved by the right auditory cortex; 2) the representation of meaningful suprasegmental acoustic sequences within the right posterior superior-temporal sulcus; and 3) the explicit retrieval of acoustic information from emotional memory within the bilateral inferior frontal cortices. Although the temporal order of these responses cannot be confirmed in this study (because data was not analysed in the time domain), enhanced activity in all three of these cortical regions (transverse temporal, superior temporal and inferior frontal gyri) was discovered in the gamma band for group A. Because acoustic prosody processing is expected for this task it is therefore necessary to cogitate as to why group A had exceptionally stronger activity during this condition.

According to Wildgruber et al's (2006) prosody processing model, the inferior, frontal gyrus is associated with the explicit retrieval of acoustic information from emotional memory irrespective of emotion-type and valence of the stimulus. In conjunction with this model, many neuroimaging studies have consistently demonstrated the functional involvement of the right prefrontal cortex during episodic retrieval (Fletcher, Frith, & Rugg, 1997; Tulving, 2002) and several specific studies have shown the strong involvement of the right inferior frontal/insular cortex during cued recall conditions (see for example: Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1998; Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002; Renier, et al., 2009). Because group A had previously encoded a multisensory version of the stimulus, it is likely then,

that the enhanced activity during subsequent audio-only exposure is due to the retrieval of this encoded emotional content, a process which involves a right hemispheric network of posterior superior-temporal and inferior-frontal/insular cortices. Future research will require time-varying spectral analysis techniques in order to investigate this hypothesis further, but given the nature of the task and the differences between groups, it is reasonable to believe that the conditions for requisite one have been met.

Gamma and Theta Oscillations

Nyhus & Curran (2010) proposed in their "unified model" of episodic retrieval that gamma and theta activity cause the reinstatement of the entire episodic memory representation in the cortex by way of feedback projections from the hippocampus and also, that directional theta couplings from the frontal cortex to the hippocampus, allow for top-down control in the retrieval of episodic memories. In line with this model, gamma band responses are thought to involve an extensive network (subsequently referred to as POITF-network) of parieto-occipitotemporal (fusiform gyrus), inferior-temporal, and right frontal (middle and precentral gyri) areas when reinstating episodic memory representations of visually presented stimuli in the cortex (Gruber & Müller, 2005; 2006; Gruber, Trujillo-Barreto, Giabbiconi, Valdés-Sosa, & Müller, 2006; Gruber, Tsivilis, Giabbiconi, & Müller, 2008).

This pattern of gamma-theta cortical activity appears to be an evident difference between group A and B during the audio-only condition. Prominent theta activity was found in the right frontal middle and precentral gyri and gamma activity was localised in right parieto-occipitotemporal, inferior-temporal, frontal and even limbic (parahippocampus) lobe.

Considering that this POITF-network has been found to be active during retrieval of visual stimulation and that group A had specifically received prior audiovisual stimulation, it is possible

that this activity is an indication of retrieval of visual imagery associated to the acoustic stimulation, which further strengthens the notion that requisite one has been met.

The question remains however as to whether this right hemispheric, gamma-theta cortical activity, which appears to be a result of episodic retrieval, is reinstating the same cortical representations formed during encoding (i.e. requisite two). Based only on the findings of this study, this is not possible to determine. Given the nature of cortical responses found in group A during the A-only task, and how applicable these responses are with models of episodic memory retrieval, it appears that a far more sophisticated approach than just source localisation in each frequency band (as adopted in this study) is required. Future research will need to employ time-varying spectral analysis and cross-frequency phase-amplitude/phase-phase techniques in order to properly compare the intrinsic spatiotemporal and cross-frequency activity of the different cortical networks involved in both encoding and retrieval (Nyhus & Curran, 2010; Fell & Axmacher, 2011). Perhaps through this approach, differences between groups in the visual-only condition will also be revealed, shedding more light in the ways in which complex multisensory stimuli are encoded, integrated and retrieved.

