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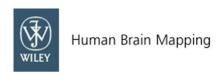
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Contextual factors multiplex to control multisensory processes

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SCHOLARONE™ Manuscripts RUNNING HEAD: Multiplexed control over multisensory processes

Contextual factors multiplex to control multisensory processes

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Abstract

This study analysed high-density event-related potentials (ERPs) within an electrical neuroimaging framework to provide insights regarding the interaction between multisensory processes and stimulus probabilities. Specifically, we identified the spatio-temporal brain mechanisms by which the proportion of temporally congruent and task-irrelevant auditory information influences stimulus processing during a visual duration discrimination task. The spatial position (top/bottom) of the visual stimulus was indicative of how frequently the visual and auditory stimuli would be congruent in their duration (i.e., context of congruence). Stronger influences of irrelevant sound were observed when contexts associated with a high proportion of auditory-visual congruence repeated and also when contexts associated with a low proportion of congruence switched. Context of congruence and context transition resulted in weaker brain responses at 228-257 ms post-stimulus to conditions giving rise to larger behavioural cross-modal interactions. Importantly, a control oddball task revealed that both congruent and incongruent audiovisual stimuli triggered equivalent non-linear multisensory interactions when congruence was not a relevant dimension. Collectively, these results are well explained by statistical learning, which links a particular context (here: a spatial location) with a certain level of top-down attentional control that further modulates cross-modal interactions based on whether a particular context repeated or changed. The current findings shed new light on the importance of context-based control over multisensory processing, whose influences multiplex across finer and broader time scales.

Keywords: cross-modal interaction; top-down; attention; audiovisual; context; congruence

Introduction

The interplay between top-down control processes (typically attention) and multisensory processing (e.g., Spence and Driver, 2004) is a topic of ongoing debate. Several studies have suggested that some varieties of multisensory integration occur at a preattentive stage and that it is largely impervious to attentional influences (e.g., Driver, 1996; Bertelson and de Gelder, 2004; Matusz and Eimer, 2011; reviewed in De Meo et al., 2015; Murray et al. 2015). This notion has been challenged by other behavioural (e.g., Sanabria et al., 2007), event-related potential (ERP; e.g., Talsma, Doty and Woldorff, 2007; Matusz and Eimer, 2013), and neuroimaging (e.g., Fairhall and Macaluso, 2009) findings, supporting the claim that attention can affect multisensory outcomes (reviewed in van Atteveldt, Murray, Thut and Schroeder, 2014).

Recently, Talsma et al. (2010) proposed a framework to account for the bidirectional relationship between attention and multisensory processes. According to this model, salient multisensory stimuli are integrated prior to effects of attention. However, when inputs to different senses provide competing information (conflicting information may constitute an extreme example of such), top-down attention mechanisms can be activated prior to multisensory interactions to facilitate efficient sensory processing. For instance, Talsma and Woldorff (2005) presented evidence of an early modulation of ERPs associated with the presentation of multisensory inputs; amplitudes were enhanced when audiovisual stimuli were selectively attended. These data suggested that top-down control was needed to select appropriate (to-be-integrated) information in situations where competing sensory representations were activated.

Aside from influences based on attention (i.e., the goals of the observer), there is a growing literature emphasising the importance of control mechanisms based on context,

where context can be understood as the immediate situation in which a stimulus is presented (van Atteveldt et al., 2014). Until recently, in studies of multisensory processes these contextual influences have been studied in terms of long-term experience and learning. Studies of speech and communication signals provide clear examples of this (e.g. Froyen et al., 2009; Matusz et al., 2015a). More recently, consideration has been given to context-based influences operating on a shorter timescale. This can include both on-line effects arising during the course of the experiment (e.g., Powers et al., 2009; Thelen et al., 2014; Matusz et al., 2015b; von Kriegstein and Giraud, 2006) as well as effects at even finer time-scales, such as those transpiring at an inter-trial level (Wylie et al., 2009; Murray et al., 2009; King et al., 2012; Sandhu and Dyson, 2013). For example, the fact of either repeating a task across two successive trials or switching from one task to another can dramatically influence performance, such that reaction times and error rates both increase after switching to perform a new task – i.e., the switch cost effect (reviewed in Wylie and Allport, 2000).

The importance of top-down control for stimulus processing has been broadly studied in cognitive control research using interference paradigms, where congruence between different dimensions of two unisensory stimuli is manipulated (e.g., the flanker task; Corballis and Gratton, 2003; Appelbaum et al., 2011). Real-world environments are typically multisensory in nature and therefore congruence (or lack thereof) permeates it. For example, the congruence of low-level spatio-temporal features has been identified as a major determinant for the occurrence of multisensory integration (reviewed in Murray and Wallace, 2012; Stein, 2012). By contrast, congruence has been largely under-investigated with regard to the interplay of top-down control and multisensory processes.

Recently, Sarmiento et al. (2012) tested how irrelevant stimuli from one sense can

interfere with the processing of stimuli in another sense by creating distinctive contexts. Participants discriminated the duration (short or long) of a visual stimulus that was accompanied by a congruent or incongruent auditory distracter. Critically, Sarmiento et al. (2012) manipulated also the likelihood of congruence between the duration of visual and auditory stimuli (hereafter context of congruence) by means of spatial locations of the auditory-visual stimuli. That is, in one spatial location (i.e., upper visual field) visual and auditory stimuli would match in their duration on the majority of trials, in contrast to the other location where on the majority of trials the stimuli would be mismatching. The difference in performance across trials containing congruent versus incongruent auditory-visual stimuli (hereafter congruence effect) was employed as an index of crossmodal interactions. The manipulation of context of congruence thus served as a proxy for understanding the importance of statistical learning for these multisensory processes (Altieri et al., 2015; Baier et al., 2006; Barakat et al., 2013; Barenholtz et al., 2014; Beierholm et al., 2009; Chandrasekaran et al., 2009).

Sarmiento et al. (2012) demonstrated that top-down attention did affect crossmodal interactions; these were larger in contexts where there was a high versus low probability of congruence. This was primarily due to a reduction in the congruence effect in the low-probability context. The authors argued that this situation triggered an attentional set for filtering out temporally incongruent auditory input that in turn resulted in larger crossmodal interactions. It is likely that these context-based adjustments of top-down attentional control are transpiring in an on-line fashion, as indicated by studies of purely visual incongruence (King et al., 2012). If this holds true also for auditory-visual congruence-based interactions, such influences should also operate on a trial-to-trial basis, which can be investigated by separately quantifying crossmodal interactions (viz. congruence effects) on

trials when the context of congruence switches versus repeats. This was the principal aim of the current study.

We achieved this by using the same paradigm as in Sarmiento et al., (2012) (hereafter, visual temporal discrimination task) (Figure 1). We expected to replicate the behavioural results of Sarmiento et al. (2012), by finding reliable influences of context on congruence-based interactions, as tested using the visual temporal discrimination task. In the present study, however, we expected that repetition of context versus a switch from one context to another on successive trials would have opposing effects on this influence. Specifically, for conditions where the context repeated we expected a larger congruence effect for the high-probability versus low-probability context, which would not only replicate the findings of Sarmiento et al. (2012) but also extend them to show that statistical learning about contingencies between the stimulus context (i.e., a spatial location) and stimulus content can take place across single trials. By contrast, for conditions where the context switched we expected a larger congruence effect for the low-probability versus high-probability context, because the attentional set cannot be reliably established.

By including electroencephalographic measurements analysed within an electrical neuroimaging framework, we were likewise able to determine the spatio-temporal correlates of context-based effects related to statistical learning as well as those related to transitioning from one to another context from one trial to the next one. We expected to differentiate between the possible contributions of modulations in brain response strength, topography, and latency that could account for the influence of context on congruence-based auditory-visual interactions. In this way, we were likewise able to situate the effects found in the visual temporal discrimination task with respect to non-linear multisensory integration processes as revealed by a control oddball task. In the latter, we expected to

observe non-linear response interactions between ERPs to AV stimuli and the summed responses to unisensory stimuli (i.e., A + V) (e.g., Cappe et al., 2010, 2012).

Methods

Participants

The participants were 28 undergraduate students from the University of Granada (19 females; age range: 18-28 years old; mean age of 24 years) who received course credits or cash payment of 20 Euro in exchange of their participation. All of the participants reported normal hearing and normal or corrected-to-normal vision and gave their informed consent to participate in the study conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. The data from two participants were removed due to technical issues with Net Station software. Additionally, EEG data from six participants were heavily contaminated by blink, muscle, or alpha-related artefacts, which resulted in less than 100 accepted EEG epochs for each condition of interest. Consequently, data from these subjects were removed from analyses. The data from the remaining 20 participants (12 women; age range: 18-28 years, mean age = 23 years) were included in the complete data analyses presented here.

Apparatus and stimuli

The experiment was conducted on an Intel Core 2 Duo PC with a 17-in. LCD monitor. E-Prime software was used for stimulus presentation and response collection (Psychology Software Tools; www.pstnet.com).

The visual stimuli consisted of a white circle (3.01° in diameter), a white equilateral triangle (3.01° in height) and a white central cross that served as the fixation point. The horizontal line of the cross (11.52° long) split the screen into upper and lower halves. Two

loudspeakers, positioned on each side of the computer screen, were used to present the auditory stimuli, which consisted of a white noise burst and a 600 Hz pure tone (60 dB[A] measured at ear level; see **Figure 1**).

