Sensory target detection at local and global time scales dissociates modality-specific and supramodal dynamics along a cortical hierarchy

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Abstract

How do cortical networks support the detection of irregular sensory events for different senses? Here we reconcile two views of cortical function according to which supramodal processing is either deferred to associative cortices in higher levels of a unimodal-to-supramodal cortical hierarchy or features across all cortical processing stages. In a series of hierarchical multisensory target detection studies using EEG, we applied a temporal cross-decoding approach to reveal the cortical dynamics elicited by rule-based global and feature-based local sensory deviations within and between the visual, somatosensory and auditory modality. We uncovered simple feature-based sensory deviations presented in temporal vicinity to a monotonous input stream triggered an MMN-like local negativity which decayed quickly and early in different sensory modalities. Conversely, complex rule-based targets tracked across time evoked a P3b-like global effect which generalised across a late time window. Ultimately, a series of temporal cross-modality decoding analyses demonstrated that global effects are maintained in supramodal networks whereas local effects propagate along modality-specific cortical networks and evolve into short-lived supramodal activity. Taken together, each sense implements a cortical hierarchy which orchestrates target detection responses operating on local and global time scales at successive processing stages. Converging evidence from different analyses and studies, we show that cortical organisation largely follows a gradient in which modality-specific processes dominate local responses and higher-order processes encode abstract supramodal information fed forward from modality-specific cortices. In conclusion, the cortex implements a hierarchy which hosts increasingly supramodal processes in each level rather than a strict hierarchy which delays supramodal function to associative cortices.

Keywords: attention, target detection, P300, Mismatch Negativity, predictive coding

Word count: 7552 words

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Introduction

The ability to detect deviant sensory events in a stream of predictable stimuli is crucial for adaptive behaviour. To enable this, each sense relies on a dedicated hierarchical system of cortices spanning from primary sensory to associative and frontal areas (Allen et al., 2016a; Chao, Takaura, Wang, Fujii, & Dehaene, 2018; Chennu et al., 2013; Cornella, Leung, Grimm, & Escera, 2012; J. Murray et al., 2014; Rao & Ballard, 1999; Wacongne et al., 2011). Are there unified principles of cortical organisation which govern target detection processes across sensory systems? A prominent proposal states each perceptual system encompasses a series of cortices arranged along a simple-to complex hierarchy according to which successive levels encode increasingly abstract sensory information (de Lange, Heilbron, & Kok, 2018; Felleman & Van Essen, 1991; Kiebel, Daunizeau, & Friston, 2008; J. Murray et al., 2014; Rao & Ballard, 1999). Indeed, there is strong evidence across different sensory modalities that neurons in primary and secondary sensory areas respond to simple features such as shapes in the primary visual cortex, pitch in the primary auditory cortex, pressure in the primary somatosensory cortex), whereas frontal regions encode more complex information such as visual landscapes, sound patterns and tactile objects (Allen et al., 2016a; Bekinschtein et al., 2009; Fardo et al., 2017; Hochstein & Ahissar, 2002; Hubel & Wiesel, 1962; Maunsell & Essen, 1983; C. Murray, 2004; Nelken & Bar-Yosef, 2008; Rao & Ballard, 1999; Riesenhuber & Poggio, 1999; Van Essen & Maunsell, 1983).

Converging evidence from target detection studies in different sensory modalities supports the notion that target detection processes are organised along a simple-to-complex gradient from modality-specific to frontal cortical regions. A rich body of literature identified the prefrontal cortex as a key site for complex rule-visual search

tasks in which simple targets are detected was found to rely on early visual regions based perceptual learning of sensory targets (Miller, 2009). In the visual system, target detection involving the spatial conjunction of multiple visual features has been shown to recruit attention-dependent frontoparietal processes (Donner et al., 2000; Kristjánsson, Vuilleumier, Schwartz, Macaluso, & Driver, 2007). Conversely, early visual cortices support visual search tasks in which simple targets are detected (Ester, Serences, & Awh, 2009). In the auditory domain, a series of studies mapping the neural basis of simple and complex auditory targets provide evidence for a hierarchical organisation of the auditory system. Higher-order frontal cortices were found to process complex targets such as auditory patterns, whereas simple pitch deviations depended on activity in early auditory cortices (Bekinschtein et al., 2009; Chennu et al., 2016; Cornella et al., 2012; Uhrig, Dehaene, & Jarraya, 2014; Wacongne et al., 2011). Taken together, these results raise the question whether the detection of complex targets relies on a common frontal activation pattern in different sensory modalities, while the detection of simple targets recruits modality-specific areas.

