Supramodal neural information supports stimulus-driven attention across cortical levels

Maria Niedernhuber [1 *], Francesca Fardo [2, 3], Micah Allen [3, 4], Tristan Bekinschtein [1]

1 Department of Psychology, University of Cambridge, Cambridge, UK
2 Danish Pain Research Center, Department of Clinical Medicine, Aarhus University and Aarhus University Hospital, Aarhus, Denmark;
3 Center of Functionally Integrative Neuroscience, Department of Clinical Medicine, Aarhus University and Aarhus University Hospital, Aarhus, Denmark
4 Department of Psychiatry, Herchel Smith Buidling for Brain & Mind Sciences, Cambridge, UK

* Corresponding author: mn473@cam.ac.uk

Abstract

Sensory systems utilise stimulus-driven attention to survey the environment for significant features. The question arises: are the cortical networks that influence stimulus-driven attention supramodal or specific to each sensory modality? Here we employed a hierarchical target detection task (n=30), examining cortical responses linked to the detection of salient targets in the somatosensory and auditory modality. In a temporal decoding analysis, we reveal a transient early supramodal process activated by target detection. We also demonstrate that both common and unique modulations of salience-related cortical responses to somatosensory and auditory targets involve modality-specific and frontal regions using Parametric Empirical Bayes. Specifically, we found that the inferior frontal gyri share information across both sensory modalities, while recurrent information transfer between ipsilateral inferior frontal gyri and associative regions was modality-specific. Finally, we showed both supramodal and modality-specific attentional modulations of effective connectivity linking regions across hierarchical levels in the cortex. Our results provide evidence for an attention network which integrates information across inferior frontal cortices to detect salient targets irrespective of their specific sensory modality. Beyond the notion of a supramodal attention system, our findings support the role of modality-specific cortices in processing inputs from other sensory modalities, highlighting that attention can bias these processes at multiple stages of the cortical hierarchy.

Author summary

A key task of the brain is to deploy attention to detect important sensory events in its environment. How does the brain coordinate information from different senses when a sensory event pops out from the environment? Here we designed a nested oddball paradigm in which expectations about somatosensory and auditory stimuli are violated while high-density EEG is recorded. We also varied the extent to which the odd stimulus pops out from its sensory environment. Using temporal decoding, we reveal a supramodal short-lived cortical process when salient targets are detected. In an effective

connectivity analysis, we also show that the detection of salient targets relies on a common interhemispheric inhibition between inferior frontal gyri. Beyond that, there are supramodal and modality-specific changes in effective connectivity linking associative and modality-specific regions in the cortex. Our results support a rapid and short-lived supramodal process in a distributed saliency detection system extending across the cortical hierarchy.

Introduction

Attention is a fundamental cognitive function used to select important sensory events for prioritised processing [1]. To monitor the sensory environment for such events, each perceptual modality implements an attention-controlled system for sensory target detection spanning from primary modality-specific to frontal supramodal regions [2–5]. A function of sensory target detection systems is to recognize salient sensory events with specific physical features which cause the stimulus to perceptually "pop out" of the background, grabbing attention in a bottom-up process [6]. To which extent is the deployment of stimulus-driven attention mediated by supramodal or unimodal cortical networks? The classical view of attention proposes that a supramodal attention system controls the detection of sensory targets. A ventral frontoparietal attention network deploys exogenous stimulus-driven attention to salient sensory events from the bottom up [7]. Conversely, a dorsal attention network binds endogenous goal-driven attention to sensory events based on top-down expectations [8,9].

Both systems are co-activated when relevant sensory targets are detected regardless of which sensory modality is stimulated [8]. Supporting the view of a supramodal system for the detection of salient targets, a series of fMRI studies identified the inferior frontal gyrus and temporal parietal junction as supramodal sites for stimulus-driven attentional control in visual, tactile and auditory change processing [9,10]. Others highlight a role for the right inferior frontal gyrus as salience detector which controls sensory information in modality-specific pathways [7,11,12]. In line with this observation, the inferior frontal gyrus has been involved in the detection of irregular sensory targets, positioned on top of a hierarchy of modality-specific cortices in different sensory modalities [13–17].

We set out to characterise commonalities and differences in the cortical dynamics and mechanisms of saliency-related target detection processes in the somatosensory and auditory modalities using Electroencephalography (EEG). Based on the previous findings outlined above, we reasoned that the detection of salient sensory targets relies on a mid-latency supramodal process driven by the inferior frontal cortex, whereas differences would emerge in modality-specific pathways. To test this hypothesis, we developed somatosensory and auditory versions of a hierarchical oddball task known as the local-global paradigm [18], where either somatosensory or auditory stimuli were presented to the left or the right side [5]. In this task, expectations about sensory inputs are selectively violated at two nested levels of hierarchy [18]: At a local level, stimulus sequences consist either of identical stimuli or occasionally end with a deviant input which creates a local sensory expectation violation in a temporally confined stimulus context. When sequences with a local deviation are compared to monotonous stimulus sequences, a "local difference" wave similar to the Mismatch Negativity (MMN) can be revealed [19,20]. In turn, at a global level, the rapid succession of monotonous stimulus sequences forms a repetitive sensory pattern which is occasionally interrupted by a deviant stimulus group. When globally frequent and rare trials are compared, a P3b-like positive distributed amplitude difference in a late time window from ˜250 ms emerges [21]. Crucially, our paradigm introduces two types of sensory deviations at each hierarchical level: salient deviations in which only the laterality of the input is

manipulated, or regular deviations in which both the laterality and the stimulus type is varied.

In line with previous findings [3,22], we found that stimulus-driven attention enhances the amplitude of cortical responses to sensory expectation violations. Using a temporal decoding approach, we show that a short-lived supramodal process supports the serial propagation of activity from ~150 ms after a salient target is detected. To examine the mechanistic basis of this supramodal process, we modelled saliency-related connectivity changes in a network involving somatosensory, auditory and frontal regions using Dynamic Causal Modelling (DCM). We constructed a General Linear Model using Parametric Empirical Bayes (PEB) over connectivity parameters in both sensory modalities to identify commonalities and differences in connectivity changes due to stimulus saliency. Our results reveal supramodal effective connections between inferior frontal gyri as well as between modality-specific cortical areas. In line with our hypothesis, we identified a supramodal process for the detection of salient targets which manifests in shared cortical dynamics and frontal information flow. Although our finding substantiates the notion that supramodal attentional processing is a function of the frontal cortex [9], supramodality in connectivity changes due to saliency-related differences extended to early modality-specific sensory regions. We also found that the inferior frontal cortex inhibits feedback to the ipsilateral secondary sensory cortex in both hemispheres for both sensory modalities relative to the other. Our findings substantiate the view that the inferior frontal cortex is a supramodal salience detector which controls modality-specific pathways [8,9]. Beyond that, we demonstrate that supramodal mechanisms supporting the detection of salient targets are ubiquitous across the cortical hierarchy, and extend from frontal to early regions canonically thought to be modality-specific [23,24].

