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Multisensory Associative Learning and Multisensory Integration

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Abstract

Human multisensory experiences with the world rely on a combination of top-down and bottom-up influences, a process that changes throughout development. The present study explored the relationship between multisensory associative learning and multisensory integration using encephalography (EEG) and behavioural measures. While recording EEG activity, participants were exposed to novel pairings of non-sociolinguistic audiovisual stimuli of varying presentation probability while performing a detection task. The same stimuli were then used in another detection task, which was followed by an analogous behavioural speeded-response task, both of which kept probabilities equal and tested for multisensory integration. Significant relationships were found in fronto-central and occipital areas between late measures of associative learning and both early and late indices of multisensory integration in frontal and centro-parietal areas, respectively. Furthermore, a significant relationship was found between the behavioural and early neural index of multisensory integration. These results highlight the influence of higher-order processes, namely, learned associations on multisensory integration.

Keywords

associative learning, multisensory integration, sensory processing, learning, sensory perception, EEG.

Summary for Lay Audience

Our experiences with the world with our senses rely on many things. What we already know about our environment is based on previous experiences with it, but also on different cues that tell us if multiple events we experience through our senses make up one event when combined, or separate events. In this study, we were interested in how learning to associate different events from our senses relates to how our brains know what events to perceive as one, or separate events. We used electrodes placed on the head to record brain activity while participants took part in our experiment. The participants saw shapes that were shown at the same time as tones and were asked to respond with their finger when they detected a specific pair. The likelihood of seeing the pairings is what we manipulated. Then, they were shown the same shapes and tones either together or separately and were simply asked to answer when they saw a red cross on the screen. Finally, they were shown the separate and paired shapes and tones and asked to respond with their finger as soon as they heard a tone or saw a shape. In this last part, we recorded how fast their responses were. As we expected, we found that individuals who learned pairs of shapes and tone well were also better at integrating information from different senses. We also found that how fast they were at responding was significantly related to how well their brain did this integration. This study shows the influence of our learning abilities for pairs of events from different senses on how well our brains integrate that information to simplify how we interact with the world.

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List of Abbreviations

Abbreviation	Meaning
°	Degrees
A	Auditory
AV	Audiovisual
C	Central
CDF	Cumulative distribution function
CI	Confidence interval
cm	Centimetre
CP	Centro-parietal
CRT	Cathode-ray tube
d	Cohen’s d
dB	Decibel(s)
EEG	Electroencephalography
EMSI	Early multisensory integration
ERP	Event-related potential
F	Frontal
FC	Fronto-central
Hz	Hertz
LMSI	Later multisensory integration
LPO	Left parieto-occipital
M	Mean
MMN	Mismatch negativity
ms	Millisecond(s)
MSI	Multisensory integration
N	Number of participants
O	Occipital (multisensory integration)
Occ	Occipital (associative learning)
p	Probability
P3a	An event-related potential component

P3b	An event-related potential component
Q	Benjamini-Hochberg false discovery rate
r	Correlation coefficient
R_2	Correlation effect size
RSE	Redundant-signals effect
RT	Response time
SC	Superior colliculus
SEM	Standard error of the mean
SNR	Signal-to-noise ratio
SPL	Sound pressure level
SD	Standard deviation
t	Student distribution value
TBW	Temporal binding window
V	Visual
α	Alpha
Δ	Delta
μV	Microvolt(s)

Introduction

All of our interactions with the world depend on how we process sensory information, which shapes how we perceive the world around us. Each sensory system transduces different types of energy to glean information about our environment. The information that each of these sensory modalities conveys is transduced independently, yet it is often integrated into a single, unified perception. Our perceptual systems must handle all of the information that is conveyed from each sensory modality, bind the information that comes from the same source, and segregate the sensory information that come from different sources. This complex process originally defined by William James (1890) is known as the *binding problem*, and is central to research on multisensory integration. To illustrate this, one can imagine having a conversation with someone at a coffee shop. As you converse with your friend, you do not separately perceive the auditory signal emitted from their mouth and the visual signal associated with the facial articulations of their speech. Instead, you perceive the auditory and visual speech signals as a single, unified perception of your friend talking to you.

Indeed, these bound, multisensory representations make up our perceptual world. This process of integrating what we see and hear into a single coherent perception is perhaps best illustrated through an audiovisual illusion known as the McGurk effect (McGurk & MacDonald, 1976). When one is presented with a visual “ba”, and an auditory “ga”, individuals often reported perceiving the syllable “da”. This illusion exemplifies the interactive nature of sensory perception, as the visual information from the lips and the auditory information from the voice are integrated into one event. Furthermore, this perception does not include the original /b/ and /g/ that were present in the auditory and visual stimulus, but is rather an entirely new phoneme /d/ that is not present in either unisensory stimulus.

In addition to the qualitative impact on how we perceive the world around us, multisensory integration also confers a number of behavioural benefits. One of the most often used measures to quantify multisensory integration and to highlight its behavioural benefits is response time (RT; Stevenson et al., 2014) Speeded RTs have consistently been a marker of the added benefits that information from multiple sensory modalities offer, as compared to solely unisensory information (Andreassi & Greco, 1975; Forster et al., 2002; Hershenson, 1962; Hughes et al., 1994; Stevenson, Fister, Barnett et al., 2012). Furthermore, when presented with multisensory (e.g., audiovisual or visual-tactile) stimuli, saccade initiation was faster than when presented only with the visual information (Amlôt et al., 2003; Colonius & Arndt, 2001; Diederich et al., 2003; Frens et al., 1995; Harrington & Peck, 1998; Hughes et al., 1994).

Another benefit of integrating information from multiple senses is more accurate detection where, for example, weak unisensory auditory and visual signals may not be detectable when presented independently, but are detectable when presented simultaneously (Frassinetti et al., 2002; Lovelace et al., 2003; Nidiffer et al., 2016; Stein & Meredith, 1993; Stevenson, Bushmakin, Kim et al., 2012). This benefit has been repeatedly observed using higher-level (e.g., audiovisual speech) and lower-level (e.g., flashes and beeps) stimuli.

Importantly, during speech perception, “multisensory gain” has been repeatedly observed where listeners benefit from an increase in intelligibility when auditory speech in noise is presented with concordant visual information (Grant & Seitz, 2000; Ma et al., 2009; Ross et al., 2007; Stacey et al., 2016; Stevenson & James, 2009; Sumby & Pollack, 1954). Other research has shown that temporal synchrony between auditory and visual events leads to better visual perception (Dalton & Spence, 2007; Vroomen & De Gelder, 2000). Interestingly, biases toward a specific sensory modality can occur. For example, in the ventriloquism effect, sound is typically shifted towards a visual event. In this effect, visual dominance is observed in the spatial domain (Slutsky & Recanzone, 2001), and auditory dominance is seen in the temporal domain (Morein-Zamir et al., 2003).

Finally, better spatial localization is also a benefit that is observed as a result of interactions between sensory information from more than one modality (Nelson et al., 1998; Stein et al., 1996; Stein et al., 1989; Teder-Sälejärvi et al., 2002).

Evidence of multisensory interactions leading to localization, perceptual, and detection benefits has continuously been shown to be dependent on spatial and temporal factors

(Frens et al., 1995; Stein et al., 1988; Stein et al., 1989; Wallace et al., 1992). While the examples above conceptually describe the process in which information from the auditory and visual systems are perceptually bound into a single percept, this process is in fact quite complicated. Each sensory system is constantly bombarded by sensory information, and determining which piece of auditory and visual information originate from the same source is paramount to this process. Learning what information goes together and is perceived as one event and what does not is integral to how easily we perceive and interpret the world. Returning to the example of having a conversation with your friend in a coffee shop, one can imagine a very busy coffee shop where there are multiple conversations happening while you are trying to converse with your friend. As a listener, you must determine which auditory signal originated from the same external event (the speaker's utterance) as the visual signal (the speaker's lips) and successfully perceptually bind these two inputs, while actively *not* binding any of the auditory and visual signals from the other conversations going on around you.

To accomplish this feat, our perceptual systems use two categories of information to determine what auditory and visual information likely originated from the same external event, and should thus be integrated; lower-level sensory features (e.g., spatial alignment, temporal congruency) and higher-level, top-down influences (e.g., learned associations, semantic congruence).

At the sensory level, the timing of the two stimuli from both modalities has been shown to be key as to whether integration occurs. If both features are too asynchronous from one another, they will usually be perceived as two separate events (Colonius & Diederich, 2004; Vroomen & Keetels, 2010). For example, our perceptual systems are attuned to account for the difference in speed at which sound and light travel (Hillock et al., 2011). With that said, if this difference is too great, multisensory integration may take place, leading to the auditory and the visual information being processed independently (Stevenson, Zemtsov, & Wallace, 2012). This is perhaps best described by the temporal binding window (TBW), which is the time window in which two asynchronous stimulus features are perceived as one event (Conrey & Pisoni, 2006; Conrey & Pisoni, 2004; Dixon & Spitz, 1980; Senkowski et al., 2007; Stevenson et al., 2010; Stevenson et al., 2017; Stevenson, Fister, Barnett et al., 2012; Stevenson et al., 2011; Stevenson & Wallace, 2013; van Eijk et al., 2008, 2010; Vroomen & Keetels, 2010; Vroomen & Stekelenburg, 2011). The width of this window, although subject to a high degree of variability, is commonly in the range of 280-425 ms (Stevenson, & Wallace, 2013).

Similarly, the location in space from which the multisensory information is perceived is key to whether the information will be bound and perceived as one event; information that is perceived as originating from the same spatial location is more likely to be bound (Hairston et al., 2003; King & Palmer, 1985; Lewald et al., 2001; Meredith & Stein, 1986a, 1996; Radeau & Bertelson, 1987; Slutsky & Recanzone, 2001). For example, in speech perception, the listener relies on the assumption that the sound that they are hearing from the speaker is originating from their lips (Colin et al., 2001).

The principle of inverse effectiveness, as opposed to being a property under which stimuli are integrated (like the temporal and spatial principles), represents the negatively proportional relationship between multisensory gain and the effectiveness of the unisensory inputs to drive a responsive (Meredith & Stein, 1986b). The principle is very robust and has been demonstrated through the use of numerous paradigms (Ross et al., 2007; Senkowski et al., 2011; Stevenson, Bushmakin, Kim et al., 2012; Stevenson & James, 2009). Generally speaking, stimuli of lower efficacy (which is usually controlled through stimulus salience) produce greater multisensory gain (Stevenson et al., 2014).

These principles were first characterized at the single-neuron level in the superior colliculus (SC), where early studies looked at subcortical single unit recordings of the convergence of sensory information from animal models (Meredith & Stein, 1983, 1986b; Stein et al., 1988; Stein & Meredith, 1993). In this important research, the number of action potentials is the dependent measure used to quantify multisensory integration, where the strongest unisensory signal is compared to the multisensory response (Stevenson et al., 2014). As for the cortical locations where multisensory integration has been identified through their generation of subadditive and superadditive responses, this activity has been identified in multiple brain regions, most notably in the superior temporal sulcus, which is responsible for integrating information about letters, objects, and speech from visual and auditory sensory modalities (Beauchamp, Argall, Bodurka et al., 2004; Beauchamp, Lee, Argall et al., 2004; Bishop & Miller, 2008; Calvert, 2001; Calvert et al., 2000; Calvert & Lewis, 2004; James & Stevenson, 2012; Macaluso et al., 2004; Stevenson et al., 2010; Stevenson et al., 2007; Stevenson & James, 2009; Stevenson et al., 2011; Van Atteveldt et al., 2004). The intraparietal sulcus has also been identified as a locus of integration, particularly in relation to spatial attention and congruency and their modulation of multisensory integration (Calvert et al., 2001; Macaluso et al., 2000). Finally, the anterior cingulate cortex has been shown to be involved in conflict monitoring, specifically in the directing of attention, as well as its involvement in the processing of unisensory and multisensory information (Laurienti et al., 2003; Tang et al., 2016; Weissman et al., 2003).

Top-down processes also play an important role in whether sensory information from more than one modality is integrated. Semantic congruence (e.g., contextual cues) are often recruited, when pertinent, in multimodal situations, from high-level (Calvert et al., 2000) to low-level stimuli (Laurienti et al., 2003). On the other hand, and perhaps more crucially for this experiment, learned associations play an integral role in whether sensory inputs are bound. Multisensory integration relies on the learned associations between sensory information from more than one modality. As typically-developing adults, when novel multisensory stimuli are encountered, there is a tendency to use a combination of the physical stimulus characteristics such as temporal synchrony and spatial location, or to rely on previously encountered associations to interpret the novel stimuli (ten Oever et al., 2013). These prior experiences are crucial for ensuring accuracy in the interpretation of incoming multisensory information, as the formation of these experiences is complex and multifaceted. These experiences can incorporate semantic, affective, and relational cues into their stored representation, which can make the integration process much more efficient (Lewkowicz, 2014), as top-down effects has been observed as early as 60 ms when exposed to multisensory stimuli (De Meo et al., 2015).

This process changes with age, where infants rely more heavily on the inherent stimulus characteristics (e.g., spatial and temporal congruence) than on statistical probabilities of occurrence and learned associations when deciding whether to integrate or segregate sensory information (Murray et al., 2016). Throughout development, there is a shift from primarily using stimulus features to using learned associations and prior experiences with the world when deciding whether to integrate, a process termed multisensory perceptual narrowing (Lewkowicz, 2014).