References

- Allen, J. J. (2008). The Electroencephalogram, Basics in Recording EEG, Frequency Domain Analysis and its Applications I -- Mood Disorders & Emotions. *Podcasts and Slides from PSYC 401A/501A Principles of Psychophysiology*. Retrieved May 6, 2013, from http://apsychoserver.psychofizz.psych.arizona.edu/JJBAReprints/PSYC501A/pdfs2008/Psychophys_Lectures_Slides_2008.htm
- Anderer, P., Pascual-Marqui, R. D., Semlitsch, H. V., & Saletu, B. (1998). Electrical sources of P300 event-related brain potentials revealed by low resolution electromagnetic

- tomography: Effects of normal aging. *Neuropsychobiology*, 37, 20-27.
- Baddeley, A. D. (2007). *Working memory, thought, and action*. Oxford: Oxford University Press.
- Calvert, G. A., Bullmore, E. T., Campbell, R., Williams, S. C., McGuire, P. K., Woodruff, P. W., . . . David, A. S. (1997). Activation of auditory cortex during silent lipreading. *Science*, 276, 593-596.
- Cannon, R. L. (2012). *Low resolution brain electromagnetic tomography (LORETA): Basic concepts and clinical applications*. Corpus Christi: BMED Press.
- Dickson, J., Drury, H., & Van Essen, D. C. (2001). "The surface management system" (SuMS) database: a surface-based database to aid cortical surface reconstruction, visualization and analysis. *Philosophical Transactions of the Royal Society London B: Biological Sciences*, 356, 1277-1292. doi:10.1098/rstb.2001.0913
- Electrical Geodesics, Inc. (2013). *Dense Array EEG Neuroimaging*. Retrieved from EGI Dense array EEG: <http://www.egi.com/clinical-division-care-center/clinical-division-dense-array-neuroimaging>
- Electrical Geodesics, Inc. (2013). *Net Station EEG Software*. Retrieved from EGI: Dense Array EEG: <http://www.egi.com/research-division-research-products/eeg-software>
- Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. *Neuroscience: Nature reviews*, 105-118. doi:10.1038/nrn2979
- Fletcher, P. C., Frith, C. D., & Rugg, M. D. (1997). The functional neuroanatomy of episodic memory. *Trends in Neuroscience*, 20, 213-218.
- Fletcher, P. C., Shallice, T., Frith, C. D., Frackowiak, R. S., & Dolan, R. J. (1998). The functional roles of prefrontal cortex in episodic memory II. Retrieval. *Brain*, 121, 1249-1256.
- Flor-Henry, P., Lind, J. C., & Koles, Z. J. (2004). A source-imaging (low-resolution

- electromagnetic tomography) study of the EEGs from unmedicated males with depression. *Psychiatry Research*, *130*(2), 191-207.
- Folkets Bio. (2009). Svensk kortfilm c/o Folkets Bio: Volym 2. Sverige:
<http://folketsdvd.se/kortfilm/svensk-kortfilm-co-folkets-bio-2>. Retrieved from Folkets Bio: <http://folketsdvd.se/kortfilm/svensk-kortfilm-co-folkets-bio-2>
- Frassinetti, F., Bolognini, N., & Làdavas, E. (2002). Enhancement of visual perception by crossmodal visuo-auditory interaction. *Experimental Brain Research*, *147*(3), 332-343.
- Furman, O., Dorfman, N., Hasson, U., Davachi, L., & Dudai, Y. (2007). They saw a movie: Long-term memory for an extended audiovisual narrative. *Learning & Memory*, *14*, 457-467. doi:10.1101/lm.550407
- Galin, D., Ornstein, R., Herron, J., & Johnstone, J. (1982). Sex and handedness differences in EEG measures of hemispheric specialization. *Brain and Language*, *16*(1), 19-55.
- Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (2009). *Cognitive Neuroscience: The biology of the mind*. New York: W.W. Norton & Company, Inc.
- Gingras, G., Rowland, B. A., & Stein, B. E. (2009). The differing impact of multisensory and unisensory integration on behavior. *Journal of Neuroscience*, *29*(15), 4897-4902. doi:10.1523/JNEUROSCI.4120-08.2009
- Gottfried, J. A., Smith, A. P., Rugg, M. D., & Dolan, R. J. (2004). Rememberance of Odors Past: Human Olfactory Cortex in Cross-Modal Recognition Memory. *Neuron*, *42*, 687-695.
- Gruber, T., & Müller, M. M. (2005). Oscillatory brain activity dissociates between associative stimulus content in a repetition priming task in the human EEG. *Cerebral Cortex*, *15*, 109-116.
- Gruber, T., & Müller, M. M. (2006). Oscillatory brain activity in the human EEG during indirect