Procedure

Participants sat in a comfortable chair at approximately 57 cm from the computer monitor in a silent, dark and electrically shielded room. The instructions that explained the tasks where displayed on the computer screen. The experiment began with an unisensory discrimination task in which participants were asked to discriminate the duration (short or long) of a white circle displayed above or below (6.52° from the centre of the circle; cf. Experiment 4 in Sarmiento et al., 2012) the fixation point (i.e., the white horizontal line) for either 100 ms or 180 ms. The unisensory block (16 short and 16 long unisensory trials) was used to ensure that participants understood the task and were responding above 60 % of accuracy overall.

After the unisensory task participants put on an elastic electrode-cap for the EEG recording (see EEG acquisition section below) during an oddball and a visual temporal discrimination task. The oddball task was conducted first in order to avoid any carryover effect from the context of congruence manipulation. However, as the visual temporal discrimination task was the main focus of the present study, we describe it first here.

Visual temporal discrimination task

The oddball task was followed by the visual duration discrimination task in which participants were asked to discriminate the duration of a white circle displayed below or above the fixation point for either 100 ms or 180 ms, while ignoring the synchronous presentation of a white noise burst that could last for 100 ms or 180 ms. Onsets were always

synchronous across sensory modalities. No unisensory trials were presented in the visual duration discrimination task. Congruent and incongruent trials emerged from the four possible stimuli combinations. The crucial manipulation consisted of the inclusion of two contexts of congruence defined by the two halves of the computer screen (upper/lower). For half of the participants, the upper spatial location was associated with a high proportion of congruent trials (80%) and the lower spatial location was associated with a low proportion of congruent trials (20%). The reverse was true for the remaining half of the participants. The congruent and incongruent stimuli had the same probability of appearance. This was also true for short and long trials. Consequently, the context of congruence could repeat or switch across trials with equal probability. Notably, stimuli with identical physical properties were presented across the two contexts. This ensured that any differences observed between these contexts could be attributed to stimulus congruence probabilities being utilised by the brain to adjust top-down attentional control to facilitate visual performance by suppressing the processing of sounds in contexts with a high proportion of auditory-visual incongruence. This interpretation is in line with emerging notions regarding the interplay between top-down attention mechanisms and stimulus expectations (e.g. Summerfield and Egner, 2009; Kok et al. 2012; Larsson and Smith, 2012; Auksztulewicz and Friston, 2015).

At the beginning of each trial, participants were presented with the fixation cross displayed in white against a black background for a random duration between 500 and 1000 ms. This fixation cross remained on throughout the whole trial. Next, the visual and auditory stimuli were presented for either 100 ms or 180 ms, and could be congruent or incongruent in duration. Feedback regarding response accuracy was provided to the participants for 500 ms. The next trial began between 1500 and 2000 ms after the feedback. Participants were encouraged to fixate and to avoid eye movements and blinks during the presentation of the

stimuli. The sequence of events is schematised in **Figure 1a**.

Accuracy, rather than response speed, was emphasised; so participants had no response time pressure. Responses were collected using a serial response box. Half of the participants were told to press the leftmost key if the circle was short in duration and the rightmost key if the circle was long in duration. The reverse stimulus-response mapping was used for the remaining participants. All responses were made with the right hand. Participants completed 8 multisensory practice trials and 8 blocks of 120 multisensory trials each, distributed as follows: 48 congruent trials and 12 incongruent trials for the high proportion-congruent context; 12 congruent and 48 incongruent trials for the low proportion-congruent context.

Oddball task

By means of a control, oddball task, we likewise assessed whether the context-based effects in the current experiment occur before or after any non-linear brain response interactions between the stimuli we employed here. Importantly, we used the same stimuli as in the visual temporal discrimination task, but made participants attend to stimulus dimensions other than stimulus duration (now visual shape and sound frequency) while removing the influence of context-based control processes (Figure 1). These manipulations enabled us to verify whether there are qualitative changes in how the congruent and incongruent stimuli from the visual temporal discrimination task are integrated when presented outside of strong top-down influences based on task-relevance or context. A corollary question here was whether congruence would further modulate these auditory-visual interactions and, if so, at what stage. While outside of the primary focus of the current study, this important issue has thus far received limited treatment (Fort et al., 2002; Molholm et al., 2004; Yuval-Greenberg and Deouell, 2009).

Participants performed an oddball task in which either a white triangle or a 600 Hz tone had to be detected via button-press. The standard stimuli, which did not require a response, were a white circle and a white noise burst (these were identical to those in the visual temporal discrimination task described above). The visual stimuli could appear above or below the fixation cross (6.52° from the centre of the circle). Participants performed two blocks of 216 trials each, 11% of which were oddballs (i.e., 24 trials). Oddballs (triangles or 600Hz tones) and standards (circles or noise bursts) could last for 100 or 180 ms and could be presented alone (unisensory stimuli) or synchronously with a stimulus of the other sensory modality (multisensory stimuli) with simultaneous onsets. The visual and auditory oddballs were never presented together. This manipulation gave rise to unisensory trials (the visual or auditory stimulus was presented alone), multisensory congruent trials (the visual stimulus was of the same duration as the auditory stimulus) and multisensory incongruent trials (the visual stimulus was of a different duration than the auditory stimulus). Unisensory and multisensory stimuli, short and long stimuli, as well as congruent and incongruent stimuli had the same probability of presentation (Figure 1b). Participants had to detect the oddballs when they appeared alone as well as when they were presented accompanied by a standard stimulus from the other modality. The fixation point was presented alone for 750 or 1250 ms, and the inter-trial interval ranged from 1500 to 2500 ms to avoid anticipation. Feedback was only displayed when participants made an error. The oddball task was used to assess multisensory integration between congruent and incongruent audiovisual stimuli when no response was required (i.e., standard stimuli).

At the end of the experiment, participants completed a questionnaire that evaluated whether or not they were aware of the congruence manipulation in the visual temporal discrimination task. They were asked whether they perceived any difference between the

two onset locations during the visual duration discrimination task, and, if so, what that difference was.

EEG Acquisition

Continuous EEG was acquired at 1000 Hz through a Geodesic Sensor Net of 129 Ag/AgCl electrodes referenced to the vertex channel (Tucker et al., 1994) and connected to an AC-coupled high-input impedance amplifier (200 M Ω , Net Amps $^{\text{TM}}$, Electrical Geodesics, Eugene, Oregon). Impedances were kept below $50k\Omega$, as recommended for these amplifiers. The signal was acquired with a 0.01-100Hz elliptical band-pass filter. Gain and zero calibration were performed prior to the start of every recording. The head-coverage included sensors lateral to and below both eyes to monitor horizontal and vertical eye movements (electrooculogram, EOG).

ERP Analyses

The EEG was high-pass (0.1Hz) and low-pass (30Hz) filtered offline. Epochs of EEG were segmented from 200 ms pre-stimulus to 800 ms post-stimulus onset. The segmented epochs were submitted to automated software processing for identification of artefacts. Epochs containing eye movements or blinks ($\pm 70~\mu V$ relative to baseline in EOG channels) were rejected. Individual channels containing other sources of transient noise ($\pm 80~\mu V$ relative to baseline in any channel) were replaced using a trial-by-trial basis with a spherical interpolation algorithm (Perrin et al., 1989). The epoch was discarded when more than 10 channels were deemed artefact-contaminated. Additionally, the data were visually inspected to ensure that all artefacts had been detected.

Epochs of EEG were averaged for each stimulus condition and from each subject to

calculate event-related potentials (ERPs). We would remind the reader that long and short duration stimuli were constituents for both congruent and incongruent stimulus conditions. By collapsing across durations, we were able to equate any contributions of offset responses to between-condition effects as well as to ensure that the comparison of responses to congruent and incongruent pairings involved equivalent stimulus energies. Data from ERPs were baseline corrected using the period of 200 ms preceding stimulus onset. ERPs were recalculated against the average reference.

For the visual temporal discrimination task, the averaging of EEG epochs was guided by the pattern of behaviour. As will be detailed below, we observed a larger congruence effect for high- than low- probability contexts when context repeats and a larger congruence effect for low- than high- probability context when context switches (see Figure 2). Consequently, we collapsed across trials with larger congruence effects as well as across trials with smaller congruence effects. This enabled us to identify brain mechanisms of the congruence effect, which serves as a proxy for audiovisual cross-modal interactions. In this way, there were 4 ERPs per participant following a 2x2 factorial design (Congruence effect size x Congruence): 1) L_{CONG} (i.e., collapsed trials when the duration was congruent and high-probability context repeated as well as when the duration was congruent and low-probability context switched), 2) Lincong (i.e., collapsed trials when the duration was incongruent and high-probability context repeated as well as when the duration was incongruent and low-probability context switched), 3) S_{CONG} (i.e., collapsed trials when the duration was congruent and lowprobability context repeated as well as when the duration was congruent and highprobability context switched), and 4) S_{INCONG} (i.e., collapsed trials when the duration was incongruent and low-probability context repeated as well as when the duration was incongruent and high-probability context switched). For each of these 4 conditions there were on average (±s.e.m.) 184(±9), 191(±9), 191(±9), and 182(±9) accepted epochs, respectively, with a minimum of 100 accepted epochs per subject and condition. Another important advantage of collapsing the data in this manner is that any differences strictly due to probability (and therefore to deviance detection) are counterbalanced across all conditions. In this way, any differences between congruent and incongruent conditions across contexts can be confidently interpreted purely in terms of top-down control.