An overwhelming amount of evidence exists supporting the notion that multisensory integration often relies on learned associations (Brunel et al., 2015; Hubel & Wiesel, 1998; Hummel & Gerloff, 2005; Laine et al., 2007; Mitchel & Weiss, 2011; Wallace, 2004). The learning of arbitrary associations between features from different sensory modalities could also be explained by a type of statistical learning (Sarmiento et al., 2016). This process is one where statistical regularities are extracted across time in order to learn about the structure of the sensory inputs (Saffran et al., 1996). The robustness of this effect is perhaps best demonstrated by presenting participants with novel spatially and temporally congruent audiovisual stimuli that were arbitrarily paired (Altieri et al., 2015). Over time, participants demonstrated neural and behavioural benefits, in concordance with learning effects. This precisely exemplifies the top-down influence of learned associations on stimuli that are otherwise maximally congruent. These learned associations are also distinct from semantic congruency, which is also a top-down process that modulates multisensory integration (Doehrmann & Naumer, 2008).

Learned associations can have an important effect on bottom-up processes. Studies have shown that experience with learned associations and their statistics can reduce the strength of temporal factors (Habets et al., 2017). These findings speak to the constant balance and re-weighting of the pre-attentive automatic processes such as temporal and spatial congruence against the higher-order, top-down processes such as attention and learned associations. Our perceptual systems tend to offer some flexibility in this dynamic process. The implications for multisensory integration are significant, as this balancing act is constantly happening and changing throughout our lives and the different experiences we encounter.

Though there is clear theoretical work supporting the link between learned associations across modalities and multisensory integration, to date there have been few studies empirically exploring the relationship between learning novel multisensory associations and how well we integrate information from these associations. Seeing as associative learning plays a key role in effective integration of sensory information (Murray et al., 2016), and that this integration process has been continually associated with behavioural benefits, we posit that multisensory associative learning will be positively related with multisensory gain, as well as its associated behavioural benefits.

This study aims to explore whether a relationship exists between one's ability to learn associations between multisensory stimuli and their ability to integrate multisensory information. By exposing adults to novel low-level (non-sociolinguistic) audiovisual stimulus pairings in a learning phase and subsequently exposing them to the separate and combined features from these pairings, we predict that their ability to integrate multisensory information will be proportionate to their associative learning. This study is designed to test participants' learning of novel arbitrary multisensory associations, and testing their multisensory integration abilities is contingent on how well they learned the pairings. The use of non-sociolinguistic stimuli is particularly crucial in exploring the learning effect as an isolated phenomenon, free from all social and linguistic cues that are usually provided with sociolinguistic stimuli (e.g., speech and faces).

While both multisensory associative learning and multisensory integration have been well established in the literature behaviourally, they have also been studied extensively through electroencephalography (EEG; Besle et al., 2009; Molholm et al., 2002; Saint-Amour et al., 2007). EEG is useful in providing high temporal resolution to understand phenomena as they are unfolding in the brain. It measures the summed activity from multiple neural generators within the brain. The continuous recorded EEG activity is segmented into time-locked events, representing individual trials, or event-related potentials (ERPs). Using this method, a three-stimulus oddball detection paradigm (Courchesne et al., 1975) can be used to assess learning, which includes frequent stimuli, an infrequent target that is difficult to discriminate from the frequent stimuli, and a distracter stimulus, which is easily discriminable and highly salient. This version of the oddball task controls for novelty effects to isolate learning (Polich & Comerchero, 2003).

Assessing multisensory integration can be done using passive exposure to a combination of audiovisual stimuli as well as their unisensory components, while attention is sustained using an irrelevant detection task (Cappe et al., 2010). Electrophysiological indices of multisensory integration can take place at multiple latencies after stimulus presentation. The first of these indices represents *early* sensory interactions. Such interactions are typically defined as occurring <100 ms post-stimulus onset (De Meo et al., 2015; Giard & Peronnet, 1999; Molholm et al., 2002), and are typically centrally or fronto-centrally located on the scalp (Talsma et al., 2007). The second index (approximately 200 ms post-stimulus presentation) represents a later-going index of integration that has been previously established (Besle et al., 2009; Besle et al., 2005; Giard & Peronnet, 1999). Its topographical scalp locations tend to be over the central, parietal, and occipital areas (Möttönen et al., 2004), and it is thought to be representative of the latest possible latency before confounds such as common activity, which is typically indicative of response selection or motor responses, appear (Besle et al., 2004; Hillyard et al., 1998).

Both of these time-windows are thought to represent sensory-perceptual activity that occurs as a result of feedforward bottom-up processes (Foxe et al., 2000; Lamme & Roelfsema, 2000), although evidence exists that argues otherwise (Talsma & Woldorff, 2005). Given the passive nature of the stimuli being presented, the audiovisual signal is expected to be subadditive (Talsma et al., 2007). Subadditivity uses the additive model to quantify multisensory integration (Stevenson et al., 2014), where the unisensory signals are summed and compared to the multisensory signal. The result of this computation is considered subadditive if the multisensory signal is smaller than the sum of the unisensory signals (e.g., Hein et al., 2007), which is thought to represent interactive processes between sensory modalities (Vroomen & Stekelenburg, 2010).

In this study, we will use EEG to quantify both multisensory associative learning with the use of a three-stimulus oddball detection task and, subsequently, multisensory integration with a simple oddball detection task. Critically, for the three-stimulus oddball detection task, the audiovisual *pairings* will comprise the standard, target, and deviant stimuli, as opposed to the unisensory component themselves. The simple oddball detection task that follows will use an irrelevant unisensory visual target. Differences in amplitudes between conditions of interest will be extracted from a combination of a priori and data-driven latency windows. To quantify associative learning, two measures at different latencies will be extracted. The first is the mismatch negativity (MMN; Näätänen, 1995; Näätänen et al., 2007), which is a measure of pre-attentive deviance detection that typically occurs in the auditory cortex (Huotilainen et al., 1998). The second component is the later going P3b, which has been shown to be representative of potentially inhibitory and encoding processes, and is thought to have parietal and frontal neural generators (Polich, 2007). This is not to be confused with the P3a component, which is more characteristic of deviance detection and exogenous attention-switching.

As for quantifying multisensory integration, a first window will be extracted to represent early multisensory interactions (Foxe et al., 2000; Giard & Peronnet, 1999; Molholm et al., 2002), which are thought to represent featural, stimulus-based integration. A later window will also be extracted in order to test for later multisensory interactions. Furthermore, a follow-up behavioural measure of multisensory integration will be used (with the same stimuli as is used in the rest of the experiment) as a validation measure for use in quantifying multisensory integration. It will also be compared to the measures of multisensory associative learning.

Methods

Participants

Participants were 65 undergraduate students aged 17-55 at the University of Western Ontario. Four participants were excluded as they failed to complete the experiment (4 female, 4 right handed). The final sample included *N* = 61 participants (21 males, 4 left-handed) participants aged 17 to 55 years (*M* = 18.97, *SD* = 5.27). Participants completed three computer tasks. The first part of the study was a multisensory associative learning task, and the second a multisensory integration task, both wherein electroencephalographic (EEG) activity was recorded at the scalp. The last part of the experiment consisted of a behavioural measure of multisensory integration.

Equipment

Electrophysiological data were collected using a 128-channel Hydrocel GSN EGI (Electrical Geodesics Inc., Eugene, OR, USA) cap and sampled at a rate of 250 Hz. All visual stimuli were presented on an LCD screen for the EEG components, and on a CRT screen for the behavioural component to collect precise response times, both with a 60 Hz refresh rate. All auditory stimuli were presented via a speaker on either side of the participant, 160 cm from their head. Responses were collected using a Serial Response Box (Model 200A; Psychology Software Tools, Inc., 2003). Experiments were conducted using E-Prime 2.0.8.252. (Psychology Software Tools, Inc., 2014) using NetStation Extensions version 2.0. The experiment took place in a sound-attenuated booth (background dB SPL = 30.4 dB).

Stimuli

Auditory stimuli consisted of pure tones created using Matlab’s Psychophysics Toolbox (Kleiner et al., 2007). The frequencies of the tones were chosen to ensure adequate perception and discriminability. The three tones of distinct frequencies (320.00 Hz, 427.15 Hz, and 570.14 Hz), were 100 ms in duration, were sampled at a rate of 8000 Hz, and played at 82-83 dB SPL. The auditory features will be referred to as A1, A2, and A3.

Visual stimuli were presented through a computer screen on a black background. Visual stimuli were three white two-dimensional shapes (circle, square, and triangle) presented on a black background, and created using Adobe Illustrator CC. The shapes were controlled for luminance by keeping their area constant. The visual angles (width x height) of the circle, square, and triangle were 8.86_o x 8.86_o, 7.82_o x 7.82_o, and 11.89_o x 10.38_o, respectively. These visual features will be referred to as V1, V2, and V3.

Procedure

Phase 1: Multisensory Associative Learning Phase

Throughout this phase, participants were presented with audiovisual tone-shape pairings, each pair with its own frequency of presentation (see Table 1 for a complete layout of presentation frequencies). Participants were tasked with responding with their right index finger, by using the serial response box, as quickly and as accurately as possible to a specific audiovisual pairing, “Target”. Two pairings, A1V1 and A2V2, were presented during 70% of total trials (35% each), and will subsequently be referred to as “Match” trials. A1V2 pairings were presented on 10% of trials, and will be referred to as “Mismatch” trials. A2V1 pairings were also presented on 10% of trials, and were target trials to which participants were instructed to respond. Finally, the A3V3 pairing was presented for 10% of trials, and will be referred to as “Deviant” trials. Deviant trials were included in order to control for attention-switching due to rare sensory features (Rohlf et al., 2017). The three visual stimuli (circle, square, triangle) and three auditory stimuli (high, medium, low), were counterbalanced across participants.

Table 1: Experimental Design of Phases 1, 2, and 3

Phase	Stimuli	Proportion		Condition	Number of Trials
	A1V1	.35	.70	Match	840
	A2V2	.35			

Phase 1: Multisensory Associative Learning	A1V2	.10	.20	Mismatch	120
	A2V1	.10		Target	120
	A3V3	.10	.10	Deviant	120
Phase 2: Multisensory Integration (EEG)	A1 A2	.33		Auditory	120
	V1 V2	.33		Visual	120
	A1V1 A2V2	.33		Audiovisual	120
Phase 3: Multisensory Integration (Behavioural)	A1 A2	.33		Auditory	120
	V1 V2	.33		Visual	120
	A1V1 A2V2	.33		Audiovisual	120

Each trial consisted of a 100 ms audiovisual stimulus presentation followed by an inter-trial interval where a white visual fixation cross was shown for a randomly jittered duration of 900-1400 ms. At the beginning of the experiment, participants were instructed to respond by pressing the leftmost button on a serial response box (‘1’) when they detected the target combination which was presented to them immediately prior to testing (Figure 1). Responses were recorded during the inter-trial interval where the white fixation cross was presented. This phase of the experiment was comprised of a total of 1200 trials, which were presented in random order, and divided into five blocks of 240 trials with short periods of rest to check the impedances on the EEG net. Thus, a total of 840 match, 120 mismatch, 120 target mismatch, and 120 deviant trials were presented during this phase of the experiment.

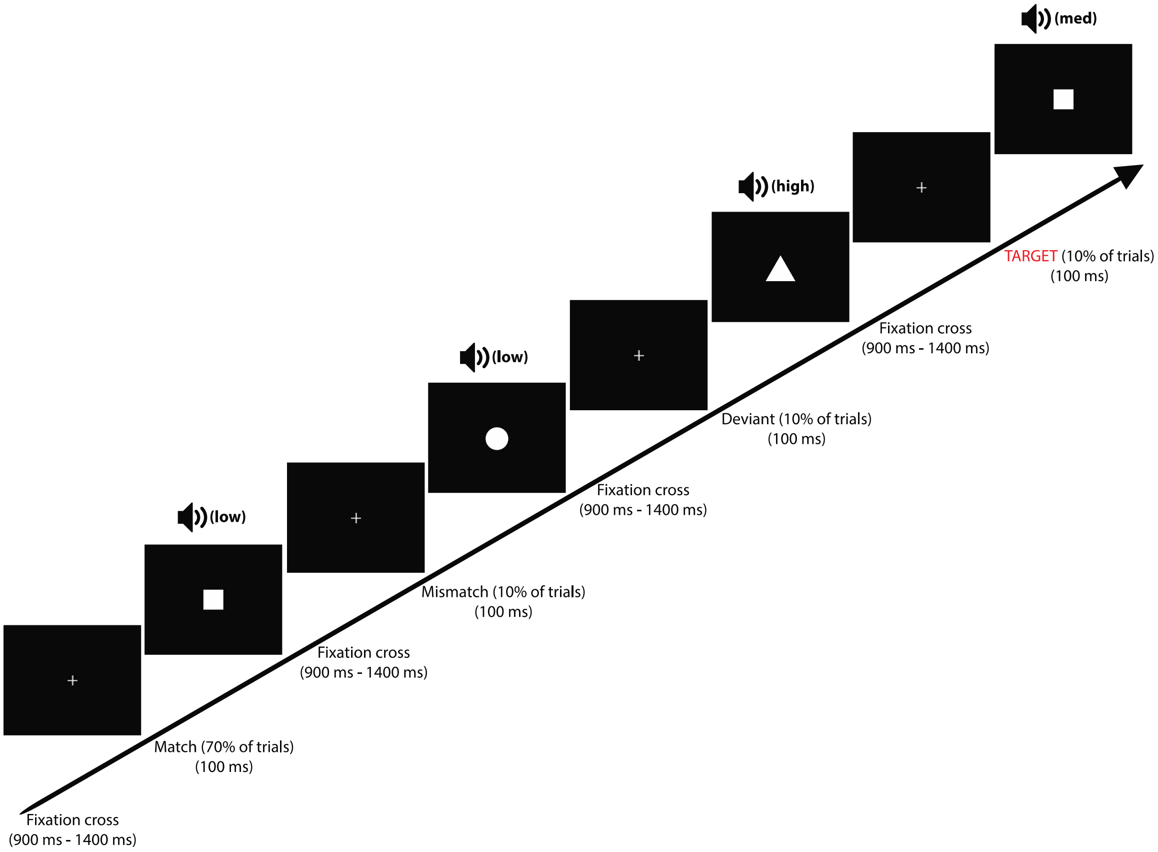

Figure 1: Trial structure for Phase 1, which tests associative learning.