- and direct memory tasks. *Brain Research*, 1097, 194-204.
- Gruber, T., Trujillo-Barreto, J. N., Giabbiconi, C. M., Valdés-Sosa, P. A., & Müller, M. M. (2006). Brain electrical tomography (BET) analysis of induced gamma band responses during a simple object recognition task. *NeuroImage*, 29, 888-900.
- Gruber, T., Tsivilis, D., Giabbiconi, C., & Müller, M. M. (2008). Induced electroencephalogram oscillations during source memory: familiarity is reflected in the gamma band, recollection in the theta band. *Journal of Cognitive Neuroscience*, 20(6), 1043–1053.
- Hamilton, W. (1859). *In Lectures on Metaphysics and Logic* (Vol. I). Gould & Lincoln.
- Hasson, U., Malach, R., & Heeger, D. J. (2009). Reliability of cortical activity during natural stimulation. *Trends in Cognitive Sciences*, 14(1), 40-48.
- Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject Synchronization of Cortical Activity During Natural Vision. *Science*, pp. 1634-1640.
- Holmes, A. P., Blair, R. C., Watson, J. D., & Ford, I. (1996). Nonparametric analysis of statistic images from functional mapping experiments. *Cerebral Blood Flow and Metabolism*, 16(1), 7-22.
- Horowitz, L. M., & Prytulak, L. S. (1969). Redintegrative memory. *Psychological Review*, 76, 519-32.
- Hulme, C., Roodenrys, S., Schweickert, R., Brown, G. D., Martin, S., & Stuart, G. (1997). Word-frequency effects on short-term memory tasks: Evidence for a redintegration process in immediate serial recall. *Journal of Experimental Psychology*, 23(5), 1217-1232.
- Jurcak, V., Tsuzuki, D., & Ippaita, D. (2007). 10/20, 10/10, and 10/5 systems revisited: Their validity as relative head-surface-based positioning systems. *NeuroImage*, 34, 1600-1611.
- Knyazev, G. (2007). Motivation, emotion, and their inhibitory control mirrored in brain

- oscillations. *Neuroscience and biobehavioral reviews*, *31*, 377-395.
- Koenig, T., & Pascual-Marqui, R. D. (2009). Multichannel frequency and time-frequency analysis. In C. M. Michel, T. Koenig, D. Brandeis, L. R. Gianotti, & J. Wackermann, *Electrical Neuroimaging* (pp. 145-168). Cambridge: Cambridge University Press.
- Lehmann, S., & Murray, M. M. (2005). The role of multisensory memories in unisensory object discrimination. *Cognitive Brain Research*, *24*, 326–334. Retrieved from www.elsevier.com/locate/cogbrainres
- Matias Palva, J., Monto, S., Kulashkhar, S., & Palva, S. (2010). Neuronal synchrony reveals working memory networks and predicts individual memory capacity. *Proceedings of the National Academy of Sciences USA*. doi:10.1073/pnas.0913113107
- Mazziotta, J., Toga, A., Evans, A., Fox, P., Lancaster, J., Zilles, K., . . . Mazoyer, B. (2001). A probabilistic atlas and reference system for the human brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *356*, 1293-1322.
- McDonald, J. J., Teder-Sälejärvi, W. A., & Hillyard, S. A. (2000). Involuntary orienting to sound improves visual perception. *Nature*, *407*(6806), 906-908.
- Murray, M. M., Foxe, J. J., & Wylie, G. R. (2005). The brain uses single-trial multisensory memories to discriminate without awareness. *NeuroImage*, *27*, 473-478.
- Murray, M. M., Michel, C. M., Grave de Peralta, R., Ortigue, S., Brunet, D., Andino, S. G., & Schneider, A. (2004). Rapid discrimination of visual and multisensory memories revealed by electrical neuroimaging. *NeuroImage*, *21*, 125-135. Retrieved from www.elsevier.com/locate/ynimg
- Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: a primer with examples. *Human Brain Mapping*, *15*(1), 1-25.