Materials and methods

Participants

30 individuals (15/15 female/male, aged 24.56 (+-4.52) mean+-STD) took part in the study. Only participants without hearing impairment and history of neurological or psychiatric disease were included in the study. Participants freely consented to participating in study in written and were paid £10 per hour for a total duration of 3-3.5 h. The study was approved by the Cambridge Psychology Ethics Committee (CPREC 2014.25).

Stimuli

The experimental design involved somatosensory and auditory stimuli (Figure 1). Somatosensory stimulation was applied with a custom-made device which applies mechanical pins to the fingertip with a Saia-Burgess 12.7mm stroke, 12v, 4W DC push-action solenoid with 0.3-0.6 N force, and no nominal delay after current onset) controlled by an Arduino Mega board. These stimuli were applied to the fingertip of either the left or the right hand. To design auditory expectation violations, we generated two auditory stimuli by mixing three sinusoidal signals of 500, 1000, and 2000 Hz for stimulus type A or 350, 700, and 1400 Hz for stimulus type B in Matlab R2016 [3]. These were audibly presented to either the left or the right ear using EARTONE 3A insert earphones. Trials consisted of five stimuli which were presented with a stimulus onset interval of 150 ms and a stimulus duration of 50 ms. In locally deviant trials, four identical stimuli were always either followed by a deviant stimulus. Locally standard trials consisted of five identical stimuli. Somatosensory standard trials consisted of five

ipsilateral pressure stimuli delivered to the index finger of either hand. Deviant trials were composed of four pressure stimuli applied to one index finger and a deviant stimulus applied to either the index finger (regular locally deviant trials) or middle finger (salient locally deviant trials) of the opposite hand. Auditory locally standard trials consisted of five stimulus type A sounds presented to one ear. In locally deviant trials, four identical ipsilateral stimulus type A sounds could either be followed by a stimulus type A sound or stimulus type B sound to the opposite ear.

The experiment contained eight somatosensory and auditory blocks [25]. Blocks were composed of 158-160 trials in total and lasted ˜4.5 min. Inter-trial intervals were randomly sampled from a uniform distribution between 800 ms and 1000 ms in steps of 50 ms. Each block started with an uninterrupted sequence of 15 globally standard trials to establish which trial type would be frequent. 15-17 globally deviant trials of each type were embedded in a sequence of 112 global standard stimulus patterns. Globally deviant trials were equally likely to be preceded by either 2, 3, 4 or 5 globally standard trials. Participants listened to white noise when somatosensory stimulation was presented to mask any possible auditory cues from the tactile stimulation device. We introduced two block types which were presented twice in each sensory modality. In block type X, a stream of locally standard trials was occasionally interspersed with locally deviant trials. In block type Y, a sequence of regular locally deviant trials were interspersed with salient locally deviant trials and locally standard trials. For each participant, blocks were pseudorandomised so that no more than two consecutive blocks were presented in the same sensory modality. The experiment always started with somatosensory blocks type Y and X.

Participants were prompted to fill out a questionnaire about their handedness [26]. Throughout the main part of the experiment, they were seated comfortably with their eyes fixated on a black cross presented on a grey background. To rule out differences in the perception of tactile inputs, the tactile stimulation device was prompted to apply tactile input to each finger. The experiment was continued only when tactile stimuli delivered to the index and middle finger of each hand were perceived to be identical in intensity. Monaural sounds alternating between ears were played to offer the opportunity to adjust the default volume for auditory stimulus presentation to a comfortable level. During the experiment, participants were instructed to attend to the sequence of stimulus patterns as closely as possible. We aimed to ensure that participants' attention was bound to the global regularity underlying the stimulus sequences while simultaneously ruling out task-related confounds. Participants were prompted to either only attend to the global rule underlying the sensory inputs in equal numbers of blocks in each modality or to count any rare stimulus patterns occurring in the sequence of stimuli. After each of these blocks, they were asked to indicate how many uncommon stimulus patterns they counted. Participants were also given the opportunity for a break between blocks.

EEG preprocessing and cluster-based permutation of ERP time course series

We recorded 128-channel high density EEG data using a Net Amps 300 amplifier developed by Electrical Geodesics. Data were preprocessed in Matlab using the EEGLAB toolbox [27]. Following the removal of channels on the neck, cheeks and forehead which record primarily artefacts resulting from head muscle and eye movements, we retained 92 channels for further analysis. We excluded the first 15 trials per block, which constitute the habituation phase in which a global prediction about incoming stimuli is generated, from further analysis. EEG data were filtered between 0.5 and 30 Hz and epoched 200 ms before and 1300 ms after trial onset. Trial and