We propose that cortical signatures of sensory targets are arranged along a gradient of supramodality according to which responses to complex rule-based targets largely rely on sustained late supramodal activation patterns while modality-specific processing dominates responses to simple targets (pre-registered https://osf.io/3mqvy/). Our approach exploits differences in the susceptibility of electrophysiological responses to bottom-up and top-down variables to dissociate their neural dynamics in different levels of the cortical hierarchy. Sensory targets are followed by two cortical responses which can be measured using EEG: the Mismatch Negativity and the P300 complex (consisting of two components called P3a and P3b). The MMN is an early local negativity associated with sensory change detection in a temporal proximity to the expected input (Mäntysalo & Näätänen, 1987; Risto Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001; Shinozaki, Yabe, Sutoh, Hiruma, & Kaneko, 1998; Wacongne, Changeux, & Dehaene,

2012). Originally discovered in the auditory modality (R. Näätänen, Simpson, & Loveless, 1982), the MMN can be detected in different sensory modalities (Allen et al., 2016b; Amado & Kovács, 2016; Czigler & Csibra, 1992; Czigler et al., 2006; Shen, Smyk, Meltzoff, & Marshall, 2018). Consistent with its early appearance, the MMN has been found to originate in primary sensory cortices dedicated to the modality in which the sensory irregularity was generated Hamm & Yuste (2016). Canonically considered to be pre-attentive (Tiitinen, May, Reinikainen, & Näätänen, 1994), the MMN is modulated by attention but resilient to distraction (Auksztulewicz & Friston, 2015; Chennu et al., 2013). The P3b is a late distributed positive potential which marks the detection of sensory targets and can be elicited in a range of sensory modalities (Polich, 2007; Yamaguchi & Knight, 1991b, 1991a), In contrast to the MMN, the P3b seems to require an active memory to track the sensory context in which irregularities are embedded. The P3b also also lasts longer (Pegado et al., 2010) and disappears without attention to the sensory irregularity (Katayama & Polich, 1998; Polich, 2007; Squires, Petuchowski, Wickens, & Donchin, 1977). Based on these properties, the auditory MMN and P3b can be located as cortical responses to simple versus complex sensory targets in lower-order auditory cortical regions and higher-order frontoparietal levels of the cortical hierarchy respectively (Bekinschtein et al., 2009; Chao et al., 2018; Wacongne et al., 2011).

Here we use multisensory versions of a hierarchical sensory target detection paradigm ("local-global paradigm") to obtain a P3b-like global top-down response as well as a MMN-like local bottom-up response. The local-global paradigm achieves this by manipulating the complexity of the sensory context in which a stimulus change appears (Bekinschtein et al., 2009). We hypothesised that the global effect as a top-down-driven sensory novelty response to complex targets in higher-order cortices might share neural signatures between the senses. In contrast, the local effect which can be regarded as a bottom-up response to simple targets might be supported by early localised modality-specific activity in primary sensory cortices. In two different multisensory

variants of the local-global paradigm, we uncovered commonalities between the cortical dynamics of responses to feature-based local and rule-based global sensory deviations using a temporal decoding approach (King & Dehaene, 2014). We show that classifiers trained to decode global effects in a specific sensory modality were able to decode other global effects in a late extended time window. In contrast, local effects shared few short-lived cortical signatures between the senses.

Results

Hierarchically nested sensory deviations elicit local and global effects in different sensory modalities