Nyberg, L., Forkstam, C., Petersson, K. M., Cabeza, R., & Ingvar, M. (2002). Brain imaging of human memory systems: between-systems similarities and within-system differences.

Cognitive Brain Research, *13*, 281-292.

Nyberg, L., Habib, R., McIntosh, A. R., & Tulving, E. (2000). Reactivation of encoding-related brain activity during memory retrieval. *Proceedings of the National Academy of Sciences USA*, *97*(20), 11120-11124.

USA, *97*(20), 11120-11124.

Nyhus, E., & Curran, T. (2010). Functional role of gamma and theta oscillations in episodic memory. *Neuroscience and biobehavioral reviews*, 1023-1035.

doi:10.1016/j.neubiorev.2009.12.014

Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology*, *112*, 713-719.

Park, H., Kang, E., Kang, H., Kim, J. S., Jensen, O., Chung, C. K., & Lee, D. S. (2011). Cross-Frequency Power Correlations Reveal the Right Superior Temporal Gyrus as a Hub Region During Working Memory Maintenance. *Brain Connectivity*, *1*(6), 460-472.

doi:10.1089/brain.2011.0046

Pascual-Marqui, R. D. (2007). *Discrete, 3D distributed, linear imaging methods of electric neuronal activity. Part 1: exact, zero error localization*. Retrieved May 6, 2013, from LORETA: low resolution brain electromagnetic tomography:

<http://arxiv.org/pdf/0710.3341>

Pascual-Marqui, R. D. (2009). Theory of the EEG inverse problem. In S. Tong, & N. Thakor, *Quantitative EEG Analysis: Methods and Applications* (pp. 121-140). Boston: Artech House.

Pascual-Marqui, R. D., Lehmann, D., Koukkou, M., Kochi, K., Anderer, P., Saletu, B., . . .

- Kinoshita, T. (2011). Assessing interactions in the brain with exact low-resolution electromagnetic tomography. *Philosophical Transactions of the Royal Society A: Mathematical Physical and Engineering Sciences*, 369(1952), 3768-3784.
doi:10.1098/rsta.2011.0081
- Pascual-Marqui, R. D., Nitschke, J. B., Oakes, T. R., Larson, C. L., Abercrombie, H. C., Schaefer, S. M., . . . Davidson, R. J. (2001). Anterior cingulate activity as a predictor of degree of treatment response in major depression: evidence from brain electrical tomography analysis. *American Journal of Psychiatry*, 158, 405-415.
- Psychology Software Tools, Inc. (2012). *E-Prime 2*. Retrieved 2013, from Psychology Software Tools, Inc. Solutions for research, assessment, and education:
<http://www.pstnet.com/eprime.cfm>
- Renier, L. A., Anurova, I., De Volder, A. G., Carlson, S., VanMeter, J., & Rauschecker, J. P. (2009). Multisensory integration of sounds and vibrotactile stimuli in processing streams for "what" and "where". *Journal of Neuroscience*, 29(35), 10950-10960. doi:10.1523/JNEUROSCI.0910-09.2009
- Shams, L., & Seitz, A. R. (2008). Benefits of multisensory learning. *Trends in Cognitive Sciences*, 12(11), 411-417. doi:10.1016/j.tics.2008.07.006
- Shams, L., Wozny, D. R., Kim, R., & Seitz, A. (2011). Influences of multisensory experience on subsequent unisensory processing. *Frontiers in Psychology*, 2(264).
doi:10.3389/fpsyg.2011.00264
- Shimamura, A. P. (2000). The role of the prefrontal cortex in dynamic filtering. *Psychobiology*, 28, 207-218.
- Teyler, T. J., & DiScenna, P. (1986). The hippocampal memory indexing theory. *Behavioral*