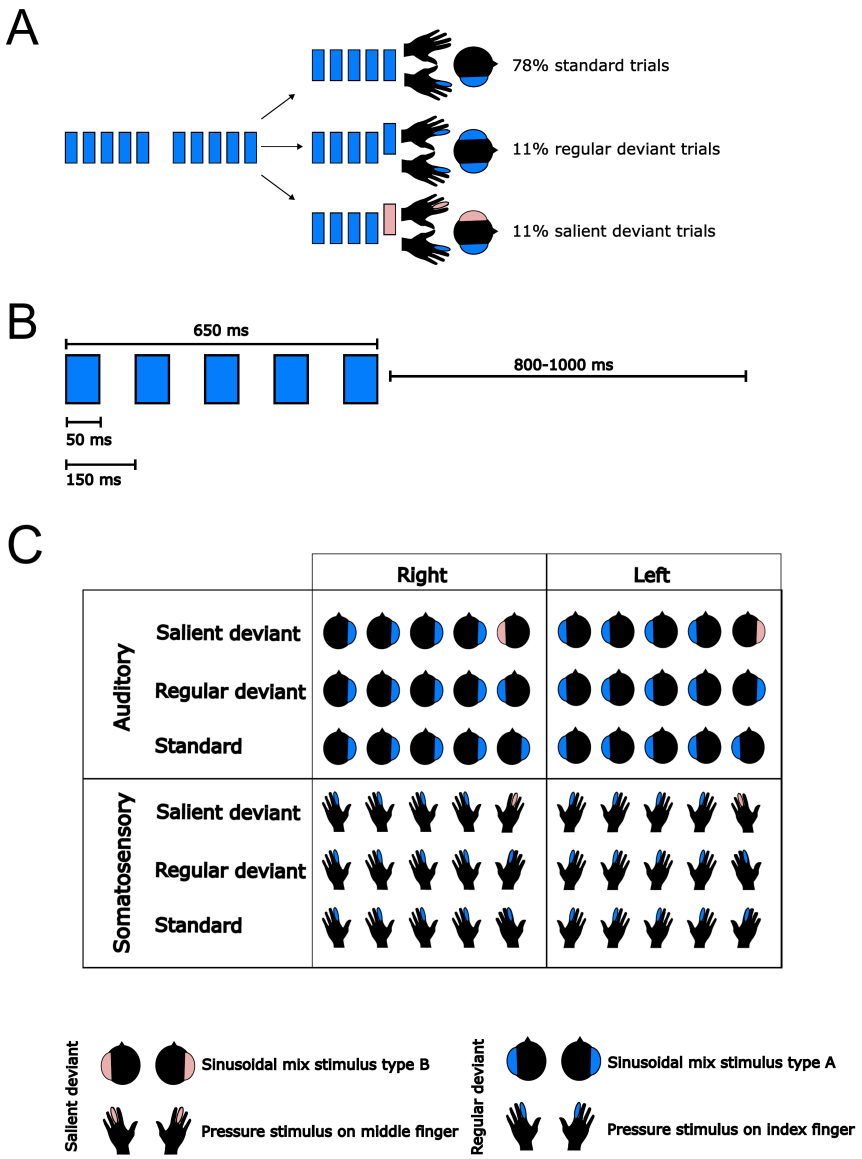

Fig 1. Experimental design. Stimulus sequences were presented in blocks of somatosensory or auditory stimulation. In a block, a stream of standard trials was occasionally interrupted by regular or salient deviant trials (A). Each trial consisted of five stimuli with a duration of 50 ms and an interstimulus interval of 150 ms. Trials were separated by an intertrial interval of 800-1000 ms (B). We presented repetitive sequences of five stimuli which consist of four ipsilateral stimuli which could either be followed by a further ipsilateral stimulus (standard trials) or a contralateral stimulus (deviant trials). In the somatosensory condition, standard stimuli were applied to the index finger. The fifth stimulus was applied either to the index finger (regular deviant trials) or the contralateral middle finger (salient deviant trials). For the auditory condition, standard trials consisted of an ipsilateral sequence of standard auditory stimuli type A presented to a target ear. Deviant trials either ended on a contralateral stimulus type A (regular deviant trials) or B (salient deviant trials). Trials in two blocks started with standard stimuli on the left side, and in the remaining two blocks on the right (C).

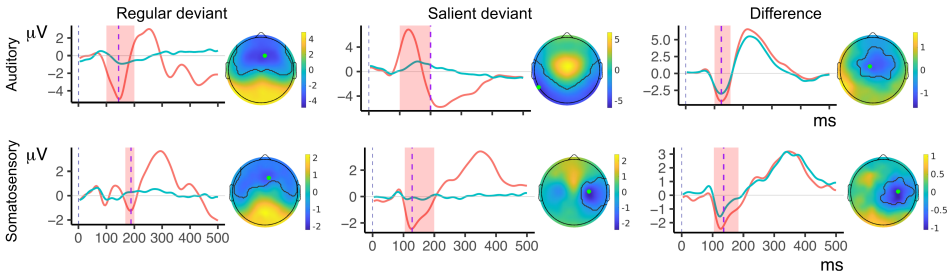

Fig 2. Cluster-based permutation test of ERP amplitude time series. Results from a cluster-based permutation test on ERP time courses reveal a difference between deviant and standard trials for the somatosensory and auditory regular and salient condition. A comparison between deviant-standard amplitude differences obtained from the salient and the regular condition showed a stronger ERP response to salient targets in both sensory modalities. For each comparison, the ERP time course plot is shown. 0 denotes the onset of the fifth stimulus in a trial. Time segments in which ERP time courses differ are highlighted in red. The time point at which the difference is maximal is specified in the figure title along with Monte Carlo summarised t-values and p-values. In the ERP voltage time course plot, this time point is marked with a red dashed line. Next to the time course plot, we show the topography corresponding to the maximal difference between conditions. On the topography plot, a green dot indicates the position of the electrode at which the maximal difference between conditions is obtained and clusters which differ from chance are delineated with a black line.

channel artefacts were rejected by visual inspection of all channels. Channels which did not record activity were excluded from further analysis and interpolated at a later stage. Artefacts originating from eye or muscle movements were visually identified and removed using independent component analysis [27]. Following the interpolation of missing channels, data were re-referenced to the average and baseline-corrected relative to a 100 ms interval before the presentation of the last stimulus in the five-stimulus trial sequence.

To demonstrate that sensory deviations elicited an ERP response in our paradigm, we examined whether locally deviant trials produce larger ERP voltage amplitudes than standard trials in each sensory modality and for each saliency level. We also tested whether salient targets triggered an enhanced response in comparison to regular targets regardless of sensory modality. For that, we obtained the amplitude difference between regular deviant and standard trials as well as salient deviant and standard trials following a baseline correction in a 100 ms time window before the onset of the last stimulus in a trial. To investigate differences between ERP voltage time courses for each condition pair, we ran a Monte Carlo cluster-based permutation test in Matlab 2017a using EEGLAB [27]. A time window of 100-200 ms typical for the MMN response to sensory deviations was chosen for the permutation test [28]. Trial numbers in both conditions were equalised by randomly removing trials in the condition with the highest trial number until equal trial numbers were achieved. We performed a baseline correction in a time window of 100 ms after onset of the last stimulus in a trial and applied the common average as a reference. Cluster permutation is a non-parametric test performed on spatiotemporal EEG data which controls for an inflation in false alarms arising from multiple comparisons of channel-time pair data points. To perform the analysis, cluster-level t-statistics were obtained using Monte Carlo partitioning with 3000 runs implemented in Fieldtrip [29]. In a Monte Carlo procedure, trial numbers from both conditions are equalised, then trials are pooled and randomly divided up in

two groups of the original size. We performed two-sided t-tests on time-channel pairs on the resulting datasets. Spatiotemporally adjacent t-values with $p < .05$ were summarised and the largest cluster-level summed t-value was retained. We determined the p-value defined as the proportion of maximal cluster-level summed t-values obtained through partitioning larger than the originally observed t-value. There is a difference between conditions if $p < .05$.