For the oddball task, ERPs (collapsed across durations) were calculated for unisensory visual trials (V), unisensory auditory trials (A), congruent auditory-visual trials (AV_{cong}), and for incongruent auditory-visual trials (AV_{incong}). The ERPs from the A and V conditions were summed (A+V) and then statistically compared with the AV_{cong} and AV_{incong} conditions in a 1-way non-parametric F-test. Non-linear multisensory interactions were identified in planned contrasts (AV_{cong} vs. A+V as well as AV_{incong} vs. A+V). Finally, planned contrasts tested for effects of congruence (AV_{cong} vs. AV_{incong}). For the AV_{cong} , AV_{incong} , and A+V conditions there were on average (\pm s.e.m.) 71(\pm 4), 71(\pm 3), and 72(\pm 4) accepted epochs, respectively, with a minimum of 34 accepted epochs per subject and condition.

ΑII analyses conducted using the freeware Cartool were (http://sites.google.com/site/fbmlab/cartool; Brunet et al., 2011) and the STEN toolbox (http://www.unil.ch/line/home/menuinst/infrastructure/software--analysis-tools.html). The analysis strategy we used followed a multi-step analysis procedure referred to as electrical neuroimaging (Murray et al., 2008). Electrical neuroimaging allowed us to identify effects using both local and global measures of the electric field at the scalp. This procedure distinguishes between effects following from modulations in the strength of responses of statistically indistinguishable brain generators and alterations in the configuration of these generators (viz. the topography of the electric field at the scalp), as well as latency shifts in brain processes across experimental conditions (Michel et al., 2004, 2009; Murray et al., 2008; Michel and Murray, 2012; Altieri et al., 2015; Stevenson et al., 2014). Additionally, we used the local autoregressive average distributed linear inverse solution (LAURA; Grave de Peralta Menendez et al., 2001, 2004) to visualise and statistically contrast the likely underlying sources of effects indentified in the preceding analysis steps.

Global modulations in the strength of the electric field at the scalp were quantified by calculating the global field power (GFP; Lehmann and Skrandies, 1980) for each subject and stimulus condition. This measure represents the spatial standard deviation of the electric field at the scalp at a given time point, and constitutes a reference-independent measure of the ERP amplitude (Murray et al., 2008; Koenig and Melie-Garcia, 2010). Stronger electric fields result in larger GFP values. GFP values were baseline corrected in order to legitimately compare between conditions with different numbers of trials. GFP modulations were analysed using a millisecond-by-millisecond non-parametric analysis of variance (ANOVA) and non-parametric planned contrasts when warranted using the Mann-Whitney test. Analyses were performed in conjunction with a 15 contiguous data-point temporal criterion for significant effects to correct for temporal auto-correlation (only those effects where p-values met the statistical threshold (p≤0.05) for more than 15 contiguous time points (i.e., ~15 ms at 1000 Hz sampling) were considered reliable; inspired by Guthrie and Buchwald, 1991).

In order to identify stable periods of electric field topography (hereafter template maps), the collective post-stimulus group-average ERPs were subjected to hierarchical clustering. The optimal number of stable ERP clusters (i.e., the minimal number of maps that accounts for the greatest variance of the dataset) was determined using a modified Krzanowski-Lai criterion (Murray et al., 2008). The clustering makes no assumption on the

orthogonality of the derived topographic template maps (De Lucia et al., 2010a, 2010b; Pourtois et al., 2008; Koenig et al., 2014). Template maps identified in the group-level ERP were entered into a fitting procedure wherein each template map was compared with the moment-by-moment scalp topography on the individual subjects' ERPs from each condition and was labelled according to the one with which it best correlated spatially. This fitting procedure allows determining the total amount of time a given template map was observed for a given condition across subjects. Statistical analysis of these values was performed with an ANOVA. The results of this analysis revealed whether a given ERP was more often described by one template map vs. another, which implied different stable map configurations across conditions at the same moments in time.

Source Estimations

The intracranial generators underlying the surface electric field were estimated using a distributed linear inverse solution based on a Local Auto-Regressive Average (LAURA) model comprising biophysical laws as constraints (Grave de Peralta Menendez et al., 2001, 2004). LAURA uses a realistic head model with a solution space of 4024 nodes, selected from a 6 x 6 x 6 mm grid equally distributed within the gray matter of the Montreal Neurological Institute's (MNI's) average brain. This algorithm selects the source configuration that better mimics the biophysical behaviour of electric vector fields, that is, the estimated activity at one point depends on the activity at neighbouring points according to electromagnetic laws (Grave de Peralta and Gonzales Andino, 2002). Prior to calculation of the inverse solution, the ERP data of each individual subject for each condition were down-sampled and affine-transformed to a common 111-channel montage. The time period for which intracranial sources were estimated and statistically compared between conditions was defined by the

results of the abovementioned topographic analysis. Statistical analyses of source estimations were performed by first averaging the ERP data across time to generate a single data point for each participant and condition. ANOVAs were performed at each of the 4024 source nodes in the inverse solution space (using across-subjects variance). For the temporal discrimination task, the ANOVA followed a 2x2 factorial design (congruence x congruence effect size). For the oddball task this ANOVA followed a 1-way design (AVcong, AVincong, A+V). Only nodes exceeding the spatial extent criterion of at least 17 contiguous significant nodes (p≤0.0002) were considered significant (see Thelen et al, 2012 for similar spatial criterion). This spatial criterion was determined using the AlphaSim program (http://afni.nimh.nih.gov) and assuming a spatial smoothing of 6mm full-width half maximum. AlphaSim performs 10,000 Monte Carlo permutations on the 4024 nodes of our lead field matrix to determine the false discovery rate for clusters of different sizes. These permutations indicated that there is a 3.54% probability of a cluster of at least 17 contiguous nodes, which gives an equivalent node-level p-value of p≤0.0002. The results of the analyses were rendered on the MNI average brain with loci of the largest statistical differences within a cluster indicated based on the Talairach and Tournoux (1988) atlas.

Results

Visual Temporal Discrimination Task

Behavioural data

Mean response accuracy for each participant and condition were submitted to a 2 Context of congruence (high congruent, low congruent) x 2 Congruence (congruent, incongruent) x 2 Context Transition (switch, repeat) parametric ANOVA. The first trial of each block was excluded from the analysis. Neither the main effect of context transition

 $(F_{(1,19)}=1.91; \ p>0.18; \ \eta_p^2=0.09)$ nor context of congruence $(F_{(1,19)}=0.153; \ p=0.7; \ \eta_p^2<0.01)$ were reliable. There was a reliable main effect of congruence $(F_{(1,19)}=42.55; \ p<0.001; \ \eta_p^2=0.69)$. None of the 2-way interactions were reliable (all F's<1.69; p's>0.20). Crucially, there was a reliable 3-way interaction $(F_{(1,19)}=18.66; \ p<0.001; \ \eta_p^2=0.49)$.

Additional 2-way ANOVAs for each level of the factor context transition were conducted to understand the bases for this 3-way interaction. For the repeat context transition 2x2 ANOVA there was a reliable effect of congruence ($F_{(1.19)}$ =36.31; p < 0.001; $\eta_p^2 = 0.66$) as well as a reliable interaction between context and congruence ($F_{(1.19)}$ =11.67; p < 0.003; η_p^2 = 0.38). There was no main effect of context ($F_{(1,19)} = 0.36$; p > 0.55; $\eta_p^2 = 0.02$). The interaction on trials involving repetition of context was driven by larger in magnitude congruence effects in the high proportion-congruent context (23.8%) than in the low proportioncongruent context (16.6%); both being significant (t's>4.6; p's<0.001) (Figure 2). For the switch context transition 2x2 ANOVA there was likewise a reliable effect of congruence $(F_{(1.19)} = 43.06; p < 0.001; \eta_0^2 = 0.69)$ as well as a reliable interaction between context and congruence ($F_{(1.19)} = 7.06$; p = 0.016; $\eta_p^2 = 0.27$). There was no main effect of context ($F_{(1.19)}$ =1.74; p > 0.20; $\eta_0^2 = 0.08$). In contrast to the context-repeat trials, the interaction on trials involving a switch in context between trials was driven by larger in magnitude congruence effects in the low proportion-congruent context (23.3%) than in the high proportioncongruent context (17.9%); both being significant (t's>5.2; p's<0.001). That is, there was a larger congruence effect when switching to a low proportion-congruent context.

Participants' reports revealed that five (25%) of the participants noticed a difference between the two contexts (e.g., "I made more errors on the upper half"). However, none of them reported being aware of the specific proportion-congruent manipulation, in accordance with previous studies (Crump et al., 2006; Heinemann et al., 2009; Sarmiento et

al., 2012; King et al., 2012).

Surface ERP data

In light of the behavioural results described above, the ERP data were analysed following a 2x2 Congruence effect size x Congruence factorial design (see Materials and Methods for details). The timepoint-wise non-parametric ANOVA on the Global Field Power waveforms revealed a significant interaction over the 228-257 ms period (**Figure 3**). Non-parametric post-hoc tests within this period showed there to be a significantly weaker GFP for L_{CONG} than L_{INCONG} over the 240-259ms period. By contrast, there was a significantly stronger GFP for S_{CONG} than S_{INCONG} over the 224-242ms period. Neither main effect yielded significant results.

A hierarchical topographic cluster analysis was performed on the collective group-average ERPs to identify periods of stable electric field topography both within and between experimental conditions. 11 template maps that explained 95.9% of the variance were identified. At the group-average level there was no evidence for different template maps across conditions (see **Supplementary Figure 1**). Consequently, no single-subject fitting was performed with these data.