Neuroscience, 100, 147-154.

- Teyler, T. J., & Rudy, J. W. (2007). The hippocampal indexing theory and episodic memory: updating the index. *Hippocampus*, 17, 1158-1169.
- Thelen, A., Cappe, C., & Murray, M. M. (2012). Electrical neuroimaging of memory discrimination based on single-trial multisensory learning. *Neuroimage*, 62, 1478–1488.
Retrieved from www.elsevier.com/locate/ynimg
- Thompson, V. A., & Paivio, A. (1994). Memory for pictures and sounds: independence of auditory and visual codes. *Canadian Journal of Experimental Psychology*, 48(3), 380-398.
- Tulving, E. (2002). Episodic Memory: From mind to brain. *Annual Review of Psychology*, 53, 1-25.
- Tulving, E., & Madigan, S. A. (1975). Memory and verbal learning. *Annual Reviews*, 26, 291-335. doi:10.1146/annurev.ps.26.020175.001451
- Wildgruber, D., Ackermann, H., Kreifelts, B., & Ethofer, T. (2006). Cerebral processing of linguistic and emotional prosody: fMRI studies. *Progress in Brain Research*, 156, 249-268.

Appendix I

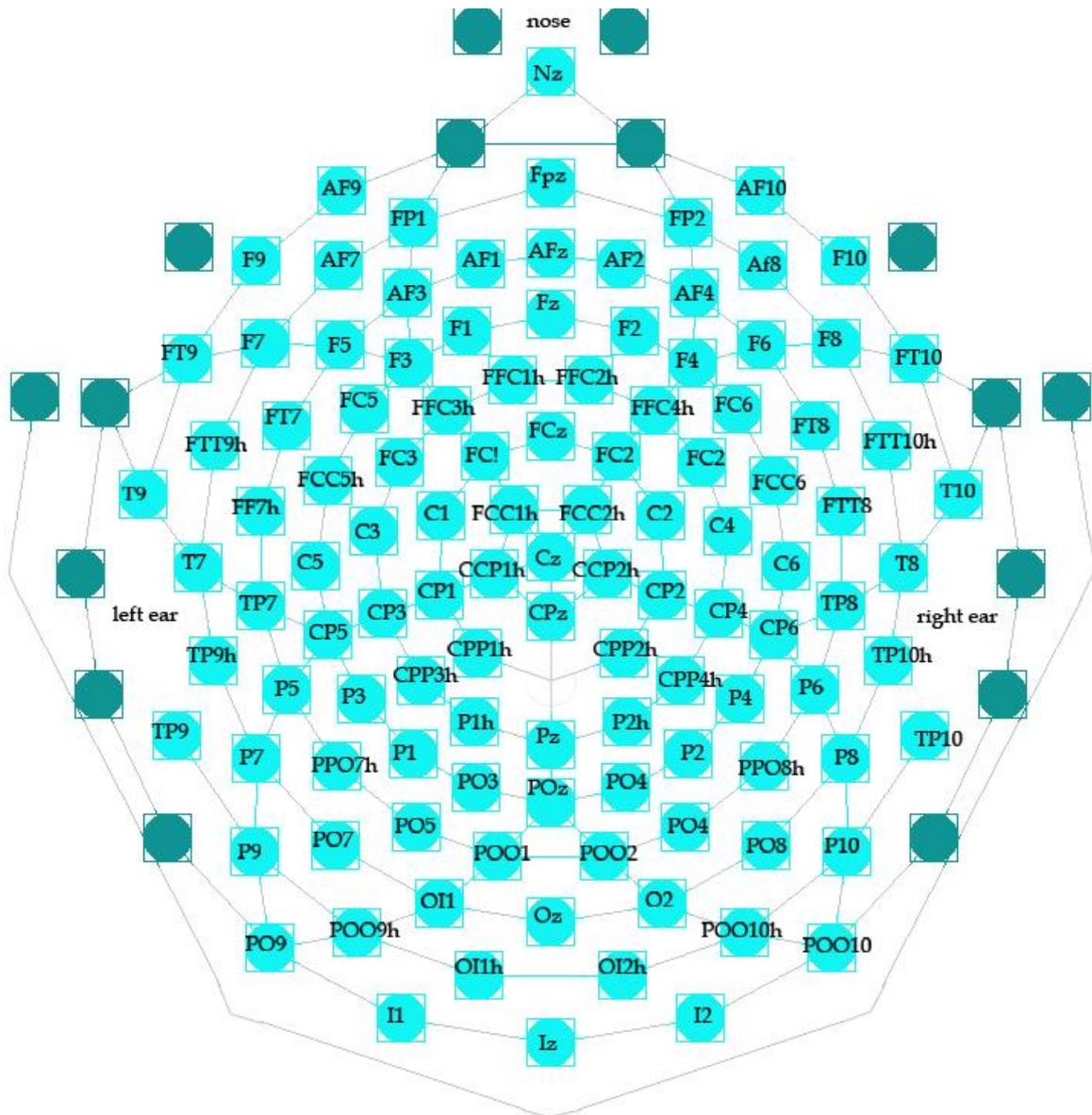


Figure I. Data was down sampled to the 10-5 system. Electrodes not included in the montage after down sampling are dark blue.

Appendix II

The number of good, artefact free epochs varied across participants and stimulus conditions: range 6 – 32 (Table I). Because averaging across epochs preserves the constant signal and gradually cancels the random noise it is likely that smaller numbers of epochs will contain more noise. However, care was taken to select epochs that did not contain any visually obvious physiological artefacts or random channel noise (likely due to changes in impedance over time).

Table I.