Phase 2: Multisensory Integration Phase (EEG)

This second phase used the same features of the stimuli from the associative learning phase to test for multisensory integration. Presentations of the visual and auditory unisensory components of the match stimuli were included (A1, A2, V1, V2), as well as matched audiovisual presentations (A1V1 and A2V2). Note that the audiovisual combinations presented in this phase were always the matched, frequently-presented pairings, never the mismatched, target, or deviant stimulus pairs from the previous phase. Trial structures were the same as in the associative learning phase, with the exception that following 10% of trials, the fixation cross turned red 100 ms after the initial fixation presentation. Participants were tasked with responding via key press when this red fixation appeared in order to assure vigilance while not contaminating EEG recordings with a motor artifact during stimulus presentations (Figure 2). There was a total of 360 trials, which were equally distributed across conditions, 120 audio-only, 120 visual-only, and 120 audiovisual trials. A break was included after 180 trials.

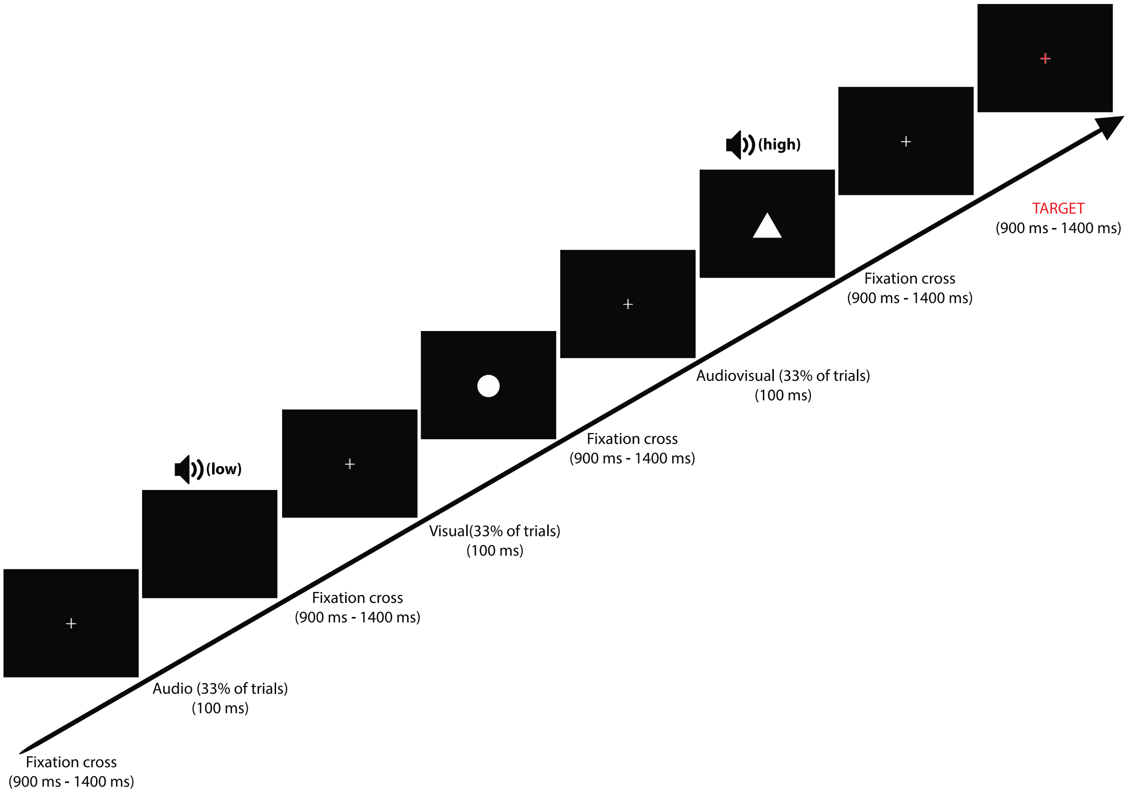

Figure 2: Trial structure for Phase 2, which tests multisensory integration.

Phase 3: Multisensory Integration Phase (Behavioural)

This portion of the experiment tested for a behavioural measure of multisensory integration using the same paradigm as its analogous EEG phase. However, in this portion of the experiment, participants were instructed to respond via response box as quickly as possible when they detected either an auditory, visual, or audiovisual stimulus with response times (RTs) recorded. No red fixation cross was presented in this portion of the experiment (Figure 3).

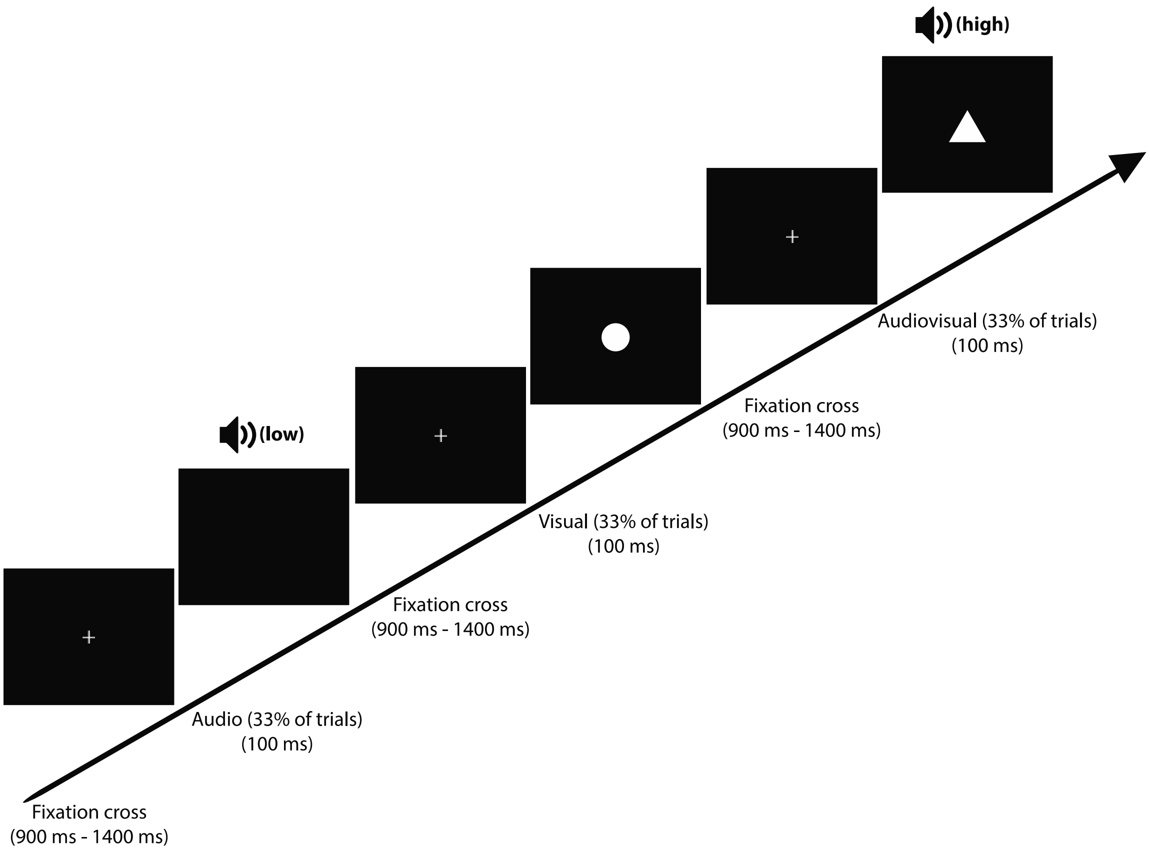

Figure 3: Trial structure for Phase 3, which tests multisensory integration behaviourally.

Analysis

Data was collected using continuous EEG recording through EGI NetStation, and analyzed using NetStation Waveform Tools and Matlab. Data were initially band-pass filtered at 0.1-100 Hz. Additionally, a 60 Hz notch filter was applied to filter out powerline interference. Only correct trials (correctly identifying the target, and correctly withholding a response for all other trials) were included in the analyses. Epochs of 1200 ms were extracted from the data, with the first 200 ms used for baseline correction, and the last 1000 ms post-stimulus presentation. Epochs in which motion artifacts such as eye blinks (>50 µV, window size = 640 ms; moving average = 80 ms) or eye movements (>50 µV, window size = 640 ms; moving average = 80 ms) were excluded. Bad channels (>150 µV, across entire segment; moving average = 80 ms) were removed based on whether 20% of the segments were identified as "bad". These channels were replaced by spherical spline interpolating the signal from the surrounding electrodes. An epoch was deemed "bad" if it contained more than 20 bad channels, contained an eye blink, or contained an eye movement. Bad epochs were excluded from analyses. An average reference was computed, and data was re-referenced to the average.

Phase 1: Multisensory Associative Learning Phase

For the associative learning phase of the experiment, the MMN and P3b time-windows were defined as time-window latencies observed in previous literature, which were 100-250 ms (Näätänen & Winkler, 1999) and 300-600 ms (Polich & Comerchero, 2003) respectively. Within these *a priori time windows,* latencies were identified where there were five consecutive time points showing a significant amplitude difference between the match and mismatch conditions for individual participants' waveform, tested with a paired-sample t-test ($\alpha = .05$ for each time point). Within these significant time-windows, *a priori* defined electrode clusters that outline anatomical regions of the brain (Tripathi et al., 2018) were extracted. Clusters with multiple electrodes showing significant amplitude differences for the MMN and P3b were used in the analysis. Significant electrodes contiguous with a predefined cluster with multiple significant electrodes were incuded in this cluster, given that they were not already assigned to a predefined cluster of activity with multiple significant electrodes.

The mean amplitude of these significant windows was used to quantify multisensory associative learning, as mean relative to peak amplitude is less sensitive to noisy data and is effective whenever the latency windows are well established (Luck & Gaspelin, 2017). Both MMN and P3b values were calculated for each individual by subtracting the match from the mismatch mean values within their respective time windows.

Participants' data were considered outliers if their mean difference scores between the conditions of interest were more than three times the value of the interquartile range for an electrode cluster at either the early or late time window. Data from participants who were outliers were imputed using a Markov Chain Monte Carlo multiple imputation with a maximum of 100 iterations. Imputations were conducted 10 times, with the mean value of these 10 imputations used.

Phase 2: Multisensory Integration Phase (EEG)

For the multisensory integration phase, the amplitudes from the unisensory and multisensory signals were compared to quantify multisensory interactions. As electrical fields detected by EEG sum linearly, interactions between auditory and visual processing are identified by summing the two unisensory signals and comparing this sum to the audiovisual signal, known as the additive criterion (Besle et al., 2004). Interactions are thus defined by significant differences:

$$A + V \neq A$$

Two windows were extracted based on previous literature, an early (~40-110 ms) and a late (140-220 ms) latency range of multisensory integration (Giard & Peronnet, 1999; Molholm et al., 2002). Criteria for identifying electrodes with significant amplitude differences and for cluster extraction were defined using the same specifications as the previous phase. Values for mean amplitudes were then extracted for both audiovisual presentations and the summed unisensory presentations. The level of multisensory integration was calculated for each individual by subtracting the summed unisensory from the audiovisual values within early and late time windows within each cluster.

Participants' data were considered outliers if their mean difference scores between the conditions of interest were more than three times the value of the interquartile range for an electrode cluster at either the early or late time window. Data from participants who were outliers were imputed using a Markov Chain Monte Carlo multiple imputation with a maximum of 100 iterations. Imputations were conducted 10 times, with the mean value of these 10 imputations used. If a participant was identified as an outlier in both Phase 1 and Phase 2, the participant's data was removed from analysis in both phases.

Phase 3: Multisensory Integration Phase (Behavioural)

The Race Model (Miller, 1982; Raab, 1962) is commonly used to test for behavioural multisensory integration, and postulates that integration could be present if the mean response times from the multisensory stimuli are smaller than that of either of their unisensory components, assuming that the processes do not interact with one another. In this case, the response times from the behavioural multisensory integration phase were compared using the same principle as their EEG counterpart. Cumulative distribution functions (CDFs) of the response times are calculated for each of the unisensory components, and then summed. These represent the predicted response times, assuming independent processing, also known as Miller's bound (Miller, 1982). The CDF of RTs during audiovisual trials was then computed and compared to Miller's bound. Violations of Miller's bound occur when the audiovisual CDF is above and to the left of Miller's bound, i.e., when RTs in response to audiovisual presentations occur faster than predicted by responses to the unisensory presentations, and are indicative of multisensory integration/facilitation. Otto's (2019) redundant signals effect (RSE) toolbox was used to compute Miller's bound, as well as the violation values. A binomial test was used to assess whether a significant number of individual participants showed multisensory enhancement.