Source estimations

Distributed source estimations were calculated using the mean potential values over the 228-257 ms period and submitted to a 2 Congruence × 2 Congruence-effect size ANOVA. The main effect of congruence yielded no significant clusters. The main effect of congruence effect size yielded significant clusters centred within the left middle occipital gyrus, the right parahippocampal gyrus, the right precuneus, and the right inferior frontal gyrus. These

regions are consistent with the literature reporting their contribution to cross-modal and multisensory processes (reviewed in Murray and Wallace, 2012), including those focusing on stimulus (a)synchrony (e.g., Macaluso et al., 2004). A significant interaction between congruence and congruence-effect size was observed in a widely distributed network of clusters within the left superior temporal cortices, the left parietal cortices, and bilateral precuneus (Figure 4a). In particular, the parietal cortices likely included pre-motor structures previously implicated in temporal processes (e.g., Grahn and Rowe, 2009; Marchant et al., 2012). Given this interaction, contrasts focused on the congruence effect for the large-size congruence effect (L_{CONG} vs. L_{INCONG}) and small-size congruence effect (S_{CONG} vs. S_{INCONG}) conditions, separately. For the large-size congruence effect conditions, clusters exhibiting significant differences were centred within the left medial frontal gyrus, the left superior temporal cortex, and the precuneus bilaterally (Figure 4b). All clusters were more strongly active in response to incongruent than congruent trials. For the small-size congruence effect conditions, clusters exhibiting stronger responses to congruent than incongruent pairings were centred within the left parietal cortices (Figure 4c).

Oddball Task

Behavioural data

Overall accuracy across participants on the oddball task was 99.77%, with a mean reaction time of 340 ms. This high performance provides an assurance that participants were appropriately engaged in the oddball task.

Surface ERP data

Analyses of data from the Oddball task focused on determining differences in the neural activation between the ERPs in response to the congruent and incongruent multisensory

conditions and the summed ERPs in response to the unisensory auditory and visual conditions (denoted by AV_{cong}, AV_{incong} and A+V, respectively). Only trials for standard stimuli were included in the analyses, because they constituted the pool of stimuli used for the visual temporal discrimination task, the analyses of which are described above.

The GFP waveforms were compared statistically using a 1-way ANOVA as a function of time (**Figure 5**). There was a significant main effect over two time intervals (130-145 ms and 249-800 ms). Follow-up planned nonparametric contrasts revealed no significant differences between AV_{cong} and AV_{incong} responses. Likewise, for both time windows, there were superadditive multisensory responses that were observed irrespective of stimulus congruence.

Next, a hierarchical spatio-temporal cluster analysis was employed again to test for topographic differences between experimental conditions within the data from the oddball task. This procedure identified a set of 11 template maps explaining 96.3% of the variance of the concatenated group-averaged ERP data set. There was no evidence for different template maps across conditions (see **Supplementary Figure 2**). Consequently, no single-subject fitting was performed with these data.

Source estimations

Estimated intracranial sources over the 130-145 ms post-stimulus time period revealed a main effect of stimulus condition centred within a distributed network of areas including the calcarine sulcus bilaterally, the left parieto-occipital cortex and left parietal cortices, the orbitofrontal cortex bilaterally and the right lateral occipital cortices (see **Figure 6a**). These areas have been repeatedly observed in studies of audiovisual integration (e.g., Calvert et al., 2000, Dhamala et al., 2007; Cappe et al., 2010, 2012), with the orbitofrontal cortices implicated in multisensory conflict (Diaconescu et al., 2011). Planned

comparisons between the AV_{cong} and A+V conditions revealed super-additive responses within the calcarine sulcus bilaterally, the left parieto-occipital cortex and left parietal cortices, and sub-additive responses within the orbitofrontal cortex bilaterally (**Figure 6b**). A similar pattern of effects was observed between AV_{incong} and A+V, with the addition of super-additive responses within the right lateral occipital cortices (**Figure 6c**). Finally, contrasts between AV_{cong} and AV_{incong} revealed stronger responses to the AV_{cong} condition within the calcarine sulcus bilaterally and stronger responses to the AV_{incong} condition within the right lateral occipital cortex, the right parietal cortex and the bilateral orbitofrontal cortex (**Figure 6d**). However, we are hesitant to over-interpret these results, given that corresponding effects were not reliably at the level of scalp ERPs.

Source estimations over the 195-275 ms post-stimulus time period revealed a main effect of stimulus condition throughout an extensive brain network including bilateral occipital, parietal, temporal, and frontal sources (Supplementary Figure 3). Planned comparisons between either AV_{cong} and A+V or AV_{incong} and A+V revealed sub-additive responses within this network. The contrast between AV_{cong} and AV_{incong} revealed stronger responses to AV_{cong} within the left temporal pole, the anterior cingulate, and dorsal prefrontal cortex. Stronger responses to the AV_{incong} condition were observed in right parietal cortices. This locus is similar to that observed for the large-size congruence effect contrast (see Figure 4b).

Discussion

It is well established that some multisensory processes can occur in a bottom-up fashion, i.e., independently of top-down control based on one's goals. Much less is known about how these processes are controlled by influences based on the context in which the

multisensory stimuli are presented as well as whether (and if so how) context-based mechanisms operating across different timescales interact with each other.

In a series of behavioural experiments, Sarmiento et al. (2012) demonstrated that the ability of an irrelevant auditory stimulus to interfere with a duration judgement on a visual stimulus can be influenced by the particular context in which the stimuli appear. Specifically, spatial locations where there was a large proportion of congruent auditory-visual stimuli were generally giving rise to stronger influences of the sound on visual processing than in spatial locations with higher proportion of incongruent auditory-visual presentations. The authors interpreted these findings in terms of specific contexts activating top-down attentional control mechanisms to a different extent. Contexts with a high proportion of incongruent pairings trigger enhanced top-down inhibition that in turn attenuated auditory-visual interactions, indexed by behavioural congruence effects. This top-down control enhancement likely occurred implicitly, as indicated by the majority of participants being unaware of the experimental manipulation.

The present study employed the same paradigm to understand whether context-based control operates at a finer 'online' time scale. To do this, we analysed trials when the context of congruence repeated versus switched on two successive trials, and electrophysiological recordings were used to understand the brain mechanisms underlying the influence of these control mechanisms. Furthermore, we added a control, oddball task, where the same stimuli as those used on the visual temporal discrimination task were both made irrelevant, so that the timing of the non-linear interactions between these stimuli could be assessed outside of influences of top-down control and then compared with the timing of the occurrence of context-based influences described above.

The visual temporal discrimination task revealed that congruence effects differed in

magnitude depending on the context of congruence as well as on whether a particular context repeated or switched. Specifically, larger-size congruence effects were observed for high-proportion congruence contexts on trials where the context repeated and for low-proportion congruence contexts on trials where the context switched (Figure 2). Our analyses of the brain responses focused on the mechanisms giving rise to large versus small congruence effects at the level of behaviour. Audiovisual interactions were modulated by context transition at ~230ms post-stimulus, with these modulations being driven by changes in brain response strength within a statistically indistinguishable configuration of brain areas (Figure 3). In the case of large-size congruence effects, brain responses were attenuated on trials with congruent than incongruent auditory-visual stimuli, and originating in the left medial frontal gyrus, the left superior temporal cortex, and the precuneus bilaterally (Figure 4). Small-size congruence effects were found to be associated with stronger responses on congruent than incongruent trials in the left parietal cortices.

Auditory-visual interactions in the visual temporal discrimination task differed in their strength depending on which context they appeared in as well as whether this context repeated or switched across two successive trails. Larger (and comparable in size) congruence effects were observed in contexts with high proportion of auditory-visual congruence on trials where this context repeated and in contexts with high proportion of cross-modal *in*congruence when this context *switched*. These results can be most readily interpreted in terms of the stimulus context (or rather contexts operating both at coarser and finer time scales) modulating the cross-modal interactions by means of a form of statistical learning.

Statistical learning is typically understood as a process by which a cognitive system learns about the underlying structure of the sensory inputs by extracting the distributional

properties from these inputs across time and/or space (Saffran et al., 1996). While the domain-general versus -specific nature of this process is a topic of current debate (Frost et al., 2015), it has been demonstrated to support a variety of cognitive functions, from auditory stimulus parsing and visual search to conditioning, to name just a few (e.g., Saffran et al., 1996; Baker et al., 2004; Courville et al., 2006; Goujon and Fagot, 2013). The importance of statistical learning has likewise been demonstrated for multisensory processing (Baier et al., 2006; Beierholm et al., 2009; Chandrasekaran et al., 2009; Barakat et al., 2013; Barenholtz et al., 2014; Altieri et al., 2015). For example, one can learn to associate arbitrary but spatially and temporally congruent auditory and visual stimuli (pure tones and Gabor patches, respectively), with reduced brain response strength corroborating increased efficiency of their recognition after a few days of training (Altieri et al., 2015). In a similar vein, learning of pairs consisting of human voices and gender-congruent faces is facilitated compared to pairs involving human voices and images of gender-incongruent faces or of plants/ rocks (Barenholtz et al., 2014).