Temporal decoding

We employed temporal decoding (also known as temporal generalisation method) to assess whether salient deviations share more extensive cortical representations between sensory modalities than regular deviations. Temporal decoding is a machine learning method implemented in MNE Python used to characterise how cognitive operations unfold in time ([30], based on tutorials here: https://mne.tools/). To perform temporal decoding, classifiers are trained to discriminate deviant trials from standard trials at each time point. Unlike point-by-point machine learning procedures, the extent to which each classifier is capable of distinguishing both trial types is not only assessed using a subset of trials obtained at the time point from which training data was sampled, but on data samples from all time points in a trial. By harnessing the potential of temporal decoding to uncover neural representations across time, we can account for latency differences in the onset and duration of sensory evoked potentials in different sensory modalities. We used temporal decoding to reveal the temporal dynamics underlying each saliency level and per sensory modality, leading to four regular deviant trials vs standard trials and salient deviant trials vs standard trials in each the auditory and the somatosensory modality. Salient deviations were always locally and globally deviant across block types and therefore bind bottom-up and top-down attention. As a result, the salient response produces both a local and a global effect regardless of block type. To extract a regular response, we selected regular trials which were both locally and globally deviant from block type X. Standard trials used for this contrast were sampled from block type X and did not deviate either at a local or global level. To assess the cortical dynamics of responses within a sensory modality, we applied a 5-fold stratified cross-validation procedure to separate deviant trials from standard trials for each condition pair. To that end, linear support vector machines were trained to discriminate deviant from standard trials on 4/5 of trials by fitting a hyperplane to best separate the two categories, and tested on the remaining 1/5 of samples. For the crossmodal analysis, we tested whether classifiers trained to decode the somatosensory contrast might generalise to the auditory contrast (and vice versa) for each the regular and salient condition. In each comparison, a classifier was fitted for each time point in a time window of 600 ms after the onset of the last stimulus in a trial. Classification performance was evaluated using Area Under the Curve Receiver Operating Characteristics (AUC-ROC) which is a non-parametric criterion-free measure of separability. We tested whether each classifier would generalise to the remaining time points in a trial using the above training-testing procedure. This resulted in a training-testing generalisation matrix with AUR-ROC values representing decoding performance for each time point in a 600 ms time window after the odd stimulus in a trial. We ran a Monte Carlo cluster-based permutation test with 1024 random partitions which applied a one-tailed paired t-tests to assess whether adjacent AUC-ROC values differ from chance using $p<.05$ as a criterion for significance. Subsequently, we determined whether salient contrasts share more extensive cortical representations than regular contrasts. For that, we performed a cluster-based permutation test to investigate whether there are differences in the extent to which classifiers trained to distinguish salient and regular contrasts at 100, 200, 300, 400, 500 and 600 ms generalise over the complete time window [31]. We compared salient and

the regular contrasts using a cluster-based permutation comparison of AUC-ROC classification score series obtained from a classifier trained at a target time point and tested on all time points in a trial per participant.

Parametric Empirical Bayes

We used a DCM-PEB approach detailed in Zeidman et al. [32] to examine commonalities and differences in effective connectivity changes associated with the detection of salient targets between the somatosensory and auditory modality. For each sensory modality (auditory/somatosensory) and saliency level (regular/salient), we used DCM for ERPs to estimate effective connections elicited in a network recruiting primary and secondary somatosensory cortices (S1, S2), primary auditory cortices (A1), both superior temporal gyri (STG) and both inferior frontal gyri (IFG). DCM for ERPs is a validated, neurophysiologically grounded Bayesian source reconstruction method. DCM is used to describe causal interactions between cortical sources elicited by a cortical response [33]. A set of differential equations describe effective connectivity, which is the rate of change at which a neuronal population in a cortical source exerts influence over another, and the modulation of effective connectivity elicited by an experimental intervention [34,35]. Based on a framework for neural mass models developed by Jansen and Rit [36], DCM for ERP relies on a neural mass model which describes neuronal activity in three cortical layers: an excitatory pyramidal cell population in the granular layer, an inhibitory interneuron population in the supra-granular layer and a subpopulation of deep pyramidal cells in the infra-granular layer. Interactions between these neuronal subpopulations are described via extrinsic connections which describe information flow between sources traversing white matter and intrinsic connections which represent coupling within a cortical source. The theoretical framework underpinning DCM assumes a hierarchical organisation of cortical areas. Based on a proposal by Felleman and Van Essen [37], connections between sources are directional and can either be forward, backward or lateral. Earlier work characterising connections in the visual cortical hierarchy [38] frame pathways in the cortex as either ascending or forward (originating in a lower-ranked cortical area and terminating in a higher-order cortical area), descending or backward (originating in a higher-order cortical area and terminating in a lower-order area), or lateral connections between two cortical areas at the same hierarchical level. In addition, DCM is extended by a spatial forward model which translates cortical activity arising from depolarised pyramidal cells to responses obtained from EEG sensors which are described as an equivalent current dipole (ECD) model which is an electrophysiological model in which sources represent equivalent current dipoles. Taken together, this renders DCM a spatiotemporal generative model of context-related changes in effective connectivity between cortical sources.

There is convergent evidence that the cortical networks underpinning local effects in different sensory modalities include primary and secondary modality-specific cortices as well as the inferior frontal gyri. DCM studies modelling the auditory MMN consistently found a network spanning from bilateral primary auditory cortices to uni- or bilateral inferior frontal gyri via superior temporal gyri [13,15,22,39–41]. Similarly, effective connectivity underpinning the somatosensory MMN has been found to recruit a network including the primary and secondary somatosensory cortices and inferior frontal regions [14,17].

We used MNI coordinates provided in [42] as dipole locations for the primary auditory cortex, superior temporal gyrus and inferior frontal gyrus for the forward projection from source to sensor space. To identify sources for the primary and secondary somatosensory cortex, we performed an auxiliary source reconstruction on somatosensory locally deviant trials using Brainstorm [43] available for download under the GNU general public licence (http://neuroimage.usc.edu/brainstorm). Following the

pipeline outlined in the Brainstorm tutorials (https://neuroimage.usc.edu/brainstorm/Tutorials/SourceEstimation), we applied the symmetric Boundary Element Method available from the open-source software OpenMEEG to estimate a forward model using the cortex surface as a source space. We removed the DC offset and estimated the noise covariance using minimum norm estimators using data from baseline activity in a 100 ms time window before the onset of the first stimulus in a trial. In a further step, we used minimum norm estimation which constrains sources to be perpendicular to the cortex surface with a current density map to obtain an inverse solution. MNI coordinates for sources were obtained using visual inspection. A model was fitted to each deviant-standard contrast within 0-250 ms after onset of the last stimulus in a trial per participant. For each sensory modality and saliency level, we modelled changes in effective connectivity due to a deviant stimulus in a network with auditory, somatosensory and frontal sources. This resulted in 30 DCMs for each of the four conditions in our 2x2 design (saliency: regular/salient, sensory modality: somatosensory/auditory). Trials in each condition pair were equalised and no Hanning window was used. Having been furnished with a forward model, the model was inverted for each participant. Model inversion approximates the posterior probability of connectivity parameters by minimising a free-energy bound on the log-evidence [44] and serves to constrain interactions between nodes to cortical sources [33]. We established a good model fit by calculating the coefficient of determination for each inverted DCM with mean R2:0.010.01 for the auditory regular and salient contrast, mean R2:0.050.05 for the somatosensory regular contrast, mean R2:0.050.039 for the somatosensory salient contrast (where a coefficient of determination of 0 represents the best possible model fit and 1 the worst possible model fit). Plots of actual ERPs and ERPs predicted by DCM are presented in the supplementary Figure 5.