Relating Learning to Integrating

Bivariate Pearson correlations were performed between the mean MMN and P3b values and the mean of the difference in both early and late MSI windows to determine whether a relationship existed between participants' multisensory associative learning performance and their multisensory integration abilities across each cluster. Corrections for multiple comparisons were performed by controlling the false discovery rate by using the Benjamini-Hochberg procedure (false discovery rate (Q) = .05) (Benjamini & Hochberg, 1995).

Relating Behavioural to EEG Multisensory Integration Measures

Bivariate Pearson correlations were also performed between the EEG and behavioural measures of multisensory integration. This analysis was included as a validation measure for the EEG measure of multisensory integration.

Results

Phase 1: Multisensory Associative Learning

An average of 1178.87 trials (98.24% of total trials) per participant were included in the analysis. Excluded trials were both incorrectly identified targets and target misses. For this phase of the experiment, a total of 7 participants' data was identified as outliers, and scores were imputed for 5 of them. The following analyses for this phase of the experiment therefore include 59 participants.

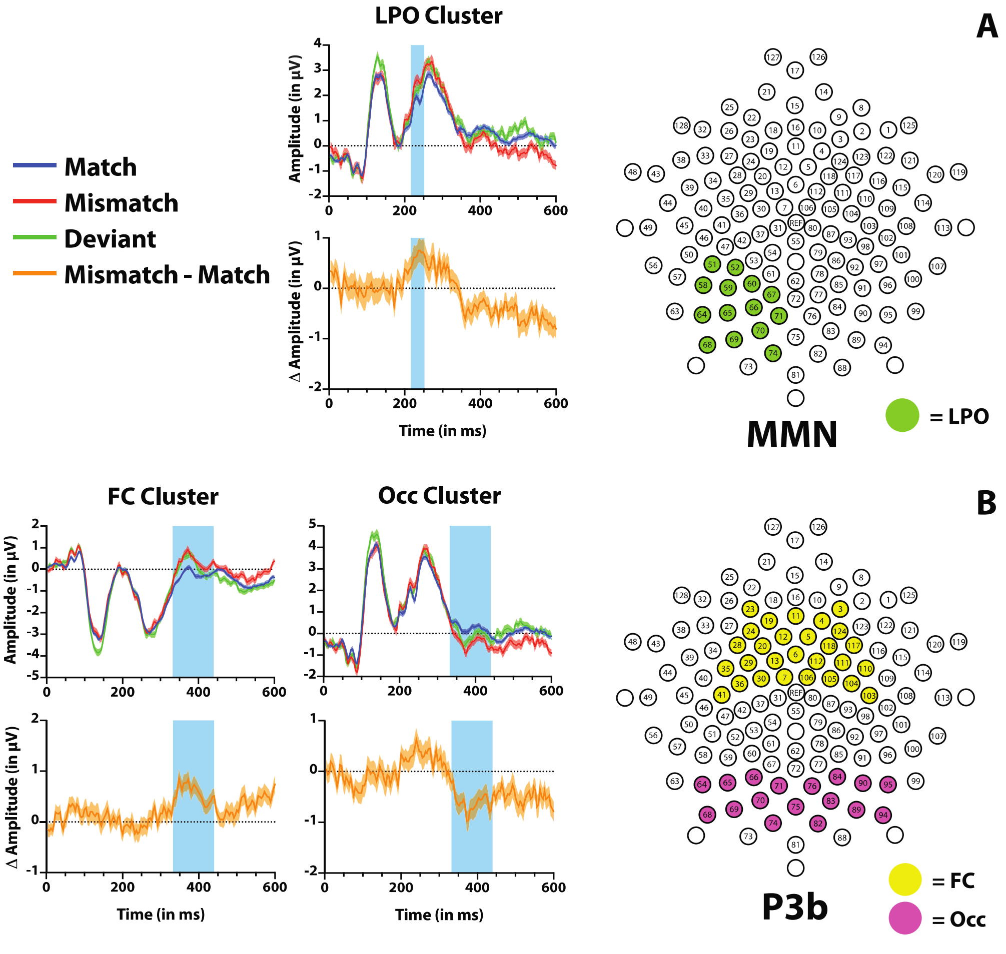

Figure 4: Scalp topography and timecourses for Phase 1, the EEG portion of the associative learning phase. The envelope around the individual time courses represents the standard error of the mean (SEM). The orange timecourse represents the activity from the Match condition subtracted from the Mismatch condition. *A),*

The extracted cluster for the MMN, the left parieto-occipital (LPO) cluster, is portrayed on the right, with the timecourses for the individual conditions on the left. *B)*, The extracted clusters for the P3b, the fronto-central (FC) cluster and the occipital (Occ) cluster are portrayed on the right, with the timecourses for the individual conditions on the left.

A cluster exhibiting a significant difference between the Mismatch and Match conditions was found in the left parieto-occipital area (LPO; electrodes 60, 52, 51, 67, 59, 58, 71, 66, 65, 64, 70, 69, 74, and 68) in the MMN latency range, between 216-252 ms (Figure 4A). Significant differences between Mismatch and Match conditions were only found in the left hemisphere, therefore, the right hemisphere was not considered for this measure. The mean amplitude difference between the Match and Mismatch conditions was *M* = .477 µV, *SEM* = .145 µV (Figure 5), which was significant (*t*(58) = 3.296, *p* = .002, *d* = .429). The mean difference between the Deviant and Match conditions *M* = .350 µV, *SEM* = .174 µV, was significant (*t*(58) = 2.004, *p* = .0498, *d* = .261).

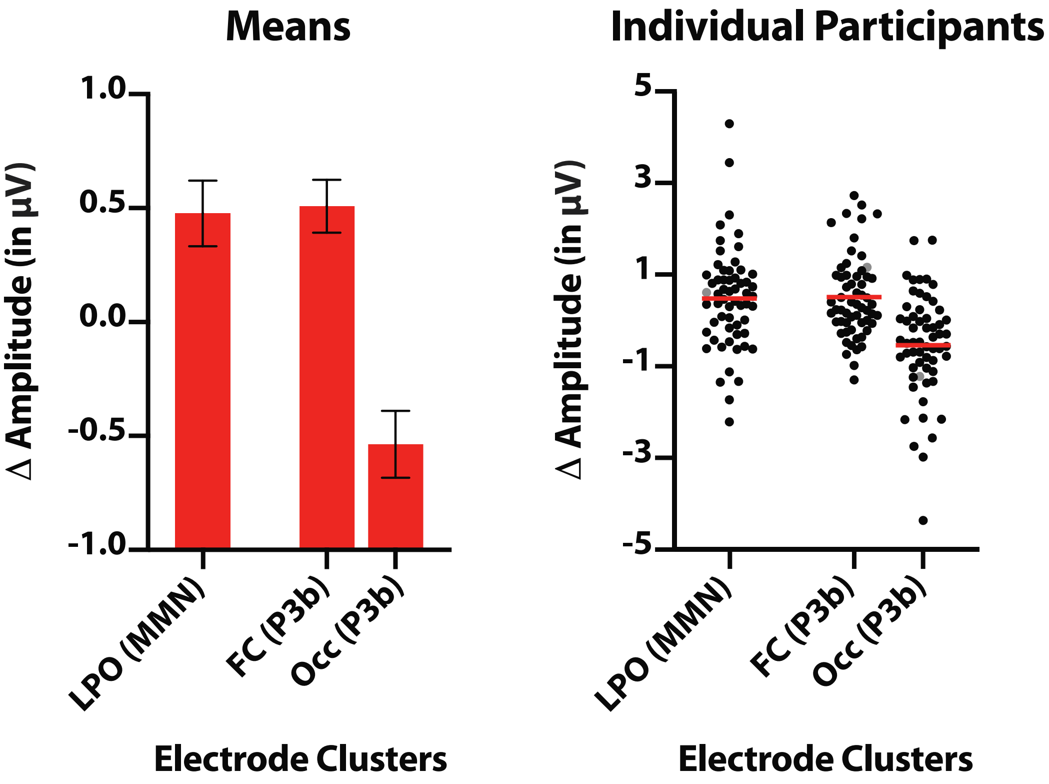

Figure 5: Group means and individual means for the electrode clusters corresponding to each measure of Phase 1, multisensory associative learning. Error bars represent SEM, and the red lines correspond to the mean. The grey individual data points represent participants who are more than 3 SD away from the age mean but were still included in analyses.

For the P3b latency range, between 332-440 ms, the first significant electrode cluster was fronto-central (FC; electrodes 11, 6, 3, 4, 124, 5, 118, 117, 23, 19, 24, 12, 20, 28, 112, 111, 110, 106, 105, 104, 103, 13, 29, 35, 7, 30, 36, and 41; Figure 4B). There were no significant hemispheric differences ($t(58) = .088$, $p = .930$, $d = .011$) and as such, both hemispheres were collapsed into one cluster. The mean difference between the Mismatch and Match conditions was $M = .509$ µV, $SEM = .116$ µV (Figure 5), which was significant ($t(58) = 4.371$, $p < .001$, $d = .569$). The difference in amplitudes between the Deviant and Match trials for this cluster was also significant ($t(58) = 3.459$, $p = .001$, $d = .450$).

In the same latency range, an occipital (Occ; electrodes 84, 76, 90, 95, 83, 89, 82, 94, 75, 71, 66, 65, 64, 70, 69, 74, and 68) (Figure 4B) electrode cluster was also extracted. There were no significant hemispheric differences (*t*(58) = .922, *p* = .360, *d* = .120) and as such, both hemispheres were collapsed into one cluster. There was a mean amplitude difference between the Mismatch and Match conditions of *M* = -.536 μV, *SEM* = .146 μV (Figure 5), which was significant (*t*(58) = 3.658, *p* < .001, *d* = .476). The difference in amplitudes between the Deviant and Match conditions was also significant (*t*(58) = 3.685, *p* < .001, *d* = .478).

Phase 2: Multisensory Integration (EEG)

An average of 359.88 trials per participant, with a task accuracy rate of 99.97% were included in the analysis for this phase of the experiment. Trials were excluded if they were incorrectly identified as the red fixation cross target, as that data was then contaminated by a motor response. All differences below refer to amplitude differences between the sum of the unisensory conditions (Audio + Visual) and the Audiovisual condition (AV). Four participants' data were identified as outliers, and following this observation, two of these were imputed. The total number of participants for this phase of the experiment was 59.

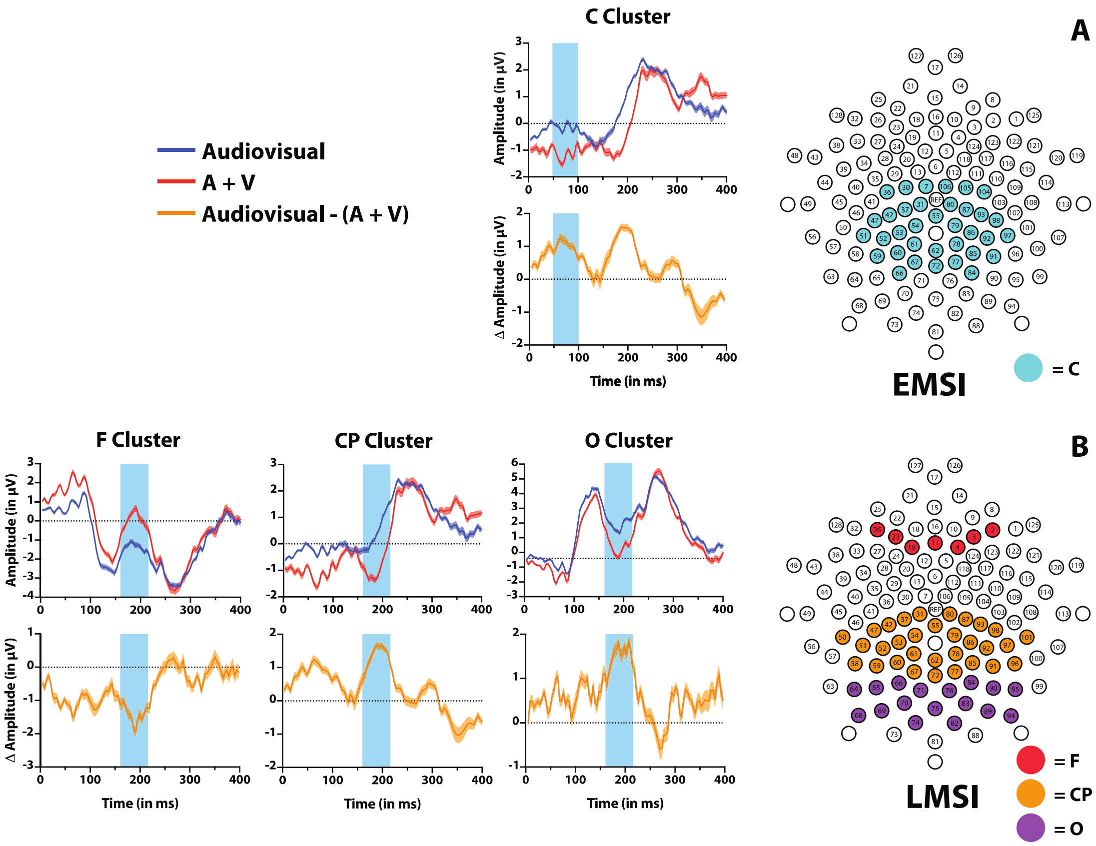

Figure 6: Scalp topography and timecourses for Phase 2, the EEG portion of the multisensory integration phase. The envelope around the individual timecourses represents the standard error of the mean (SEM). The orange timecourse represents the activity from the summed Auditory and Visual conditions (A + V) subtracted from the Audiovisual condition (AV). *A),* The extracted cluster for the early window of multisensory integration (EMSI), the central (C) cluster, is portrayed on the right, with the timecourses for the individual conditions on the left. *B),* The extracted clusters for the later window of multisensory integration (LMSI), the frontal (F) cluster, the centro-parietal (CP) cluster, and the occipital (O) cluster are portrayed on the right, with the timecourses for the individual conditions on the left.