How do the current results fit in with our understanding of the role of statistical learning and context in controlling multisensory processing? Top-down attentional control would be a prime candidate for a mechanism that could to link a particular location, a particular audiovisual stimulus (congruent or incongruent) and, crucially, a particular context of congruence (Treisman, 2006 and 1996). Indeed, research on implicit learning has repeatedly shown that selective attention is critical in order to establish a link between predictive dimensions of a particular stimulus (probability of congruence and spatial location in this case), given that such associations only emerge when these dimensions are relevant to the observer (Jiménez and Méndez, 1999; Crump et al., 2008; see also Kok et al., 2012; Larsson and Smith, 2012; Auksztulewicz and Friston, 2015 for evidence on interactions

between top-down attention and expectations). In the present study, the location was crucial since the participant needed to localize the target (displayed in one of two possible locations) in order to perform the task. Once the association between proportion of congruence and location was established, top-down attentional control of differing strength was applied to perform the task within the particular context (see e.g. Vossel et al., 2014 for a recent study modelling saccadic response—times data from a spatial-attention task). As a result, the very same stimulus (e.g., congruent) was processed differently as a function of the location where it was presented (that determined the context of congruence) and whether this context had repeated or switched. An additional contributing factor may therefore be whether or not the stimulus itself was repeated or switched (in addition to whether the context itself repeated or switched). Unfortunately, in the present study, it was infeasible to include this additional factor, principally because it would have severely reduced the signal-to-noise ratio of the ERP data. Notwithstanding, stimulus repetition effects in the current paradigm would be a particularly interesting avenue to pursue in future research, given recent evidence for the interplay between stimulus repetition and factors such as expectancy, attention, and memory (e.g., Henson et al., 2000; Turk-Browne et al., 2007; Doehrmann et al., 2010; Recasens et al. 2014; reviewed in Segaert et al., 2013).

In a functional neuroimaging study employing a visual face-gender classification version of the flanker task involving a location-based contextual manipulation of conflict frequency, King et al. (2012) demonstrated that reduced interference in contexts with high proportion of conflict is associated with stronger engagement of top-down control areas (predominantly the medial superior parietal lobule), with their comparatively weak engagement in contexts with a low proportion of conflict. The current results are in line with differing engagement of top-down attentional control across the two contexts of

congruence. If a particular location becomes associated with a high proportion of congruence between the visual and auditory stimuli, there is no need for heightened top-down control as the presence of the irrelevant sounds would typically improve the visual duration discrimination. The interactions arising between the auditory and visual stimuli are likely to be larger in the case of a repeated context that involves weak top-down inhibition of the irrelevant sounds. Along the same lines, a repeated context involving stronger top-down inhibition, as in the case of the context involving a low proportion of cross-modal congruence, is bound to lead to attenuated auditory-visual interactions when compared with a switch within such a context.

Several important aspects of the current results support the interpretation in terms of online and implicit adjustment of top-down attentional control based on a particular context of congruence as well as whether it repeated or switched. First, we hasten to remind the reader that the stimuli appearing in the two contexts were identical in their physical properties (i.e., same number of auditory-visual congruent and incongruent trials). This excludes the possibility that differences in brain responses were due to differences in stimulation or stimulus-response associations for each context. Second, by collapsing the ERP across conditions involving high-probability and low-probability contexts we also have minimised any confounding influences on the brain activity stemming strictly from detection of improbable events (e.g., P300, whose latency would coincide with the latency of our effects; reviewed in Polich, 2007). Thus, the observed ERP differences can reasonably be interpreted in terms of the brain utilising the probabilities with which stimuli were congruent in particular contexts to adjust top-down attentional control. Lastly, the lack of explicit awareness in the majority of participants regarding the congruence manipulation in the visual temporal discrimination task accords with previous findings using similar paradigms (e.g., Crump et al, 2008; Heinemann et al., 2009; King et al., 2012; Sarmiento et al., 2012). This result suggests that the top-down attention adjustments were likely occurring outside of the voluntary control of participants. This notion is further reinforced by the differences observed between repeated and switched contexts, indicating the online (i.e., trial-by-trial) nature of these implicit top-down attention adjustments.

The current study demonstrates how important for cross-modal interactions is the context in which multisensory stimuli appear, with its effects multiplexing across finer and broader time scales to influence these interactions. A predominance of congruence between signals across different senses will determine the level of top-down inhibition the brain associates with a particular context. This will have a cascading effect, with stronger cross-modal interactions transpiring across contexts associated with both high and low proportion of auditory-visual congruence, on trial-to-trial variations in the magnitude of cross-modal interactions (Murray et al., 2009; Shandu and Dyson, 2013). Importantly, the current results point to the fact that incongruity does not necessarily trigger heightened top-down control. More broadly, the current study sheds new light on the ongoing debate regarding the influence of top-down control on multisensory processes (Talsma et al., 2010; van Atteveldt et al., 2014; De Meo et al., 2015; Murray et al., 2015; ten Oever et al., in revision).

The employment of a control, oddball task enabled us to compare the timing of non-linear multisensory interactions with that of cross-modal interactions elicited by the same stimuli when under top-down control. Non-linear multisensory interactions first occurred in the present dataset at 130-145ms post-stimulus, independent of the stimulus congruence. By contrast, effects in the visual temporal discrimination task occurred first at ~230ms post-stimulus (i.e. some 100ms later). While the bases for this latency difference remain to be fully identified, these results corroborate an emerging consensus that timing of multisensory

interactions at the brain level might be one way of distinguishing processes less and more dependent on top-down control (reviewed in De Meo et al., 2015). Some multisensory processes, such as those based on simultaneity, seem to occur independently of top-down attention and context influences, being observed across paradigms and task demands, as well as across different species. These bottom-up, early multisensory interactions (eMSI) are typically observed within 100ms post-stimulus onset (De Meo et al., 2015). Some of the strongest support for their independence of top-down attention or context is provided by studies reporting eMSI in anaesthetised preparations (reviewed in reviews in Sarko et al., 2012; Rowland and Stein, 2014). In contrast, multisensory processes based on congruence (e.g., perceptual as in the current study; see also Fort et al., 2002; semantic in Molholm et al., 2004; Yuval-Greenberg and Deouell, 2009) typically transpire at later post-stimulus stages. In the case of the present study, the timing differences across the two tasks may also be linked to the fact that the visual temporal discrimination can at the earliest be completed only after 100ms post-stimulus (i.e. at the duration of the shorter stimulus). Future work will need to either modify the task to allow for its potential completion upon stimulus onset or otherwise manipulate parametrically the said timing to more fully dissociate multisensory effects differently dependent on top-down attention. Collectively, the documentation of multisensory effects across multiple time scales corroborate a novel framework differentiating top-down control processes based on attention (i.e., goals), context and content (ten Oever et al., in revision). The current results support this proposal by showing that both congruent and incongruent stimuli triggered non-linear multisensory response interactions at ~140ms post-stimulus; in some instances stimulus congruence might not play a role in modulating multisensory processing unless it is relevant to the current task (see also Molholm et al., 2004, for similar multisensory findings; see Matusz et al., in revision, for cross-modal results on predictability enabling the suppression of task-irrelevant sounds).

Conclusions

In a visual temporal discrimination task, stronger influences of irrelevant sound were observed in repeated contexts associated with a high proportion of auditory-visual congruence and following switch in context associated with a low proportion of congruence. Multisensory processes are therefore subject to control both by context as well as by statistical learning, where the latter operates on at least two time scales, but only in situations where congruence across the senses is relevant for task demands. These findings provide important insights into the interactions between expectations and top-down attention occurring in environments closely resembling naturalistic ones, i.e. where stimuli differ in their relevance to the current goals of the observer as well as the sensory modality in which they appear.

Figure Captions

Figure 1. A schematic of the experimental paradigms is displayed. a. The visual temporal discrimination task involved a white circle presented above or below the horizontal meridian and a white noise burst presented from two loudspeakers on each side of the computer monitor. The stimuli could either be 100 ms or 180 ms in duration and could either be congruent or incongruent in their duration across the senses. The location of the circle provided a context of congruence (i.e., the probability of congruent or incongruent durations; see inset). b. The oddball task used the identical stimuli as in the visual temporal discrimination task as standard stimuli. Oddball stimuli to which participants made a button-press response were a triangle and 600 Hz tone. As above the duration of stimuli could either be 100 ms or 180 ms, and when multisensory the stimuli could either be congruent or incongruent in their duration. See Materials and Methods for full details.

Figure 2. Accuracy on the visual temporal discrimination task displayed as the difference in percent correct performance between congruent and incongruent trials (i.e., the congruence effect). Mean congruence effects across participants (s.e.m. indicated) are displayed as a function of context and context transition. The congruence effect was larger for the high-than for the low- probability context when the context repeated (asterisk indicates p<0.001), while the reverse was true when the context switched (asterisk indicates p<0.001).

Figure 3. Group-averaged global field power waveforms from the visual temporal discrimination task are displayed for the L_{CONG} , L_{INCONG} , S_{CONG} , and S_{INCONG} conditions as a function of time. The yellow area plot displays the time period when a significant 2-way interaction was observed (228-257 ms). The inset displays an enlarged view of the 200-300 ms post-stimulus period.

Figure 4. The results of statistical analyses of distributed source estimations from the visual

temporal discrimination task are displayed. **a**. The 2x2 interaction yielded significant clusters (p<0.05; kE>17 contiguous nodes) centred within the left middle occipital gyrus, the right parahippocampal gyrus, the right precuneus, and the right inferior frontal gyrus. **b**. Follow-up planned contrasts for the large-size congruence-effect revealed significant clusters centred within the left medial frontal gyrus, the left superior temporal cortex, and the precuneus bilaterally. All clusters were more strongly active in response to incongruent than congruent trials. **c**. Follow-up planned contrasts for the small-size congruence-effect revealed significant clusters centred within the left parietal cortices with stronger responses to congruence than incongruent pairings.