(The Bayesian Model Average of) PEBs can be described as a General Linear Model:

$$\theta^{(1)} = X\theta^{(2)} + \in^{(1)}$$

$\theta^{(1)}$ refers to the connection weights for each participant. $X\theta^{(2)}$ represent the estimated influence of each covariate on each connection entered into the model. A design matrix X describes the regressors which model the impact of each covariate on each connection. $\in^{(1)}$ adds an error term which models random effects variability between participants [32,45]. We assessed commonalities and differences in effective connectivity elicited by the detection or salient targets in the somatosensory and auditory modality using a PEB-of-PEBs approach. Following a pipeline detailed in Zeidman et al. [32,45], we identify the most likely modulation of connections by inverting a DCM including all plausible connections between auditory, somatosensory and frontal sources for each participant and for each contrast type (using spm_dcm_erp.m). We proceeded to construct a PEB over DCM parameters modelling commonalities and differences in effective connections between salient and regular targets (B-Matrix) for each sensory modality (using spm_dcm_peb.m). Each PEB included the group mean of each connectivity parameter and the effect of saliency on the group mean as regressors. This procedure outputs a somatosensory and an auditory PEB encoding the group mean and the effect of saliency for each connection. Finally, we examined commonalities and differences in effective connectivity between sensory modalities. For that, we constructed a PEB over somatosensory and auditory PEB parameters using the mean of all participants and the difference between groups as regressors. We performed Bayesian Model Reduction of posterior densities over PEB parameters to remove connections which do not contribute to the model evidence using a greedy search algorithm (using spm_dcm_peb_bmc.m). Having pruned redundant connections, we carried out Bayesian Model Averaging across the 256 models with the best fit identified by the search. The resulting PEB encodes parameters for the mean connectivity over participants, the main

effect of sensory modality and saliency as well as their interaction for each connection. We retained connections with a posterior probability of at least 95% which can be interpreted as strong evidence.

Results

Salient targets produce stronger cortical responses across sensory modalities

Our goal was to assess whether cortical networks governing the influence of stimulus-driven attention on target detection are supramodal and/or modality-specific. We test the theory that the frontoparietal cortex is crucial for the deployment of stimulus-driven attention when salient targets are detected [9]. To that end, we uncovered supramodal cortical dynamics specific to the detection of salient targets using Temporal Decoding. Using a DCM-PEB approach, we characterised commonalities and differences in saliency-related connectivity changes between sensory modalities in a network spanning somatosensory, auditory and frontal cortices.

In the first step shown in Figure 2, we identified cortical responses to salient and regular targets using cluster-based permutation tests of ERP voltage time courses in a time window between 100-200 ms. We established differences between deviant and standard trials in each the auditory regular (cluster t = -5832.2, $p < 0.001$, max. diff. at 144 ms), salient (cluster t = -5862.7, $p < 0.001$, max. diff at 200 ms), somatosensory regular (cluster t = -702.17, $p = 0.01$, max. diff at 188 ms) and salient condition (cluster t = -1646.5, $p < 0.001$, max. diff at 128 ms). In line with previous work [22], we observed that salient targets produce a stronger ERP response amplitude than regular targets in the auditory (cluster t = -849.42, $p = 0.004$, max. diff at 124 ms) and somatosensory modality (cluster t = -619.75, $p = 0.034$, max. diff at 136 ms).

Early transient supramodal cortical information supports salient targets

Building up on previous studies showing that sensory deviations elicit activity in supramodal brain areas [5,46,47], we investigated whether salient and regular targets lead to different supramodal dynamics in the cortex. Temporal decoding within and between sensory modalities revealed differences in the cortical processing of regular and salient deviations (Figure 3, A). In line with previous work [5,48], classifiers trained to distinguish regular deviant and standard trials generalised from 200 ms after oddball onset until the end of the trial. We observed this temporal generalisation pattern in both the auditory (mean AUC = 0.511 ± 0.01, max. AUC = 0.547 at 20 ms training time and 152 ms testing time, mean cluster t = 4.662 ± 1.415, $p < 0.05$) and somatosensory modality (mean AUC = 0.507 ± 0.012, max. AUC = 0.533 at 144 ms training time and 144 ms testing time, mean cluster t = 3.987 ± 1.286, $p < 0.05$). Corroborating past work [5], cross-decoding between sensory modalities revealed that this temporal generalisation pattern was shared between sensory modalities (auditory-to-somatosensory: mean AUC = 0.506 ± 0.011, max. AUC = 0.535 at 172 ms training time and 448 ms testing time, mean cluster t = 3.945 ± 1.189, $p < 0.05$; somatosensory-to-auditory: mean AUC = 0.508 ± 0.011, max. AUC = 0.539 at 116 ms training time and 240 ms testing time, mean cluster t = 3.994 ± 1.235, $p < 0.05$). In sum, our findings support the notion of a higher-order supramodal network for sensory target detection [5,9,49]. Auditory salient deviations could be decoded along the diagonal between ˜100-200 ms and only generalised across the remaining time window from ˜200 ms (mean AUC = 0.509 ± 0.028, max. AUC = 0.613 at 488 ms training time

and 132 ms testing time, mean cluster t = 8.092 ± 2.876, $p < 0.05$). This finding can be interpreted as a serial cortical process in a mid-latency time window which transitions to a sustained activation pattern. For its somatosensory counterpart, we observed temporal generalisation from ˜100 ms until trial end. This finding suggests that cortical activity is maintained in a single cortical network (mean AUC = 0.51 ± 0.011, max. AUC = 0.541 at 52 ms training time and 196 ms testing time, mean cluster t = 7.425 ± 2.902, $p < 0.05$). When classifiers were trained and tested on salient contrasts in different sensory modalities, we identified shared signatures along the diagonal between 100-200 ms which transition to an extensive temporal generalisation pattern from ˜200 ms (auditory-to-somatosensory: mean AUC = 0.496 ± 0.017, max. AUC = 0.537 at 632 ms training time and 380 ms testing time, mean cluster t = 5.831 ± 2.08, $p < 0.05$, somatosensory-to-auditory: mean AUC = 0.496 ± 0.017, max. AUC = 0.537 at 632 ms training time and 380 ms testing time, mean cluster t = 5.831 ± 2.08, $p < 0.05$). This decoding pattern is most consistent with the notion that serial propagation of cortical activity along supramodal cortical regions contributes to the processing of salient targets.