A single significant central electrode cluster for the early latency window was identified between 48-100 ms (C; electrodes 106, 105, 104, 80, 87, 93, 7, 30, 36, 55, 31, 37, 42, 79, 86, 92, 98, 97, 78, 85, 77, 91, 76, 84, 54, 53, 47, 62, 72, 61, 60, 52, 51, 67, 59, 71, and 66) (Figure 6A). No significant difference between hemispheres was detected (*t*(58) = -

.211, *p* = .833, *d* = .028) and as such, hemispheres were collapsed into a single cluster. A mean difference of *M* = .628 µV, *SEM* = .119 µV (Figure 7) was found to be significant (*t*(58) = 5.289, *p* < .001, *d* = .689), where the Audiovisual condition was subadditive in comparison to the sum of the auditory and visual components.

Three significant electrode clusters for a later latency window of 160-216 ms were extracted. A small frontal cluster (F; electrodes 2, 3, 4, 11, 26, 23, and 19) (Figure 6B) showed no significant hemispheric differences (*t*(58) = -.124, *p* = .902, *d* = .016), and as such the data were collapsed across hemispheres. This cluster showed subadditivity, where the amplitudes of the sum of the unisensory components was greater than the audiovisual component, with a mean difference of *M* = -1.571 µV, *SEM* = .216 µV (Figure 7), which was significant (*t*(58) = 7.264, *p* <.001, *d* = .946).

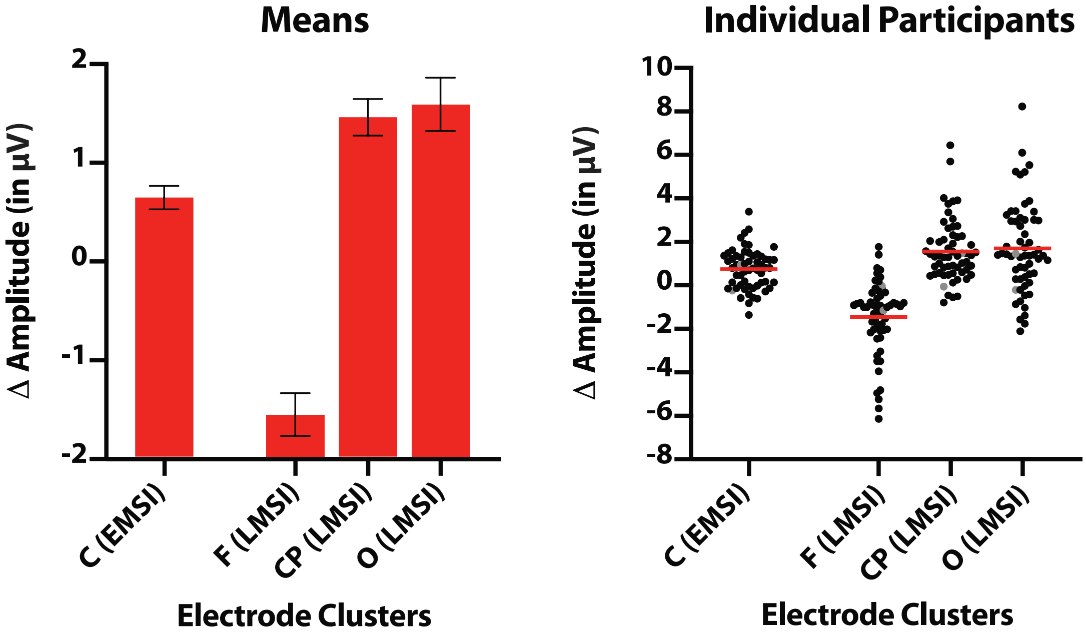

Figure 7: Group means and individual means for the electrode clusters corresponding to each measure of Phase 2, multisensory integration. Error bars represent SEM, and the red lines correspond to the mean. The grey individual data points represent participants who are more than 3 SD away from the age mean but were still included in analyses.

A second, centro-parietal cluster (CP; electrodes 80, 87, 93, 55, 79, 86, 92, 98, 97, 101, 78, 85, 62, 77, 91, 96, 72, 31, 37, 42, 54, 53, 47, 61, 60, 52, 51, 50, 67, 59, and 58) was also extracted (Figure 6B). The cluster collapsed electrodes across hemispheres, as no significant hemispheric differences were detected ($t(58) = -.784$, $p = .436$, $d = .102$). This cluster showed subadditivity, where a difference of $M = 1.441$ µV, $SEM = .185$ µV (Figure 7) was found. This difference was significant ($t(58) = 7.812$, $p < .001$, $d = 1.017$).

A final, occipital cluster (O; electrodes 71, 66, 65, 64, 70, 69, 74, 68, 84, 75, 76, 90, 95, 83, 89, 82, and 94) was extracted (Figure 6B). The electrodes were collapsed across hemispheres, as no significant hemispheric differences were observed ($t(58) = 1.643$, $p = .106$, $d = .214$). This cluster showed subadditive activity, where a difference of $M = 1.572$ µV, $SEM = .269$ µV (Figure 7) was found, which was significant ($t(58) = 5.848$, $p <.001$, $d = .762$).

Phase 3: Multisensory Integration (Behavioural)

The mean violation of Miller's bound was $M = .001$, $SEM = 2.45\text{e-}04$ (Figure 8). A binomial analysis revealed that the proportion of participants showing race model (Miller's bound) violations, in 45 out of 58 participants, was significantly greater than chance ($p = .000023$).

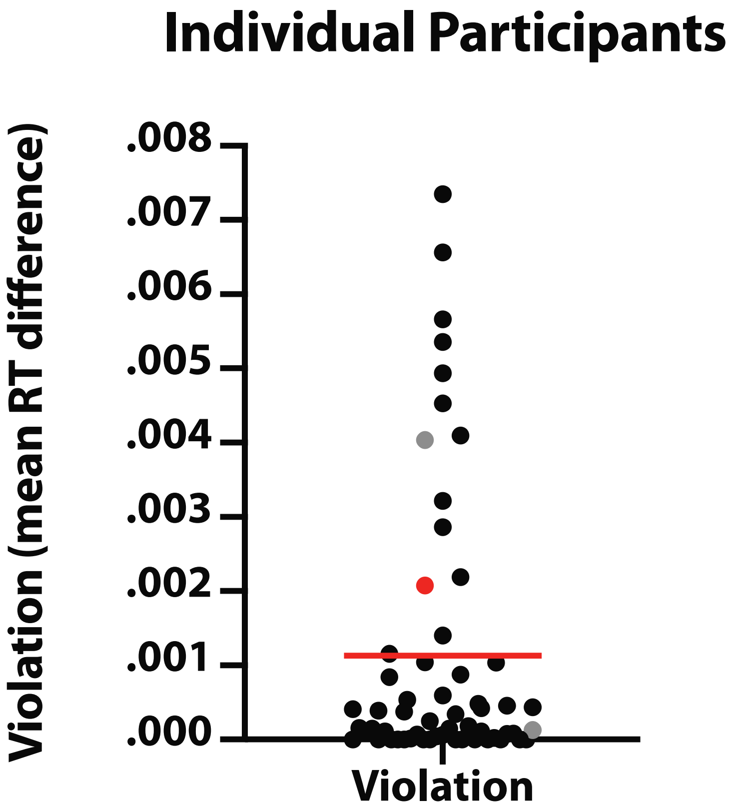

Figure 8: Race model violation, representing Miller's bound violation for individual participants. This value represents the area of the violation or the mean RT difference. The red line represents the group mean and the grey individual data points represent participants who are more than 3 SD away from the age mean but were still included in analyses. The red data point is used as an example in Figure 9.

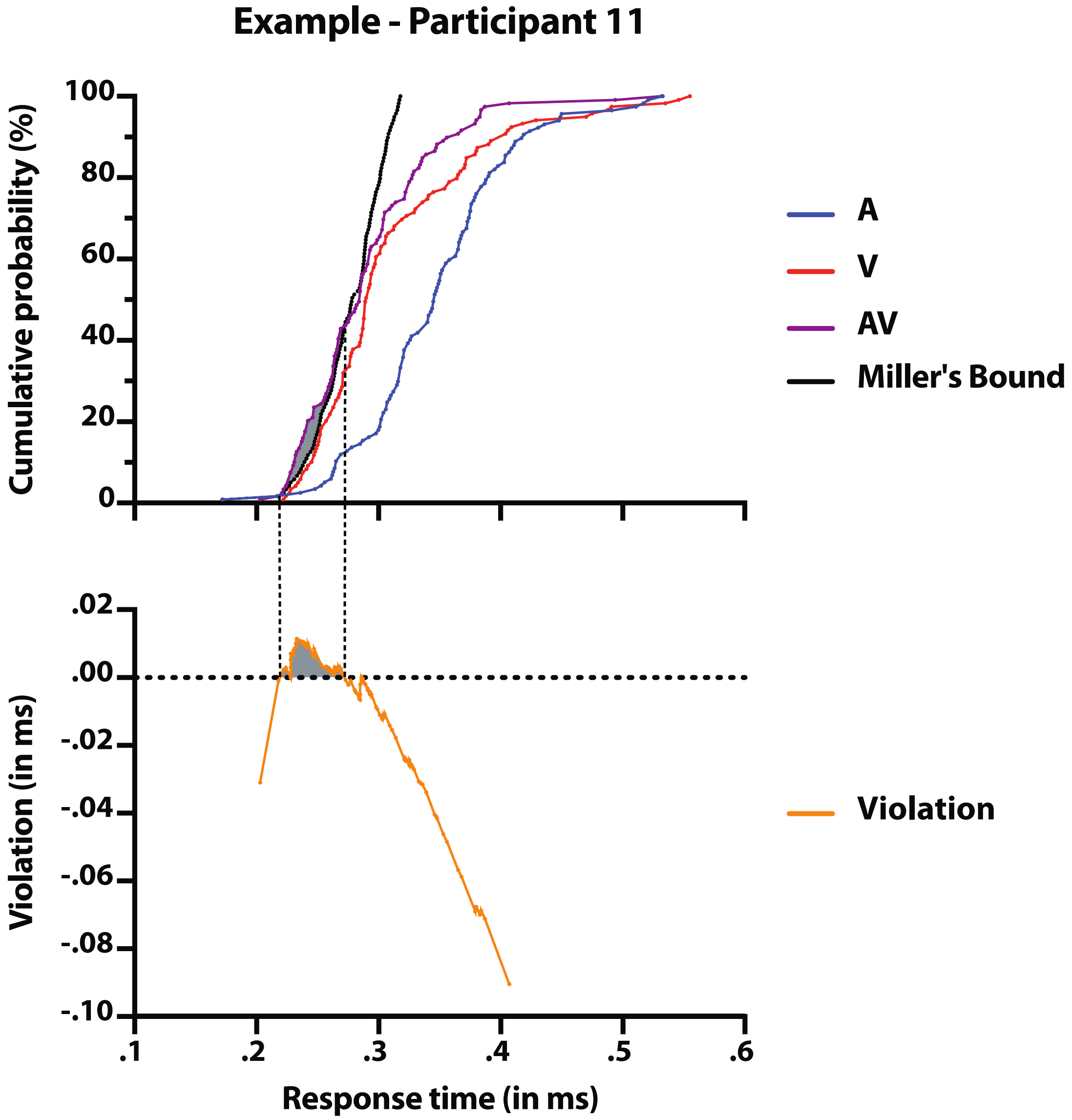

Figure 9: Example participant, illustrating the cumulative distribution functions of the multisensory condition as well as both unisensory conditions and Miller's bound. The violation is represented by the shaded area.

Relating Learning to Integrating

Early measures of multisensory associative learning (the MMN) in the left parieto-occipital cluster were not significantly correlated with any index of multisensory integration (see Table 2). Conversely, associative learning as measured by the P3b in the fronto-central cluster was significantly correlated to both early multisensory integration in the central cluster (*r*(57) = -.544, *p* = 8.466e-06) (Figure 10A), and later multisensory integration in the centro-parietal scalp area (*r*(57) = -.404, *p* = .001) (Figure 10C). Similarly, the occipital scalp area during later associative learning had a significant correlation between early integration in the central cluster (*r*(57) = .446, *p* = 4.033e-04) (Figure 10B), and later multisensory integration in the centro-parietal scalp area (*r*(57) = .352, *p* = .006) (Figure 10D). All of the significant correlations reported here have been deemed significant using the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995) with a false discovery rate of Q = .05.

The same analysis was performed on electrodes identified in previous studies (Besle et al., 2005; Wronka et al., 2012; Teder-Sälejärvi et al., 2002; Gondan & Röder, 2006; Giard & Peronnet, 1999) as opposed to our data-driven electrode cluster selection, and results showed the similar patterns of correlation (Appendix D, Table 3; Appendix E, Figure 11). Specifically, the P3b was still significantly correlated with the early index of multisensory integration, and its relationship with the later index of multisensory integration was patterned similarly but was only marginally significant. Furthermore, the marginally significant correlation between the MMN and the later index of multisensory integration was significant in this supplemental analysis. Thus, the pattern of relationships remained consistent across these two analyses.