Figure 5. Group-averaged global field power waveforms from the oddball task are displayed for the AV_{cong} , AV_{incong} , and A+V conditions as a function of time. The red area plot displays the time periods when a significant 1-way interaction was observed (130-145 and 249-800 ms; truncated in the figure at 500 ms).

Figure 6. The results of statistical analyses of distributed source estimations over the 130-145 ms time period from the oddball task are displayed. a. The 1-way ANOVA yielded significant clusters (p<0.05; kE>17 contiguous nodes) centred within a distributed network of areas including the calcarine sulcus bilaterally, the left parieto-occipital cortex and left parietal cortices, the orbitofrontal cortex bilaterally and the right lateral occipital cortices. b. Follow-up planned contrasts between AV_{cong} and A+V revealed super-additive responses within the calcarine sulcus bilaterally, the left parieto-occipital cortex and left parietal cortices, and sub-additive responses within the orbitofrontal cortex bilaterally. c. A similar pattern of effects was observed between AV_{incong} and A+V, with the addition of superadditive responses within the right lateral occipital cortices. d. The contrast between AV_{cong} and AV_{incong} revealed stronger responses to the AV_{cong} condition within the calcarine sulcus

bilaterally and stronger responses to the AV_{incong} condition within the right lateral occipital cortex, the right parietal cortex and the orbitofrontal cortex (bilaterally).

References

- Altieri, N., Stevenson, R.A., Wallace, M.T. and Wenger, M. J. (2015). Learning to associate auditory and visual stimuli: Behavioral and neural mechanisms. *Brain Topogr*, 28(3). 479-493. doi: 10.1007/s10548-013-0333-7.
- Appelbaum, L.G., Smith, D.V., Boehler, C.N., Chen, W.D., and Woldorff, M.G. (2011). Rapid modulation of sensory processing induced by stimulus conflict. *J Cogn Neurosci 23(9)*, 2620-2628. doi: 10.1162/jocn.2010.21575
- Auksztulewicz, R. and Friston, K. (2015). Attentional enhancement of auditory mismatch responses: A DCM/MEG Study. *Cereb Cortex* 1-11. doi: 10.1093/cercor/bhu323
- Baier, B., Kleinschmidt, A., and Müller, N. G. (2006). Cross-modal processing in early visual and auditory cortices depends on expected statistical relationship of multisensory information. *J Neurosci*, 26(47), 12260-12265. doi: 10.1523/JNEUROSCI.1457-06.2006
- Baker, C.I., Olson, C.R., and Behrmann, M. (2004). Role of attention and perceptual grouping in visual statistical learning. *Psyc Sci*, *15*(7), 460-466. doi: 10.1111/j.0956-7976.2004.00702.x
- Barakat, B.K., Seitz, A.R., Shams, L. (2013). The effect of statistical learning on internal stimulus representations: Predictable items are enhanced even when not predicted. *Cognition*, *129*, 205–211. doi:10.1016/j.cognition.2013.07.003
- Barenholtz, E., Lewkowicz, D.J., Davidson, M., Mavica, L. (2014). Categorical congruence facilitates multisensory associative learning. *Psyc Bull Rev, 21*, 1346–1352. doi: 10.3758/s13423-014-0612-7
- Beierholm, U.R., Quartz, S.R., Shams, L. (2009). Bayesian priors are encoded independently from likelihoods in human multisensory perception. *J Vision*, 9, 23. doi: 10.1167/9.5.23

- Belin, P., Zilbovicius, M., Crozier, S., Thivard, L., Fontaine, A., Masure, M.C. and Samson, Y. (1998) Lateralization of speech and auditory temporal processing. *J Cogn Neurosci*, 10, 536–540. doi: 10.1162/089892998562834
- Bertelson, P., and de Gelder, B. (2004). The psychology of multimodal perception. In C. Spence and J. Driver (Eds.), Crossmodal space and crossmodal attention (pp. 141-177). Oxford: Oxford University Press.
- Brunet, D., Murray, M.M. and Michel, C.M. (2011). Spatiotemporal analysis of multichannel EEG: CARTOOL. *Comput Intell Neurosci 2011*, 813-870. doi: 10.1155/2011/813870
- Calvert, G.A., Campbell, R., and Brammer, M.J. (2000). Evidence from functional magnetic resonance imaging of crossmodal binding in the human heteromodal cortex. *Curr Biol* 10, 649–657. doi: 10.1016/S0960-9822(00)00513-3
- Cappe, C., Thut, G., Romei, V. and Murray, M.M. (2010). Auditory-visual multisensory interactions in humans: timing, topography, directionality, and sources. *J Neurosci* 30(38), 12572–12580. doi: 10.1523/JNEUROSCI.1099-10.2010
- Cappe, C., Thelen, A., Romei, V., Thut, G. and Murray, M.M. (2012). Looming signals reveal synergistic principle of multisensory integration. *J Neurosci 32*, 1171–1182. doi: 10.1523/jneurosci.5517-11.2012
- Chandrasekaran, C., Trubanova, A., Stillittano, S., Caplier, A., Ghazanfar, A.A. (2009). The natural statistics of audiovisual speech. *PLoS Comput Biol*, 5, e1000436. doi: 10.1371/journal.pcbi.1000436
- Corballis, P.M. and Gratton, G. (2003). Independent control of processing strategies for different locations in the visual field. *Biol Psychol 64*, 191-209. doi: 10.1016/S0301-0511(03)00109-1
- Courville, A.C., Daw, N.D., and Touretzky, D.S. (2006). Bayesian theories of conditioning in a

- changing world. *Trends Cogn Sci*, 10(7), 294-300. doi:10.1016/j.tics.2006.05.004
- Crump, M.J., Gong, Z. and Milliken, B. (2006). The context-specific proportion congruent stroop effect: location as a contextual cue. *Psychon Bull Rev, 13,* 316-321. doi:10.3758/BF03193850
- Crump, M. J. C., Vaquero, J. M. M., and Milliken, B. (2008). Context- specific learning and control: The role of awareness, task relevance, and relative salience. *Conscious Cogn*, 17, 22–36. doi:10.1016/j.concog.2007.01.004
- De Lucia, M., Clarke, S. and Murray, M.M., (2010a). A temporal hierarchy for conspecific vocalization discrimination in humans. *J Neurosci, 30 (33)*, 11210–11221. doi: 10.1523/JNEUROSCI.2239-10.2010.
- De Lucia, M., Michel, C.M. and Murray, M.M., (2010b). Comparing ICA-based and single-trial topographic ERP analyses. *Brain Topogr 23 (2)*, 119–127. doi: 10.1007/s10548-010-0145-y
- De Meo, R., Murray, M.M., Clarke, S. and Matusz, P.J. (2015). Top-down control and early multisensory processes: Chicken vs. egg. *Front Integr Neurosci*, *9*, 17.
- Dhamala, M., Assisi, C.G., Jirsa, V.K., Steinberg, F.L. and Kelso, J.A.S. (2007). Multisensory intergation for timing engages different brain networks. *NeuroImage*, *34*, 764–773. doi: 10-1016/j.neuroimage.2006.07.044
- Doehrmann, O., Weigelt, S., Altmann, C.F., Kaiser, J., and Naumer, M.J. (2010). Audiovisual functional magnetic resonance imaging adaptation reveals multisensory integration effects in object-related sensory cortices. *J Neurosci* 30(9), 3370-3379. doi: 10.1523/JNEUROSCI.5074-09.2010.
- Driver, J. (1996). Enhancement of selective listening by illusory mislocation of speech sounds due to lip-reading. *Nature 381 (6577)*, 66-68. doi: 10.1121/1.1907309.

- Fairhall, S.L., and Macaluso, E. (2009). Spatial attention can modulate audiovisual integration at multiple cortical and subcortical sites. *Eur J Neurosci, 29,* 1247-1257. doi:10.1111/j.1460-9568.2009.06688.x
- Fort, A., Delpuech, C., Pernier, J. and Giard M.H. (2002). Dynamics of cortico-subcortical cross-modal operations involved in audio-visual object detection in humans. *Cereb Cortex*, *12* (*10*), 1031–1039. doi: 10.1093/cercor/12.10.1031
- Frost, R., Armstrong, B. C., Siegelman, N., and Christiansen, M. H. (2015). Domain generality versus modality specificity: the paradox of statistical learning. *Trends Cogn Sci*, *19*(3), 117-125. doi:10.1016/j.tics.2014.12.010
- Froyen,. D., van Atteveldt, N., Bonte, M., Blomert, L. (2009). Crossmodal enhancement of the MMN to speech-sounds indicates early and automatic integration of letters and speech-sounds. *Neurosci Lett, 430*, 23-28.
- Goujon, A., and Fagot, J. (2013). Learning of spatial statistics in nonhuman primates: contextual cueing in baboons (Papio papio). *Beh Brain Res*, 247, 101-109. doi:10.1016/j.bbr.2013.03.004
- Grahn, J.A., and Rowe, J.B. (2009). Feeling the beat: Premotor and striatal interactions in musicians and non-musicians during beat perception. *J Neurosci*, 29(23), 7540-7548. doi: 10.1523/JNEUROSCI.2018-08.2009
- Grave de Peralta Menendez, R., Gonzalez Andino, S., Lantz, G., Michel, C.M., Landis, T. (2001). Noninvasive localization of electromagnetic epileptic activity. I. Method descriptions and simulations. Brain Topogr. 14 (2), 131–137. doi: 10.1023/A:1012944913650
- Grave de Peralta, R. and Gonzalez Andino S. (2002). Comparison of algorithms for the localization of focal sources: Evaluation with simulated data and analysis of

- experimental data. Int J Bioelectromagn, 4 (1).
- Grave de Peralta Menendez, R., Murray, M.M., Michel, C.M., Martuzzi, R., Gonzalez Andino, S.L., 2004. Electrical neuroimaging based on biophysical constraints. *Neuroimage*, *21* (2), 527–539. doi: 10.1016/j.neuroimage.2003.09.051
- Guthrie, D. and Buchwald, J.S. (1991). Significance testing of difference potentials.