We compared classification score matrices using a cluster-based permutation test (Figure 3, B) and showed that decoding performance along the diagonal was enhanced for the salient relative to the regular condition for each decoding condition: somatosensory (mean AUC = 0.008 ± 0.019, max. AUC = 0.056 at 60 ms training time and 184 ms testing time, mean cluster t = 4.116 ± 1.882, $p < 0.05$), auditory (mean AUC = 0.0 ± 0.025, max. AUC = 0.07 at 128 ms training time and 488 ms testing time, mean cluster t = 3.968 ± 1.835, $p < 0.05$), auditory-to-somatosensory (mean AUC = 0.0 ± 0.023, max. AUC = 0.072 at 540 ms training time and 352 ms testing time, mean cluster t = 3.809 ± 1.653, $p < 0.05$), and somatosensory-to-auditory (mean AUC = 0.003 ± 0.022, max. AUC = 0.052 at 696 ms training time and 312 ms testing time, mean cluster t = 3.553 ± 1.383, $p < 0.05$). We also observed better decoding performance in the salient condition in a later time window. This pattern was most evident in the somatosensory condition from ˜300 ms until trial end but also in the remaining three conditions in a mid-range time window between 300 and 400 ms (Figure 3, C).

In sum, both regular and salient sensory deviations lead to a late temporal generalisation pattern, but salient deviations were found to elicit an earlier supramodal activity pattern. Since we only focus on trials in which local deviations are succeeded by global deviations, and the decodability of the global response is very strong relative to the local response, the shape of the local response differs from previous work [5,48]. Overall, our findings reveal that the somatosensory response can be decoded earlier than the auditory response. To corroborate our finding of an enhanced supramodal early response to salient deviations, we performed a cluster-based permutation test on AUC-ROC classification score matrices between the salient and regular contrast for each of the four temporal decoding conditions. Across all four comparisons, classification scores for the salient contrast exceed the regular contrast in a mid-range time window between 100-300 ms (with regular deviant decoding scores at chance level or only slightly above chance). This finding suggests that these shared serial activation patterns are specific to the salient contrast. We also observed that classification scores for salient contrasts are higher than for their regular counterparts in a late time window from ˜300 ms to trial end. This pattern was particularly prominent in the somatosensory condition where classification scores for the salient contrast consistently exceeded its regular counterpart from ˜300 ms until trial end at 300, 400, 500 and 600 ms. Converging these results, we discovered a serial supramodal process evolving into sustained cortical activation from ˜200 ms in the salient but not the regular condition. Whereas the novel results demonstrate that both regular and salient sensory deviations elicit a late