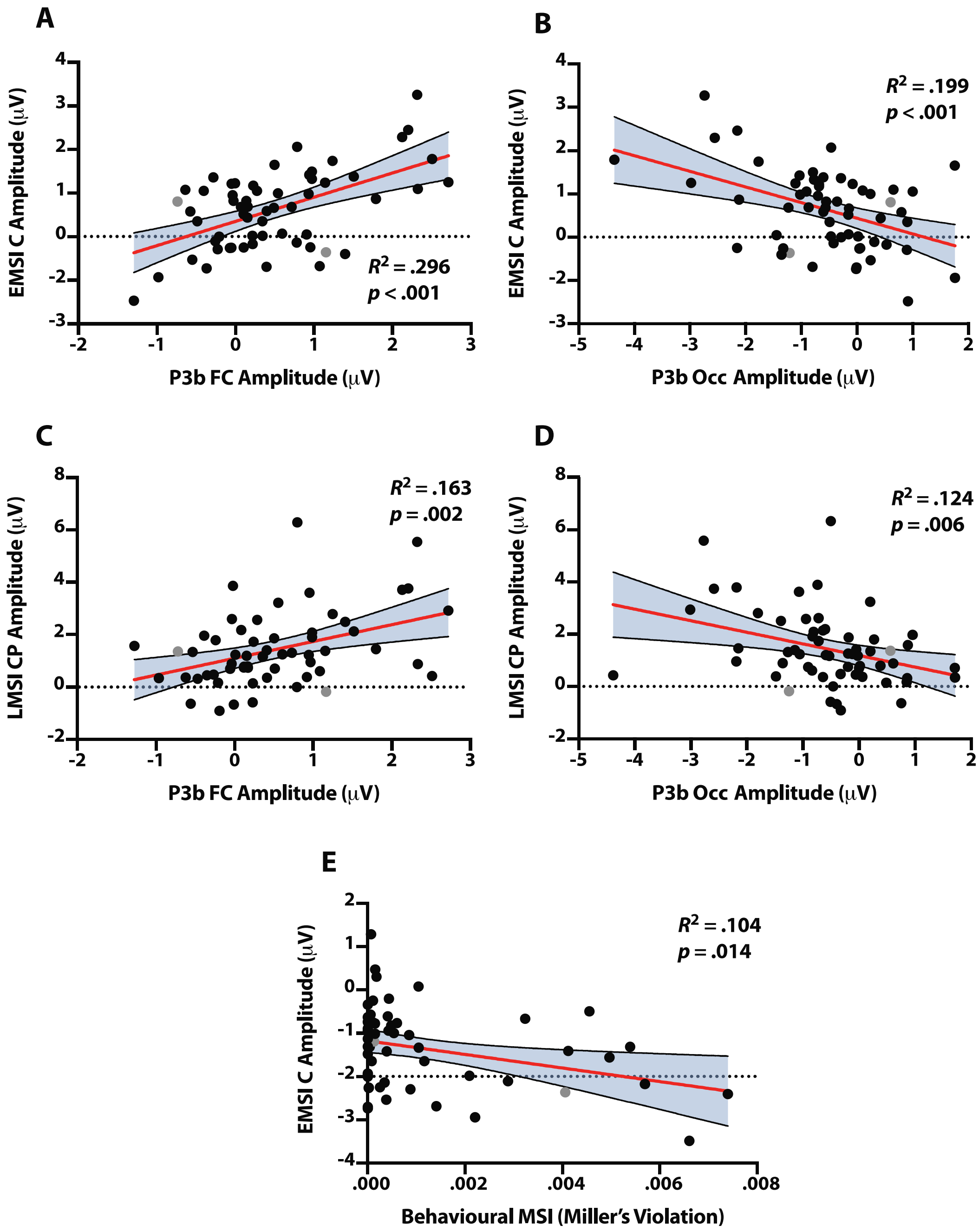

Figure 10: Significant correlations of interest with a 95% confidence interval envelope around the regression line. The grey individual data points represent participants who are more than 3SD away from the age mean, but were still included in analyses. *A)* Correlation between fronto-central cluster of the P3b and the central cluster of EMSI. *B)* Correlation between the occipital cluster of the P3b and the central cluster of EMSI. *C)* Correlation between fronto-central cluster of

the P3b and the centro-parietal cluster of LMSI. *D)* Correlation between the occipital cluster of the P3b and the centro-parietal cluster of LMSI. *E)* Correlation between the behavioural measure of multisensory integration and the central cluster of EMSI.

Relating Behavioural to EEG Multisensory Integration Measures

As for the behavioural measure of multisensory integration, the only significant correlation observed was with the early EEG measure of multisensory integration ($r(56) = .322$, $p = .014$) (Figure 10E). When participants showing no significant violation were excluded from the correlation, the only significant correlation with the behavioural measure was still exclusively with the early EEG measure of multisensory integration ($r(44) = -.406$, $p = .006$). Therefore, including all participants did not change the significance of the relationship of the behavioural measure of multisensory integration with the other measures. There were no other significant correlations throughout but see Table 2 for all comparisons.

Table 2: Correlations – correlation coefficient (*p* value)

Correlation clusters	EMSI C	LMSI F	LMSI CP	LMSI O	Behavioural MSI
MMN LPO	-.199 (.130)	.162 (.219)	-.231 (.079)	-.097 (.463)	.083 (.537)
P3b FC	.544 (8.466e-06**)	-.085 (.521)	.404 (.001*)	.046 (.727)	-.092 (.491)
P3b Occ	-.446 (4.033e-04**)	.115 (.387)	-.352 (.006*)	-.032 (.809)	.123 (.357)
Behavioural MSI	-.322 (.014*)	.086 (.522)	-.070 (.603)	-.063 (.640)	--

Note: * $p < .05$, ** $p < .01$

Discussion

The purpose of this study was to determine whether a relationship exists between multisensory associative learning and multisensory integration abilities. We conducted an EEG experiment to evaluate early implicit measures of associative learning and multisensory integration, with three novel findings. First, confirming our hypothesis, we observed a significant correlation between associative learning bilaterally in fronto-central and occipital scalp areas, as indexed by the P3b, and early multisensory integration in the central scalp region. Second, this same index of multisensory associative learning was also related to the later measures of multisensory integration bilaterally in the centro-parietal scalp area. Finally, our behavioural measure of multisensory integration validated our EEG measure of multisensory integration. Our results showed that individuals who exhibited stronger neural markers of audiovisual associative learning also displayed better performance in overall integration of audiovisual information.

The most consistent observation in our data was a significant relationship between associative learning, as indexed by the P3b, and early multisensory integration. Overarchingly, this highlights the effect of higher-order processes (i.e., learned associations) in the earliest window of integration (i.e., a top-down effect). Particularly, integration was observed as early as 48 ms post stimulus presentation, and until 100 ms, which is in line with the current literature (Giard & Peronnet, 1999; Luck et al., 1997; Molholm et al., 2002). Top-down effects have been previously established to have an effect, although limited, in sensory interaction prior to 100 ms (De Meo et al., 2015; Talsma et al., 2007; Talsma & Woldorff, 2005). This early index has been identified as having a centro-parietal scalp distribution (Cappe et al., 2010; Foxe et al., 2008), which supports the current study’s findings.

In regard to the direction of the violation of the additive model, a good amount of previous studies have found superadditivity in their measures of early multisensory integration (Gondan & Röder, 2006; Gondan et al., 2007; Vidal et al., 2008), which goes contrary to the subadditive findings that were found in this study. The results seem to indicate that prior learned associations may be playing a role in *how* sensory information is integrated. As the present study finds, top-down influences such as associative learning thus seem to be related to subadditive violations of the additive rule, which could reflect more efficient processing. A possible explanation for why only subadditivity was observed could be attributed to the salience of the choice of stimuli. The present study was comprised of bimodal stimuli presented at very high effectiveness, which could be responsible for activating a certain type of multisensory neuron, which have a high dynamic range and fire in an increasingly subadditive manner as stimulus effectiveness grows (Cappe et al., 2010; Perrault et al., 2003, 2005). Furthermore, if near-ceiling effects are observed as a result of the high-salience stimuli, subadditive effects may be representative of more efficient processing as a result of the reweighting between sensory features, or rather of top-down influences such as attention (Werner & Noppeney, 2010) or, crucially, learned associations.

The P3b in both clusters is thought to be representative of inhibitory processes and of updating/encoding of the memory representation (Polich, 2007). It is worth mentioning that although we did observe a significant relationship with multisensory integration in our established time window for late associative learning, frontal activity is usually associated with P3a generation, as opposed to the typical parietal activity which is associated with the P3b. This is an important distinction, as the P3a is thought to be representative of exogenous attention-switching elicited by distractors, as opposed to memory-encoding processes by the P3b. However, there is increasing evidence highlighting the neural relationship between both components (Ebmeier et al., 1995; Soltani & Knight, 2000), which supports the notion that the relationship between bottom-up and top-down processing and their neural generators is interactive.

Later associative learning and late MSI

The later index of multisensory associative learning was also significantly correlated with the later index of multisensory enhancement exclusively in the centro-parietal cluster. As with the early measure of multisensory integration, this cluster showed subadditivity and was significantly correlated with the associative learning measures. Furthermore, the early and the late measure of multisensory integration share similar topographical profiles, which could imply that they have similar neural generators. The idea that multisensory processing possesses some level of flexibility and synchrony is becoming increasingly prevalent (Talsma, 2015) through connecting pathways between sensory cortices directly to each other (Falchier et al., 2002) or through cortico-thalamic-cortical pathways (Hackett et al., 2007; Lakatos et al., 2007; Van Den Brink et al., 2014). It is difficult to rule out that the significant relationship between associative learning in late multisensory integration is fully independent from the one in early multisensory integration. It is possible that the learned associations acted as top-down influences on the integration process as a whole. It could be stipulated, then, that later multisensory integration is independent from early integration, or rather the change in early multisensory integration could be responsible, in a downstream manner, for the multisensory integration observed later. The lack of any significant relationship between associative learning and the occipital scalp area where late multisensory enhancement was observed could be attributed to the rather low-level visual cortex activity where multisensory integration is known to occur (Foxe & Schroeder, 2005).

Early associative learning

While the later, more attention-driven index of perceptual learning, the P3b was related to multisensory integration, the earlier, more feature-driven response, the MMN, was not related to integration. A potential reason for not seeing any effect between the early index of associative learning and overall multisensory integration could be an indication that multisensory associative learning relies on more complex higher-order processes and not simply sensory characteristics. However, it is likely that the MMN is indexing a neural process that is not related to multisensory integration

Quantifying associative learning

In the learning phase, participants were also presented with a Deviant condition, which was different than the Mismatch condition. As expected, both the Mismatch and the Deviant conditions yielded significant MMN and P3b components. The Deviant condition was included to control for exogenous attention switching, as opposed to a detection in a deviation from the statistical pattern of shape-tone associations (Rohlf et al., 2017). As such, the infrequently-presented Mismatch pairings tended to elicit a P3b wave of lower amplitude than the Deviant stimuli, because in the latter stimuli, attention is reoriented towards the presentation of novel features themselves as opposed to the violation in pairing expectation in the Mismatch condition. The use of a three-stimulus oddball detection task was vital to providing this evidence, at the very least providing a more conservative and valid measure of differences in amplitude between the Mismatch and Match conditions. This more conservative measure is based on the fact that the Deviant stimulus is only elicited by exogenous attention switching and the lower-amplitude P3b is elicited by the Mismatch. Without the inclusion of a Deviant condition, the effect could have been difficult to isolate in the EEG signal.

Behavioural MSI and early EEG MSI

Early neural signatures of multisensory integration in the EEG signal were significantly related to behavioural benefits in RT during a detection task. While this provides evidence that this early neural index of multisensory integration successfully captures a component of the behavioural benefits of multisensory integration, this behavioural measure did not relate to associative learning. Indeed, the magnitude of behavioural enhancement was quite small as the stimuli were very salient and were presented with no noise. The principle of inverse effectiveness explains that degraded signal from multisensory inputs result in a greater degree of multisensory gain than when the unisensory components are presented individually (Meredith & Stein, 1986b). Therefore, the small multisensory behavioural benefit identified in this study is most likely as a result of including stimuli with a high signal-to-noise ratio (SNR). In this experimental design, the same novel arbitrarily-paired stimuli were used throughout this study with the purpose of preserving the validity of the measures from one phase to the other. This would ensure that any relationship between associative learning and multisensory integration that was found would be due to our experimental manipulations, and not the SNR of the stimuli themselves. We would predict that the use of less salient stimuli would result in stronger multisensory behavioural benefits, and perhaps a stronger relationship with associative learning.

Developmental implications

These results confer many interesting developmental implications. Throughout development, there is a gradual shift towards using and relying on learned associations as opposed to solely the sensory features (e.g., timing and spatial congruence). Particular attention would be warranted when testing children in a study such as this, as they do not tend to rely on learned associations when integrating sensory information. Similarly, poor abilities in learning associations, especially from multiple sensory modalities could lead to an overreliance on stimulus features.