 Psychophysiology 28 (2), 240–244. doi: 10.1111/j.1469-8986.1991.tb00417.x
- Heinemann, A., Kunde, W., and Kiesel, A. (2009). Context-specific prime-congruency effects:

 On the role of conscious stimulus representations for cognitive control. *Conscious Cogn 18*, 966–976. doi: 10.1016/j.concog.2009.08.009
- Henson, R., Shallice, T., and Dolan, R. (2000). Neuroimaging evidence for dissociable form of repetition priming. *Science*, *287*, 1269-1272. doi: 10.1126/science.287.5456.1269
- Jiménez, L., and Méndez, C. (1999). Which attention is needed for implicit sequence learning? *J Exp Psychol Learn Mem*, *25*, 236–259. doi:10.1037/0278-7393.25.1.236
- King, J.A., Korb, F.M., Egner, T. (2012). Priming of control: implicit contextual cuing of top-down attentional set. *J Neurosci 32(24)*, 8192-8200. doi: 10.1523/JNEUROSCI.0934-12.2012
- Koenig, T. and Melie-Garcia, L. (2010). A method to determine the presence of averaged event-related fields using randomization tests. *Brain Topogr 23 (3)*, 233–242. doi: 10.1007/s10548-010-0142-1
- Koenig, T., Stein, M., Grieder, M. and Kottlow, M. (2014). A tutorial on data driven methods for statiscally assesing ERP topographies. *Brain Topogr*, *27*, 72-83. doi: 10.1007/s10548-013-0310-1
- Kok, P., Rahnev, D., Jehee, J.F.M., Lau, H.C and de Lange, F. P (2012). Attention reverses the effect of prediction in silencing sensory signals. *Cereb Cortex*, *22*, 2197-2206. doi:

10.1093/cercor/bhr310

- Larsson, J., & Smith, A.T. (2012). fMRI repetition suppression: neuronal adaptation or stimulus expectation? *Cereb Cortex*, *22*, 567-576. doi: 10.1093/cercor/bhr119
- Lehmann, D. and Skrandies, W. (1980). Reference-free identification of components of checkerboard evoked multichannel potential fields. *Electroen Clin Neuro, 48,* 609–621. doi: 10.1016/0013-4694(80)90419-8
- Macaluso, E., George, N., Dolan, R., Spence, C. and Driver, J. (2004). Spatial and temporal factors during processing of audiovisual speech: a PET Study. *Neuroimage*, *21(2)*, 725-732.
- Marchant, J. L., Ruff, C. C., and Driver, J. (2012). Audiovisual synchrony enhances BOLD responses in a brain network including multisensory STS while also enhancing target-detection performance for both modalities. *Hum Brain Map*, 33(5), 1212-1224. doi: 10.1002/hbm.21278
- Matusz, P.J., Retsa, C., and Murray, M.M. (in reviews). Cross-modal activation of visual cortex: Task-irrelevant yet not automatic.
- Matusz, P.J., Broadbent, H., Ferrari, J., Forrest, B., Merkley, R., Scerif, G. (2015a). Multi-modal distraction: Insights from children's limited attention. *Cognition*, *136*, 156-165. doi:10.1016/j.cognition.2014.11.031
- Matusz, P.J., Thelen, A., Amrein, S., Geiser, E., Anken, J., Murray, M.M. (2015b). The role of auditory cortices in the retrieval of single-trial auditory-visual object memories. *Eur J Neurosci*, *41*, 699-708. doi: 10.1111/ejn.12804.
- Matusz, P.J. and Eimer, M. (2013). Top-down control of audiovisual search by bimodal search templates. *Psychophysiology, 50,* 996-1009. doi: 10.1111/psyp.12086
- Matusz, P.J. and Eimer, M. (2011). Multisensory enhancement of visual attentional capture

- in visual search. *Psychon Bull Rev, 18*(5), 904-909. doi: 10.3758/s13423-011-0131-8.
- Michel, C.M., Murray, M.M., Lantz, G., Gonzalez, S., Spinelli, L. and Grave de Peralta, R. (2004). EEG source imaging. *Clin Neurophysiol*, *115*, 2195–2222. doi: 10.1016/j.clinph.2004.06.001
- Michel, C.M., Koenig, T., Brandeis, D., Gianotti. L.R. and Wackermann, J. (2009). *Electrical neuroimaging*. Cambridge, UK: Cambridge UP.
- Michel, C. M. and Murray, M. M. (2012). Towards the utilization of EEG as a brain imaging tool. *Neuroimage 61*, 371–385 doi 10.1016/j.neuroimage.2011.12.039
- Molholm, S., Ritter, W., Murray, M.M., Javitt, D.C., Schroeder, C.E and Foxe J.J. (2002)

 Multisensory auditory-visual interactions during early sensory processing in humans:

 a high-density electrical mapping study. *Cogn Brain Res* 14(1), 115-128. doi: 10.1016/S0926-6410(02)00066-6
- Müller, N.G., Strumpf, H., Scholz, M., Baier, M., & Melloni, L. (2013). Repetition Suppression versus Enhancement It's Quantity That Matters. *Cereb Cortex, 23,* 315-322. doi: 10.1093/cercor/bhs009
- Murray, M.M., Brunet, D. and Michel, C.M. (2008) Topographic ERP analyses: a step-by-step tutorial review. *Brain Topogr 20*, 249 –264. doi 10.1007/s10548-008-0054-5
- Murray, M. M., De Santis, L., Thut, G., and Wylie, G. R. (2009). The costs of crossing paths and switching tasks between audition and vision. *Brain Cogn*, 69(1), 47-55.
- Murray, M.M. and Wallace, M.T. (2012). *The Neural Basis of Multisensory Processes*. Boca Raton, FL: CRC Press.
- Murray, M. M., Thelen, A., Thut, G., Romei, V., Martuzzi, R., & Matusz, P. J. (2015). The multisensory function of the human primary visual cortex. *Neuropsychologia*. doi:10.1016/j.neuropsychologia.2015.08.011Perrin, F., Pernier, J., Bertrand, O. and

- Echallier, J.F. (1989). Spherical splines for scalp potential and current density mapping. *Electroen clin Neuro 72(2),* 184-187. doi:10.1016/0013-4694(89)90180-6
- Powers, A.R., Hillock, A.R., and Wallace, M.T. (2009). Perceptual training narrows the temporal window of multisensory binding. *J. Neurosci*, 29(39), 12265–12274. doi:10.1523/JNEUROSCI.3501-09.2009
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clin Neurophys*, *118*(10), 2128-2148.
- Pourtois, G., Delplanque, S., Michel, C. and Vuilleumier, P. (2008). Beyond conventional event-related brain potential (ERP): Exploring the time-course of visual emotion processing using topographic and principal component analyses. *Brain Topogr 20 (4)*, 265–277. doi: 10.1007/s10548-008-0053-6
- Recasens, M., Leung, S., Grimm, S., Nowak, R., & Escera, C. (2014). Repetition suppression and repetition enhancement underlie auditory memory-trace formation in the human brain: an MEG study. *Neuroimage*, doi: 10.1016/j.neuroimage.2014.12.031.
- Rowland, B.A., and Stein, B.E. (2014). A model of the temporal dynamics of multisensory enhancement. *Neurosci Biobeh Rev, 41*, 78–84. doi: 10.1016/j.neubiorev.2013.12.003
- Saffran, J. R., Aslin, R. N., and Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, *274*(5294), 1926-1928. doi: 10.1126/science.274.5294.1926
- Sanabria, D., Soto-Faraco, S. and Spence, C. (2007). Spatial attention and audiovisual interactions in apparent motion. *J Exp Psychol Hum Percept Performan, 33 (4),* 927-937. doi:10.1037/0096-1523.33.4.927
- Sanabria, D., Spence, C. and Soto-Faraco, S. (2007). Perceptual and decisional contributions to audiovisual interactions in the perception of apparent motion: A signal detection study. *Cognition*, *102*, 299-310. doi: 10.1016/j.cognition.2006.01.003

- Sandhu, R., and Dyson, B. J. (2013). Modality and task switching interactions using bi-modal and bivalent stimuli. *Brain Cogn*, 82(1), 90-99. doi:10.1016/j.bandc.2013.02.011
- Sarko, D. K., Nidiffer, A. R., Powers, I. I. I., A. R., Ghose, D., and Wallace, M. T. (2012). In: *The Neural Basis of Multisensory Processes*, ed M. M. Murray and M. T. Wallace (Boca Raton, FL: CRC Press), 191–215.
- Sarmiento, B.R., Shore, D., Milliken, B., and Sanabria, D. (2012). Audiovisual interactions depend on context of congruency. *Atten Percept Psychophys*, *74*, 563-574. doi: 10.3758/s13414-011-0249-9
- Segaert, K., Weber, K., de Lange, F.P., Petersson, K. M., and Hagoort P. (2013). The suppression of repetition enhancement: A review of fMRI studies. *Neuropsychologia*, 51, 59–66 10.1016/j.neuropsychologia.2012.11.006
- Spence, C., and Driver, J. (Eds.). (2004). *Crossmodal space and crossmodal attention*. Oxford, UK: Oxford UP.
- Stein, B.E. (2012). The New Handbook of Multisensory Processing. MIT Press: Cambridge, MA.
- Stevenson, R.A., Ghose, D., Fister, J.K., Sarko, D.K., Altieri, N.A., Nidiffer, A.R., Kurela, L.R., Siemann, J.K., James, T.W., and Wallace, M.T. (2014). Identifying and quantifying multisensory integration: A tutorial review. *Brain Topogr, 27(6),* 707-730. doi: 10.1007/s10548-014-0365-7
- Summerfield, C. and Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends*Cogn Sci, 13(9), 403-409. doi: 10.1016/j.tics.2009.06.003
- Talairach, J., and Tournoux, P. (1988). Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: an approach to cerebral imaging. G. Thieme Medical Publishers, Stuttgart; New York.