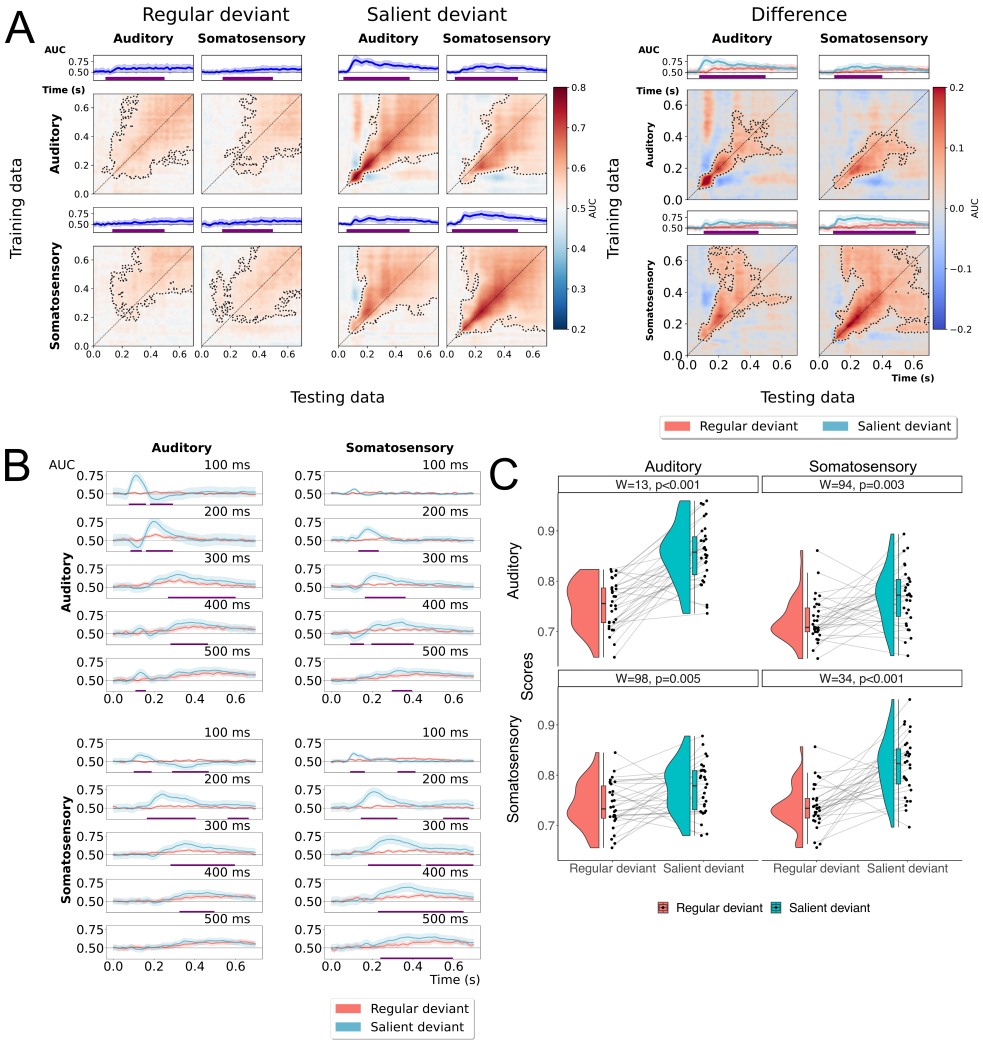

Fig 3. Temporal decoding. AUC-ROC classification score matrices plotted on a red-to-blue gradient. Adjacent classification score clusters which differ from chance were identified in a cluster-based permutation test and delineated using a dotted line. The left top panel shows the average diagonal classification performance in which time course segments different from chance were highlighted with a purple bar. Differences in classification score matrices between the regular and salient condition are shown. Significant clusters were delineated with a dotted line. The right top panel plots the diagonal decoding performance time courses of both conditions with significant differences delineated with a purple bar (Panel A). Each panel displays results from a cluster-based permutation test comparing classification scores from two subsets of classification scores. Each subset represents scores obtained from a classifier trained at a target time point (100, 200, 300, 400, or 500 ms) and tested on all remaining time points. Mean classification scores across participants obtained from decoding salient deviant and standard trials are printed in salmon and regular deviant and standard trials in teal (with the shaded area representing the standard deviation). Purple bars highlight significant differences between regular and salient AUC-ROC score series with $\alpha = 0.5$ (Panel B). Raincloud plots showing that distributions of subject-wise maximal AUC-ROC scores differ between the salient and regular conditions using a Wilcoxon Signed Rank test (Panel C).

supramodal activation pattern, only responses to salient targets were supported by a supramodal transient serial process which later progresses into a stable activity pattern (Figure 3). With these results, we replicated and extended earlier findings that deviations of sensory stimulus groups elicit a P3b-like difference wave from ˜200 ms until trial end in either sensory modality [5,48]. We also provide corroborating evidence for our own finding that shared sustained representations between the auditory and the somatosensory modality emerge from ˜200 ms in both the salient and regular contrast [5].

Salient target detection relies on networks spanning all levels of the cortical hierarchy

Having identified a supramodal serial process for the detection of salient sensory deviations, we examined whether there might be changes in connectivity due to salient sensory deviations which are shared between somatosensory and auditory modalities. We also determined whether there are differences in connectivity changes due to salient deviations between these senses. Subsequently, we describe results from a DCM-PEB approach used to assess commonalities and differences in cortical information flow in a network involving the somatosensory and auditory hierarchy spanning from primary sensory to frontal cortices. We designed a DCM with all plausible bidirectional connections between primary and secondary sensory as well as frontal cortices in the somatosensory and auditory hierarchy (Figure 4).

Our analysis revealed commonalities and differences at early and late stages of the somatosensory and auditory hierarchy. Differences in saliency processing between sensory modalities became evident across associative somatosensory and frontal cortices. As shown in Figure 4, B), we observed decreased saliency-related modulation of connectivity between the right secondary somatosensory cortex and inferior frontal gyrus as well as interhemispheric connectivity between secondary somatosensory cortices in the somatosensory relative to the auditory condition. Saliency modulated connectivity from the left secondary to primary somatosensory cortex more strongly in the somatosensory modality. Conversely, saliency-related connectivity changes from the inferior frontal gyrus to the superior temporal cortex were reduced in the auditory modality in each hemisphere. We also discovered commonalities in saliency-related connectivity modulations between sensory modalities (Figure 4, A). Supporting the notion of a supramodal network for spatial attention shifts [9], we identified a common inhibition in an interhemispheric connection between inferior frontal gyri. Interestingly, we also found commonalities in information flow between frontal, associative and early sensory cortices thought to be unisensory in the literature. Networks for somatosensory and auditory saliency processing share an excitation placed on a connection descending from the right inferior frontal gyrus to the ipsilateral secondary somatosensory cortex and between secondary somatosensory cortices. We also identified a common excitatory input from the right secondary to the right primary somatosensory cortex. In sum, commonalities in information flow linked to saliency processing can be identified between lower, intermediate and higher levels of the cortical hierarchy. Our results complement earlier findings demonstrating direct interactions between early and associative auditory and somatosensory cortices [50,51]. Our results support the view that information processing in the cortex is multisensory in early and late stages of sensory processing [23].