This phenomenon could, for example, be an issue in autistic populations, where there tends to be a bias towards processing local features over global stimulus features (Fiebelkorn et al., 2013). It is therefore possible that populations with multisensory integration difficulties also have deficits in multisensory associative learning. For example, research in autism reveals that individuals on the spectrum show atypical looking patterns to faces (Stevenson et al., 2017), and also show decreased multisensory integration (Stevenson et al., 2017) opening the possibility that a lack of exposure to the visual components of speech (e.g., the lips moving and mouthing the syllables) is related to poorer performance in multisensory integration. This could in turn play a key role in the reason why individuals in this population tend to have an overreliance on the sensory cues to bind (i.e., spatial and temporal congruence), as opposed to a balanced re-weighting between stimulus features and learned associations.

Limitations and future directions

Future studies should parametrically manipulate the choice of stimuli to include stimuli that have a lower SNR. This would be key in determining the extent of the relationship between learned associations and multisensory integration, insofar as stimulus manipulations allow. Furthermore, studies including more ecologically-valid higher-level stimuli, such as multisensory speech, could be useful in extending the generalizability of the important relationship between associative learning and multisensory integration. From a measurement perspective, using mean amplitude measurement, as this present study has, could potentially offer a more accurate quantifier of brain activity (Luck &

Gaspelin, 2017). Furthermore, future studies could attempt to maximize multisensory associative learning at different developmental stages, which already is showing some promising results (Rohlf et al., 2017). These studies could also test for multisensory integration with the use of the learned associations to see what could be modulating performance for multisensory integration. Furthermore, these studies could investigate further into how these relationships changed across age groups.

The present study was able to establish a direct link between associative learning and the capacity to integrate information from multiple sensory modalities. Participants who showed stronger indices of associative learning also exhibited stronger indices of multisensory integration of the stimuli they learned to associate. Specifically, fronto-central and occipital scalp areas exhibiting significant P3b signatures were significantly correlated with central scalp areas showing neural signatures of early integration and one centro-parietal scalp area showing later multisensory integration. Furthermore, our behavioural index was significantly related to our early measure of multisensory integration, thus serving as a validation for our measure. This study highlights the key influence of top-down effects such as multisensory associative learning on multisensory integration.

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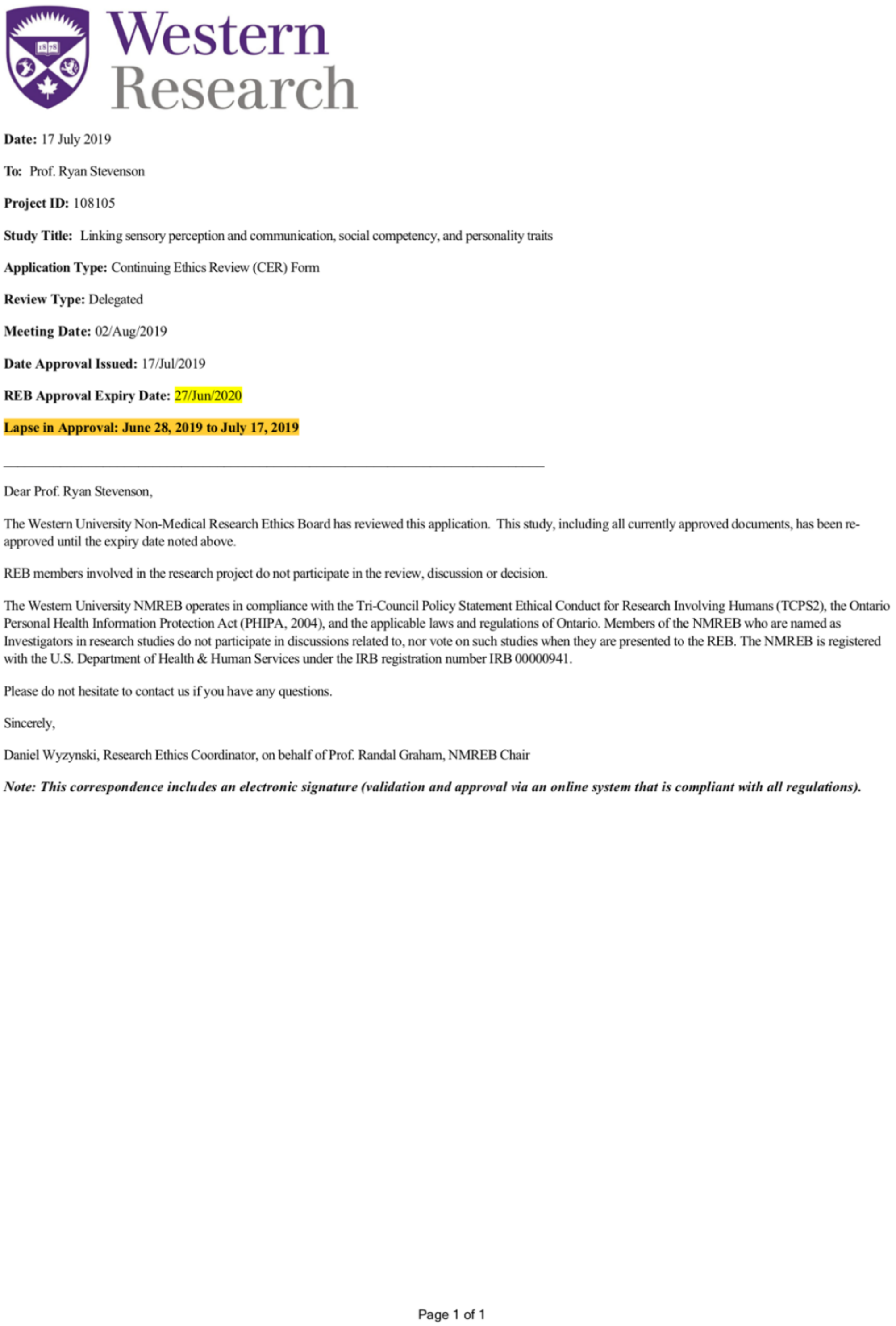
Appendix A

Ethics Approval



Western Research

Date: 17 July 2019

To: Prof. Ryan Stevenson

Project ID: 108105

Study Title: Linking sensory perception and communication, social competency, and personality traits

Application Type: Continuing Ethics Review (CER) Form

Review Type: Delegated

Meeting Date: 02/Aug/2019

Date Approval Issued: 17/Jul/2019

REB Approval Expiry Date: 27/Jun/2020

Lapse in Approval: June 28, 2019 to July 17, 2019

Dear Prof. Ryan Stevenson,

The Western University Non-Medical Research Ethics Board has reviewed this application. This study, including all currently approved documents, has been re-approved until the expiry date noted above.

REB members involved in the research project do not participate in the review, discussion or decision.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario. Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB. The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.

Please do not hesitate to contact us if you have any questions.

Sincerely,

Daniel Wyzynski, Research Ethics Coordinator, on behalf of Prof. Randal Graham, NMREB Chair

Note: This correspondence includes an electronic signature (validation and approval via an online system that is compliant with all regulations).

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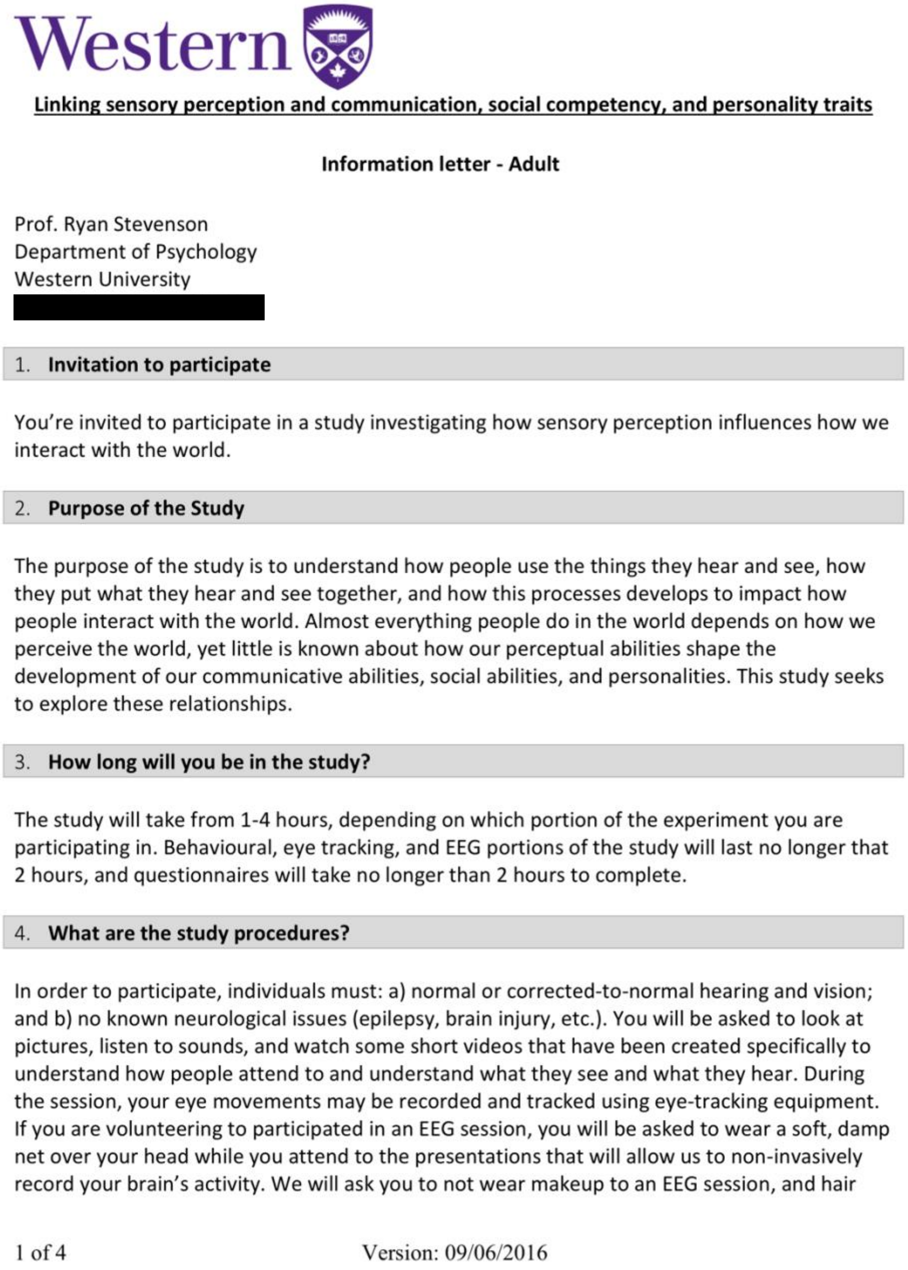
Appendix B

Letter of Information



Western

Linking sensory perception and communication, social competency, and personality traits

Information letter - Adult

Prof. Ryan Stevenson
Department of Psychology
Western University
[redacted]

1. **Invitation to participate**

You're invited to participate in a study investigating how sensory perception influences how we interact with the world.

2. **Purpose of the Study**

The purpose of the study is to understand how people use the things they hear and see, how they put what they hear and see together, and how this processes develops to impact how people interact with the world. Almost everything people do in the world depends on how we perceive the world, yet little is known about how our perceptual abilities shape the development of our communicative abilities, social abilities, and personalities. This study seeks to explore these relationships.

3. **How long will you be in the study?**

The study will take from 1-4 hours, depending on which portion of the experiment you are participating in. Behavioural, eye tracking, and EEG portions of the study will last no longer that 2 hours, and questionnaires will take no longer than 2 hours to complete.

4. **What are the study procedures?**

In order to participate, individuals must: a) normal or corrected-to-normal hearing and vision; and b) no known neurological issues (epilepsy, brain injury, etc.). You will be asked to look at pictures, listen to sounds, and watch some short videos that have been created specifically to understand how people attend to and understand what they see and what they hear. During the session, your eye movements may be recorded and tracked using eye-tracking equipment. If you are volunteering to participated in an EEG session, you will be asked to wear a soft, damp net over your head while you attend to the presentations that will allow us to non-invasively record your brain's activity. We will ask you to not wear makeup to an EEG session, and hair

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products (i.e. a hair dryer, shampoo, towels) will be provided following the EEG. This portion of participation may last up to two hours.

You may be asked to complete several questionnaires about a range of personal skills and characteristics, and may be asked to complete a problem solving task and vocabulary test. This portion of participation may last up to two hours. Participation will take place at Western Universities London campus or online.

5. **What are the risks and harms of participating?**

There are no known or anticipated risks or discomforts associated with participating in this study.

6. **What are the benefits of participating in this study?**

You may not directly benefit from participating in this study but information gathered may provide benefits to society as a whole which include understanding the role that sensory perception plays in typical development, which may lead to theories and practices to help individuals who exhibit impaired sensory perception.

7. **Can participants choose to leave the study?**

Participation is completely voluntary, *you can withdraw from the study at any time*. If you decide to stop participating, you will still be eligible to receive the promised compensation for agreeing to be in this project. In the event you withdraw from the study, all associated data collected will be immediately destroyed wherever possible.

8. **How will participants' information be kept confidential?**

All information obtained during the study will be held in strict confidence to the fullest extent possible by law. While we do our best to protect your information there is no guarantee that we will be able to do so. The inclusion of your date of birth may allow someone to link the data and identify you. The mitigate this risk to the greatest extent possible, all data will be de-identified immediately following collection and labelled with a Participant ID, and the file linking your identifying information and Participant ID will be kept under lock and key. Representatives of The University of Western Ontario Non-Medical Research Ethics Board may require access to your study-related records to monitor the conduct of the research. The experimental data acquired in this study may, in an anonymized form that cannot be connected to you, be used for teaching purposes, be presented at meetings, published, shared with other scientific researchers or used in future studies. Your name or other identifying information will not be used in any publication or teaching materials without your specific permission.