- Talsma, D. and Woldorff, M.G. (2005). Selective attention and multisensory integration:multiple phases of effects on the evoked brain activity. *J Cogn Neurosci* 17 (7), 1098-1114. doi:10.1162/0898929054475172
- Talsma, D., Doty, T.J., Woldorff, M.G. (2007). Selective attention and audiovisual integration: is attending to both modalities a prerequisite for early integration? *Cereb Cortex, 17,* 679-690. doi:10.1093/cercor/bhk016
- Talsma, D., Senkowski, D., Soto-Faraco, S. and Woldorff M.G. (2010). The multifaceted interplay between attention and multisensory integration. *Trends Cogn Sci* 14, 400-410. doi:10.1016/j.tics.2010.06.008
- Ten Oever, S., Romei, V., van Atteveldt, N., Soto-Faraco, S., Murray, M.M., and Matusz, P.J. (in review). Control mechanisms put COGs (Context-Object-Goals) into multisensory processing.
- Thelen, A., Cappe, C., and Murray, M. M. (2012). Electrical neuroimaging of memory discrimination based on single-trial multisensory learning. *NeuroImage 62*, 1478–1488. doi: 10.1016/j.neuroimage.2012.05.027
- Thelen, A., Matusz, P.J., and Murray, M.M. (2014). Multisensory context portends object memory. *Curr Biol*, *15*, R734-735. doi: 10.1016/j.cub.2014.06.040.
- Treisman, A. (1996). The binding problem. *Curr Opin Neurobiol*, *6*, 171-l 78. doi: 10.1016/S0959-4388(96)80070-5
- Treisman, A. (2006). How the deployment of attention determines what we see. *Vis Cogn, 14* (4-8), 411-443. doi: 10.1080/13506280500195250
- Tucker, D.M., Liotti, M., Potts, G.F., Russell, G.S., and Posner, M.I. (1994). Mapping the working brain: Spatiotemporal analysis of brain electrical fields. *Hum Brain Mapp*, 1, 134-152. doi: 10.1002/hbm.460010206

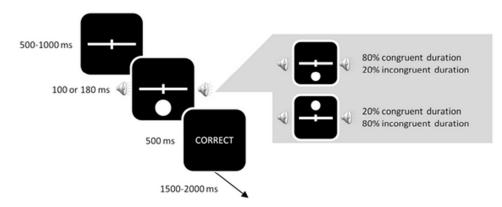
- Turk-Browne, N.B., Yi, D.J., Leber, A.B., and Chun, M.M. (2007). Visual quality determines the direction of neural repetition effects. *Cereb Cortex*, *17*, 425-433. doi: 10.1093/cercor/bhj159
- van Atteveldt, N., Murray, M.M., Thut, G., and Schroeder, C.E. (2014). Multisensory integration: flexible use of general operations. *Neuron*, *81*, 1240-1253. doi: 10.1016/j.neuron.2014.02.044
- Von Kriegstein, K., and Giraud, A.L. (2006). Implicit multisensory associations influence voice recognition. *PLoS Biol*, *4*(10), e326.
- Vossel, S., Mathys, C., Daunizeau, J., Bauer, M., Driver, J., Friston, K.J., Stephan, K.E. (2014).

 Spatial attention, precision, and Bayesian inference: A study of saccadic response speed. *Cereb Cortex*, 24(6), 1436-1450. doi: 10.1093/cercor/bhs418.
- Wylie, G., and Allport, A. (2000). Task switching and the measurement of "switch costs". *Psyc Res*, *63*(3-4), 212-233. doi: 10.1007/s004269900003
- Wylie, G.R., Murray, M.M., Javitt, D.C., and Foxe, J.J. (2009). Distinct neurophysiological mechanisms mediate mixing costs and switch costs *J Cogn Neurosci*, *21*(1), 105-118.
- Yuval-Greenberg, S., and Deouell, L. Y. (2009). The dog's meow: asymmetrical interaction in cross-modal object recognition. *Exp Brain Res, 193*(4), 603-14. doi: 10.1007/s00221-008-1664-6.

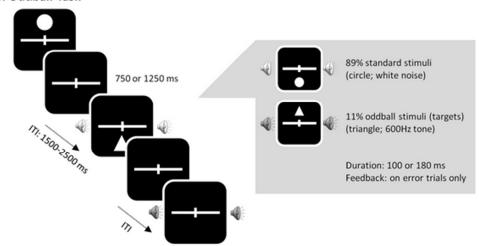
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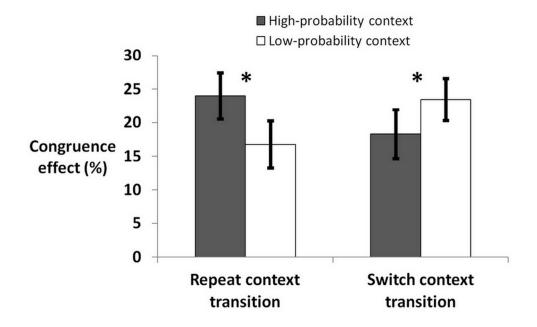
a. Visual Temporal Discrimination Task



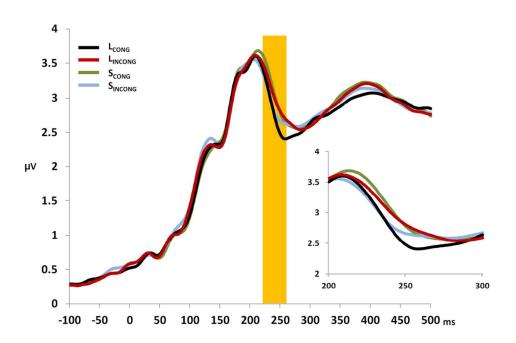
b. Oddball Task



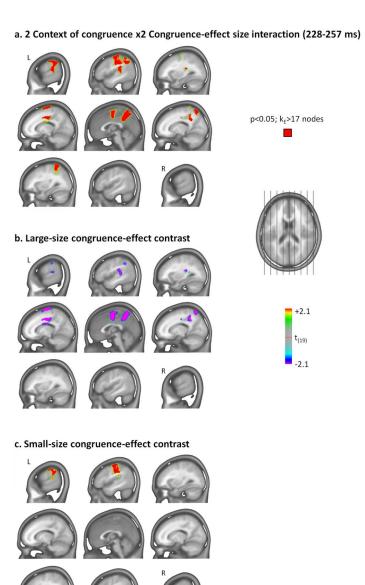
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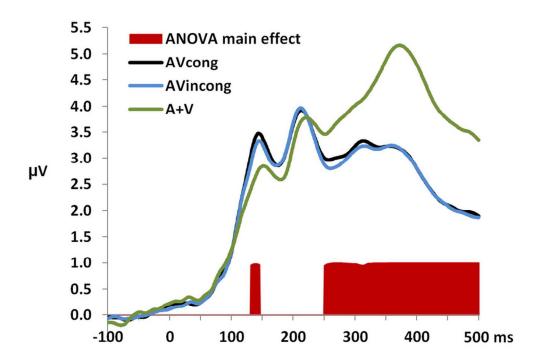
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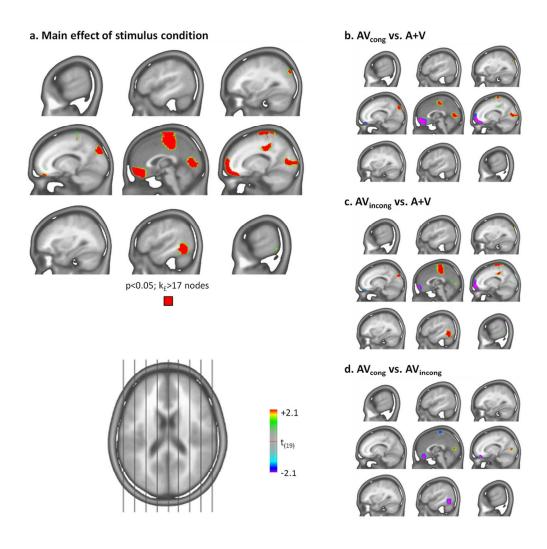
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