Number of extracted artefact free 3-second epochs per participant and stimulus condition. Epochs for the A (audio-only) and V (visual-only) conditions were extracted from circa 90 s of data and epochs for the AV (audiovisual) condition were extracted from circa 180 s of data.

Participant	Group A			Group B		
	<u>Stimulus Condition</u>			<u>Stimulus Condition</u>		
	A	V	AV	A	V	AV
1	8	12	16	17	9	23
2	12	6	16	6	6	12
3	11	9	26	18	10	19
4	17	18	25	19	7	23
5	6	10	23	19	8	18
6	20	14	32	9	11	10
7	20	12	32	9	10	17
8	17	11	24	7	15	26
9	15	9	18	17	12	26
10	8	9	26	16	7	13
11	21	12	29	8	9	16
12	13	10	13	15	7	22

Appendix III

Linköping University Electronic Press



Copyright

The publishers will keep this document online on the Internet – or its possible replacement – from the date of publication barring exceptional circumstances.

The online availability of the document implies permanent permission for anyone to read, to download, or to print out single copies for his/hers own use and to use it unchanged for non-commercial research and educational purpose. Subsequent transfers of copyright cannot revoke this permission. All other uses of the document are conditional upon the consent of the copyright owner. The publisher has taken technical and administrative measures to assure authenticity, security and accessibility.

According to intellectual property law the author has the right to be mentioned when his/her work is accessed as described above and to be protected against infringement.

For additional information about the Linköping University Electronic Press and its procedures for publication and for assurance of document integrity, please refer to its www home page: <http://www.ep.liu.se/>.

© Rina Blomberg