9. Are participants compensated to be in this study?

Yes. Participants from the SONA system will be compensated with 1 research credit per hour toward PSYC1000 for participating in this study. If you are enrolled in a course other than Psych 1000, your compensation will be based on your course outline. If you have any questions about the time or compensation, please feel free to contact the investigators before you consider signing the consent. Otherwise, compensation will be $5.00 for every 30 minutes of participation.

10. What are the Rights of Participants?

Your participation in this study is voluntary. You may decide not to be in this study. Even if you consent to participate you have the right to not answer individual questions or to withdraw from the study at any time. If you choose not to participate or to leave the study at any time it will have no effect on your academic standing if you are a student.

We will give you new information that is learned during the study that might affect your decision to stay in the study.

You do not waive any legal right by signing this consent form.

11. Whom do participants contact for questions?

If you have questions about this research study please contact: Prof. Ryan Stevenson at the Department of Psychology, Western University, [redacted]

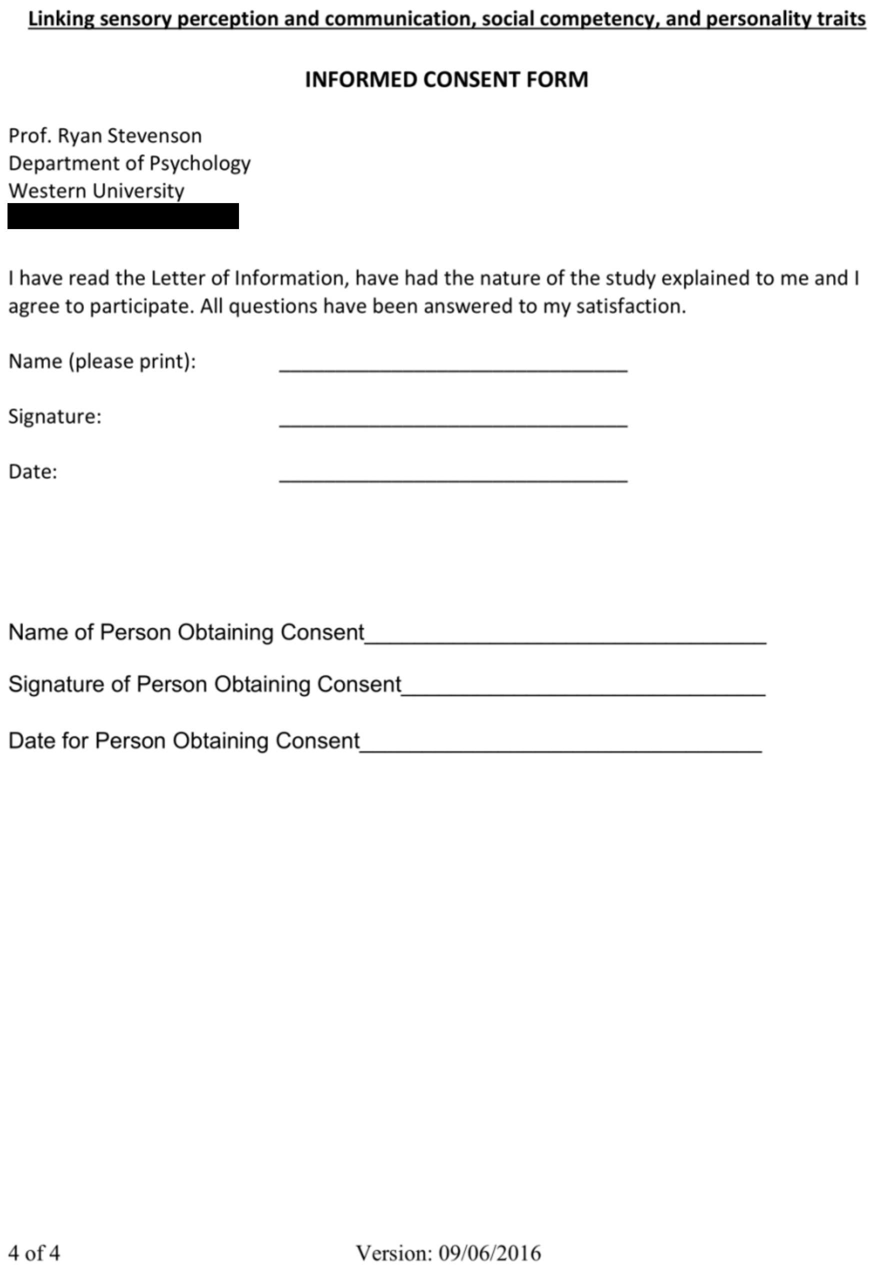
If you have any questions about your rights as a research participant or the conduct of this study, you may contact The Office of Research Ethics [redacted], email: [redacted].

Thank you for your interest and participation in this study, it is greatly appreciated!

This letter is yours to keep for future reference.

Appendix C

Consent Form



Linking sensory perception and communication, social competency, and personality traits

INFORMED CONSENT FORM

Prof. Ryan Stevenson
Department of Psychology
Western University
[redacted]

I have read the Letter of Information, have had the nature of the study explained to me and I agree to participate. All questions have been answered to my satisfaction.

Name (please print): ________________________________

Signature: ________________________________

Date: ________________________________

Name of Person Obtaining Consent________________________________

Signature of Person Obtaining Consent______________________________

Date for Person Obtaining Consent________________________________

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Appendix D

Table 3: Literature-based regions' correlations – correlation coefficient (*p* value)

		EMSI			LMSI							
					CP				Occ			
	Electrode	61	62	78	7	31	55	80	106	77	83	96
MMN	59	-.143	.181	.125	.049	**.254***	**.301***	**.362****	.130	.207	.145	.189
		(.270)	(.163)	(.336)	(.707)	(.049)	(.018)	(.004)	(.319)	(.109)	(.264)	(.145)
	60	-.064	.130	.073	.059	**.322***	**.297***	**.309***	.097	**.273***	**.274***	.006
		(.625)	(.317)	(.578)	(.652)	(.011)	(.020)	(.015)	(.457)	(.033)	(.033)	(.966)
	66	-.113	.058	-.064	-.160	.046	.055	.062	-.158	.082	.226	.127
		(.385)	(.659)	(.623)	(218)	(.724)	(.676)	(.634)	(.224)	(.528)	(.079)	(.330)
P3	62	-.011	-.084	-.182	-.197	-.163	-.174	-.162	-.217†	-.097	.063	.245†
		(.933)	(.521)	(.160)	(.127)	(.209)	(.179)	(.213)	(.093)†	(.456)	(.628)	(.057)†
	70	-.168	-.138	-.201	.154	.190	.204	.160	.135	.183	.053	.039
		(.196)	(.289)	(.120)	(.235)	(.142)	(.114)	(.217)	(.300)	(.159)	(.683)	(.764)
	75	-.201	-.139	-.146	.148	.150	.157	.219†	.197	.134	-.047	.004
		(.120)	(.286)	(.262)	(.256)	(.248)	(.228)	(.090)†	(.127)	(.302)	(.717)	(.977)
	83	**-.273***	**-.389****	**-.413****	.040	-.220†	-.187	-.204	-.017	-.217†	.073	.144
		(.033)	(.002)	(.001)	(.757)	(.088)†	(.150)	(.114)	(.895)	(.093)†	(.579)	(.268)

Note: † $p < .10$* $p < .05$, ** $p < .01$

Appendix E

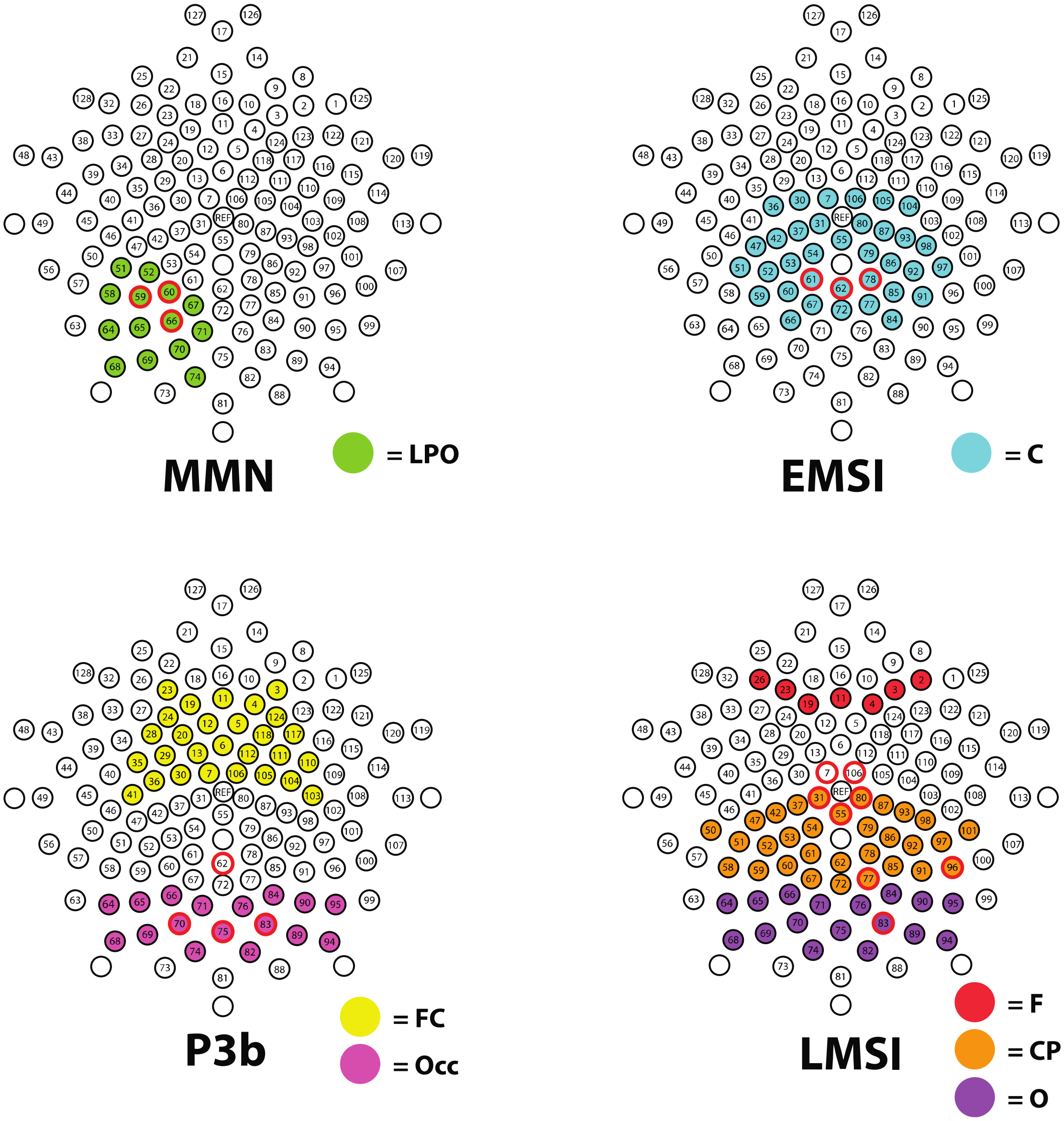

Figure 11: Scalp topographies that were included in the study's analyses and subsequent analyses using previously defined areas identified in other studies (electrodes identified in red).

Curriculum Vitae

Name:	Sébastien Lauzon
Post-secondary Education and Degrees:	University of Waterloo Waterloo, Ontario, Canada 2013 – 2017 B.A. (Psychology)
	The University of Western Ontario London, Ontario, Canada 2017 – 2020 M.Sc. (Psychology)
Honours and Awards:	University of Waterloo President’s Scholarship 2013 Distinction, University of Waterloo 2017 Dean’s List, University of Waterloo (GPA 3.90) 2017
Related Work Experience	Graduate Teaching Assistant The University of Western Ontario 2017 – 2019

Presentations:

Lauzon, S. A., Schulz, S. E., Cohen, Z. I., Stevenson, R. A. (2018). Multisensory integration and autistic traits. *International Society for Autism Research 2018 Annual Meeting*. Rotterdam, Netherlands.

Lauzon, S. A., Schulz, S. E., Cohen, Z. I., Stevenson, R. A. (2018). Multisensory integration and autistic traits. *Third Annual Developmental Disabilities Research Day*. London, ON, Canada.

Lauzon, S. A., MacLeod, C. M. (2017). Shapes, tones, and associations: Exploring cross-modal contingency learning. *The 47th Annual Ontario Psychology Undergraduate Thesis Conference*. Ottawa, ON, Canada.

Leblanc, V., Durand, G., **Lauzon, S. A.**, Turgeon, A., Cousineau, D. (2016). Clusters of response time distribution in the same-different task. *Psychonomic Society's 57th Annual Meeting*. Boston, MA, USA.

Lauzon, S. A., Cousineau, D. (2016). L’effet des stimuli d’une complexité contrôlée sur les temps de réponse lors de la tâche même-différent [The effect of controlling stimuli complexity on response times during the same-different task]. *38ième Congrès annuel de la Société Québécoise de Recherche en Psychologie*. Trois-Rivières, QC, Canada.