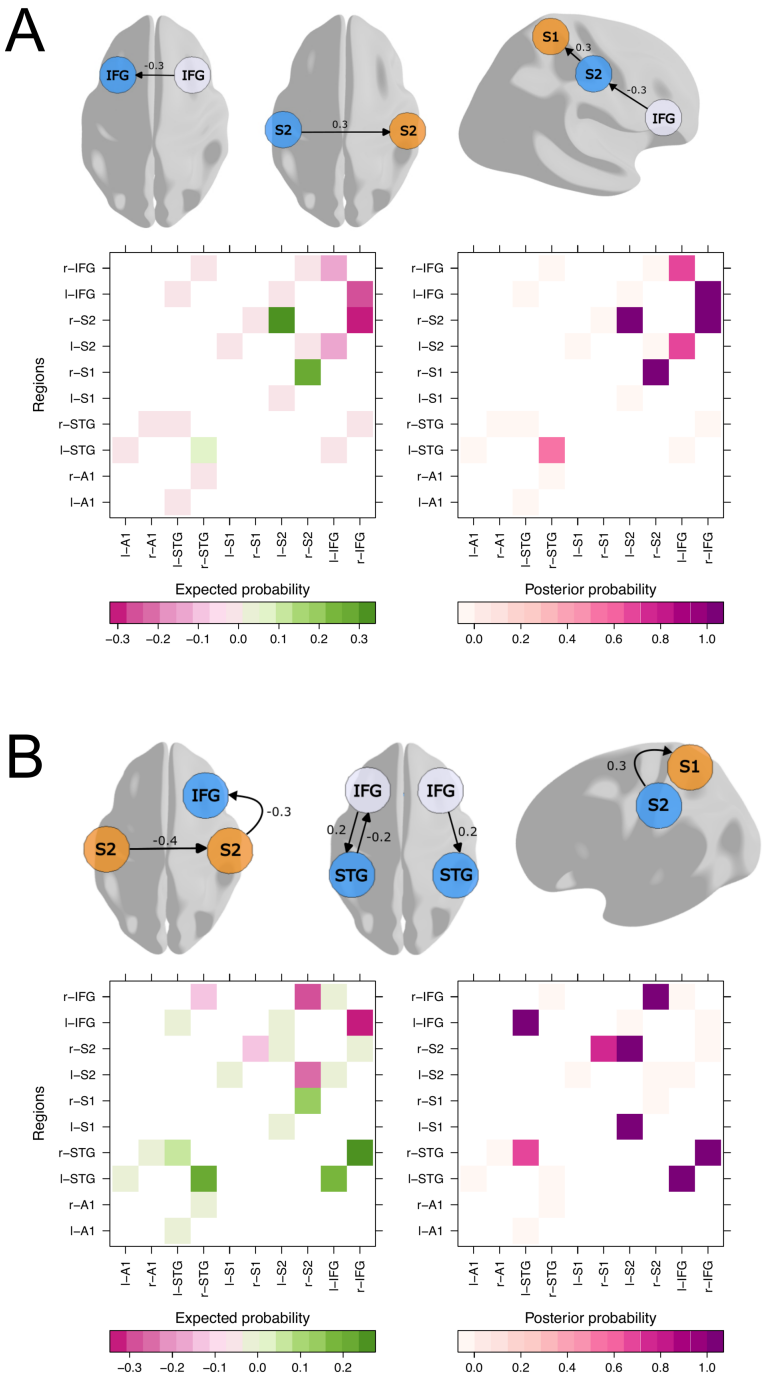

Fig 4. Effective connectivity modelling. The top panel shows commonalities (Panel A) and differences (Panel B) in saliency-related modulations of effective connections modelled using PEB. Each glass brain model highlights a subset of results from the full PEB model. Arrows represent forward and backward connections between cortical regions and posterior expectations of connectivity parameters resulting from a multivariate normal probability density computation over PEB parameters that plotted next to each connection. Only extrinsic connections thresholded at a 95% posterior probability based on free energy (corresponding to very strong evidence) are shown. The bottom panel displays a heatmap depicting the posterior expected connectivity parameters adjacent to a heatmap with the corresponding posterior probabilities.

Discussion

Our study examined to which extent the detection of salient targets relies on supramodal or modality-specific attention networks. Converging evidence from behavioural tasks in patients and healthy individuals [52–54] as well as studies of cortical function [10,11,49,55,56] supports the hypothesis that target detection recruits a supramodal attention-related network. Other studies point towards a modality-specific contribution to networks orienting attention towards a target [57,58]. To reconcile these findings, we compared the cortical dynamics and mechanisms of saliency-related target responses between the somatosensory and auditory modality. We made three key observations: First, we identified a minimal but significant difference in voltage amplitude time courses between regular and salient responses in each sensory modality. Second, we showed that both salient and regular targets elicit sustained supramodal activity in a late time window using temporal decoding. However, only salient targets were found to produce a mid-latency process which relies on common cortical dynamics. Lastly, we performed a follow-up comparison of saliency-related connectivity changes between both sensory modalities. Using forward generative modelling, we identified commonalities in connectivity changes between sensory modalities not only between bilateral inferior frontal cortices but also in lower-order sensory cortices. Differences in saliency-related connectivity changes between sensory modalities manifested in early and late stages of cortical processing.

The detection of salient targets recruits a supramodal process

In a series of analyses, we provide evidence for a mid-latency supramodal process linked to the detection of salient targets in the auditory and somatosensory modality. This finding fits well with the canonical theory that a supramodal frontoparietal network supports attention deployment on behaviourally relevant targets [8–10]. Cortical responses to sensory targets manifest in a late and sustained supramodal activation pattern regardless of targets being regular or salient. Characteristics of this response are consistent with the P3b, an attention-related positive difference wave which occurs ˜300 ms after a deviant stimulus [48] and has been found to rely on a supramodal network in earlier studies [5,47]. While regular deviations only trigger a P3b-like temporally extended activity pattern, salient deviations involve a supramodal serial mid-latency process which evolves into sustained activity from ˜300 ms. In other words, the detection of deviant stimulus groups using top-down attention leads to a supramodal sustained activation pattern regardless of whether the expectation violation is salient. However, when attention is drawn to a rare sensory deviation through a bottom-up process, a short-lived supramodal response precedes this pattern. This result suggests that there are some shared processes between sensory systems when activity is propagated along the cortical hierarchy in response to a salient target. Based on earlier work [30], the early response is likely supported by a series of generators with some overlap between the senses. From ˜300-700 ms, a single supramodal network is active.

Stimulus-driven attention elicits supramodal and modality-specific information flow across cortical processing stages

Having demonstrated that saliency-related responses share cortical dynamics between sensory modalities, we characterised whether this process manifests in common connectivity changes in a somatosensory/auditory-to-frontal network. In line with the notion of a supramodal frontoparietal attention network [8–10], we identified supramodal connectivity changes in interhemispheric information flow between inferior

frontal gyri due to saliency. Our finding substantiates accumulating evidence for a role for the inferior frontal gyrus in sensory target detection in different sensory modalities [8,10]. Across a series of studies, the right inferior frontal gyrus has been found to selectively respond to rare targets in the visual [12,16], auditory [13,22,40,42,59], and somatosensory modality [2,14,17]. Although these findings substantiate earlier proposals that the inferior frontal cortex might serve a supramodal function for target detection [8], they are largely based on an inferior frontal response to rare targets in different sensory modalities alone. By uncovering a common interhemispheric inhibition in the inferior frontal cortex, our results demonstrate a common mechanistic base for the influence of saliency on target detection in a supramodal saliency network. We also observed differences between the senses in the extent to which salient targets modulate interactions between inferior frontal and modality-specific cortices. We observed that feedback from ipsilateral frontal cortices to superior temporal gyri is inhibited in the auditory relative to the somatosensory modality. Likewise, we found an inhibition sent from the frontal cortices to the secondary somatosensory cortex in the somatosensory relative to the auditory modality. In line with earlier studies [11], this finding indicates that the frontal cortex might control ipsilateral associative cortices dedicated to a specific sensory modality from the top-down in a modality-specific manner. In summary, our findings support a role for the inferior frontal cortex as a key region for saliency processing with supramodal and modality-specific interactions between other regions in modality-specific hierarchies. Beyond this, we identified supramodality in modulations placed on connections between secondary somatosensory cortices and even between the primary and secondary somatosensory cortex. This finding challenges models which states that primary sensory cortices exclusively process sensory inputs from a specific modality [37]. Evidence from a wide range of studies refutes the notion of primary and secondary sensory cortices as unisensory processors which led to proposals that the cortical function is multisensory at all processing stages [23]. Indeed, the secondary somatosensory cortex borders the temporoparietal junction and auditory cortex where patches of somatosensory but also multisensory neurons have been found [60,61]. White-matter projections between the secondary somatosensory cortex and auditory cortex have been documented in the literature [51]. Beyond audiotactile integration, the somatosensory cortex has been found to respond to purely auditory inputs [50]. Collectively, our findings contradict the idea that the cortex is organised along a strictly unimodal-to-supramodal gradient [37]. Instead, stimulus-driven attention drives supramodal and modality-specific interactions between the inferior frontal gyrus and modality-specific regions. This way, our findings unify the view that attention influences activity in early cortical processing stages [62–64] and that early cortical function is not specific to a sensory modality [23].

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