We investigated commonalities in cortical responses to rule-based global and feature-based local sensory deviations using multisensory versions of the local-global paradigm. In this task, expectations about sensory stimuli are selectively violated at two hierarchical levels: the local and global level. To achieve this, the paradigm varies the temporal extent of the sensory context in which a deviant stimulus is presented (Bekinschtein et al., 2009). Sensory deviations are introduced either at a local level (by occasionally varying the last stimulus in a stimulus group) or at a global level (by introducing rare stimulus groups in blocks of frequently appearing stimulus groups), as shown in Figure 1. Capitalising on differences in the responsiveness of cortical processes to top-down manipulation, this design enables us to extract local and global cortical markers which can be located at successive hierarchical levels in the cortex. MMN-like local effects can be extracted from feature-based sensory deviations and manifest as an early amplitude enhancement when locally standard trials (groups of five identical ipsilateral stimuli) are contrasted with locally deviant trials (groups of four identical ipsilateral stimuli followed by a contralateral input). Rule-based sensory deviations evoke P3b-like global effects which are established by contrasting ERP time courses extracted from globally deviant trials with

standard trials in a late time window between 250-600 ms after onset of the last stimulus in a trial. As such, the global effect is associated with top-down target detection processes which require the retention of the preceding sensory input stream in memory in different sensory systems. To examine commonalities in local or global cortical responses between different sensory modalities, we developed two versions of the local-global paradigm in which sensory inputs are sampled from different sensory modalities. In the bimodal version of the paradigm, we presented blocks of auditory or somatosensory hierarchical sensory stimulation. The trimodal version of the paradigm contained unisensory blocks of either visual, somatosensory or auditory sensory inputs.

In a first step, we established that hierarchical manipulations of sensory context elicit a MMN-like local effect and a P3b-like global effect in the auditory, somatosensory and visual modality in both experiments. To that end, we performed cluster-based permutation of ERP amplitude time courses (Maris & Oostenveld, 2007) displayed in Figure 1. Replicating earlier findings (Bekinschtein et al., 2009; Chennu et al., 2013), the auditory local effect in the bimodal paradigm manifested as a frontotemporal bipolar two-peak difference wave (cluster $t = -12000$, $p < 0.001$) and a one-peak difference wave in the trimodal paradigm (cluster $t = -5396.6$, $p = 0.001$). A somatosensory local effect emerged as a central negativity between ~50-150 ms in the bimodal paradigm (cluster $t = -752.31$, $p = 0.003$) and as a two-peak negativity between ~100-350 ms the trimodal paradigm (cluster $t = -3298.4$, $p = 0.004$). We also identified a visual local effect as a negativity in a mid-range time window between ~100-350 ms (cluster $t = -6178.9$, $p < 0.001$) shown in Figure 1.

At a global level, a comparison of globally deviant and standard trials revealed a positive difference wave in a time window from ~250 ms until the end of the trial regardless of sensory modality (with some shifts in onset of the effect). In the bimodal (cluster $t = 22143$, $p < 0.001$) and trimodal study (cluster $t = 27934$, $p < 0.001$), we revealed an auditory global effect as a positive deflection with a posterior distribution. A

somatosensory global effect presented with a similar posterior distribution in both the bimodal (cluster $t = 18351$, $p < 0.001$) and trimodal study (cluster $t = 21421$, $p < 0.001$). Ultimately, a visual global effect emerged as a positive difference wave in a relatively late time window from ~400 ms until the end of the trial (cluster $t = 12857$, $p = 0.001$) shown in Figure 1. These results show that complex targets which require the conscious tracking of sensory patterns across time elicit a global effect in different sensory modalities. Our finding that the global effect manifests as a large, late and posterior positive deflection regardless of sensory modality complements previous studies which characterise the related P300 as a late positivity (Bekinschtein et al., 2009; Bledowski et al., 2004; Chennu et al., 2013; Walz et al., 2013), Taken together, our results show that the functional dissociation of local and global effects is a supramodal property of target detection systems in different sensory domains.

Cortical responses to rule-based but not feature-based sensory targets are sustained across time in each sensory modality

Previous work has shown that functional differences between cortical responses to auditory rule-based and feature-based targets are reflected in the extent to which they are maintained in auditory networks. Cortical activation patterns in response to auditory rule-based targets are sustained in time, whereas feature-based auditory deviations decay quickly (King & Dehaene, 2014). Is the temporal evolution of cortical target detection responses a property common to different sensory domains? We examined whether global effects are linked to a sustained cortical activation pattern whereas local effects are supported by short-lived activity regardless of sensory modality. We employed temporal decoding to characterise neural activation patterns elicited by local and global effects in different sensory modalities. In short, temporal decoding is a machine learning approach used to characterise the temporal evolution of cortical activation patterns linked to sensory events. A classifier trained at a time point t is not only tested at t but at all other

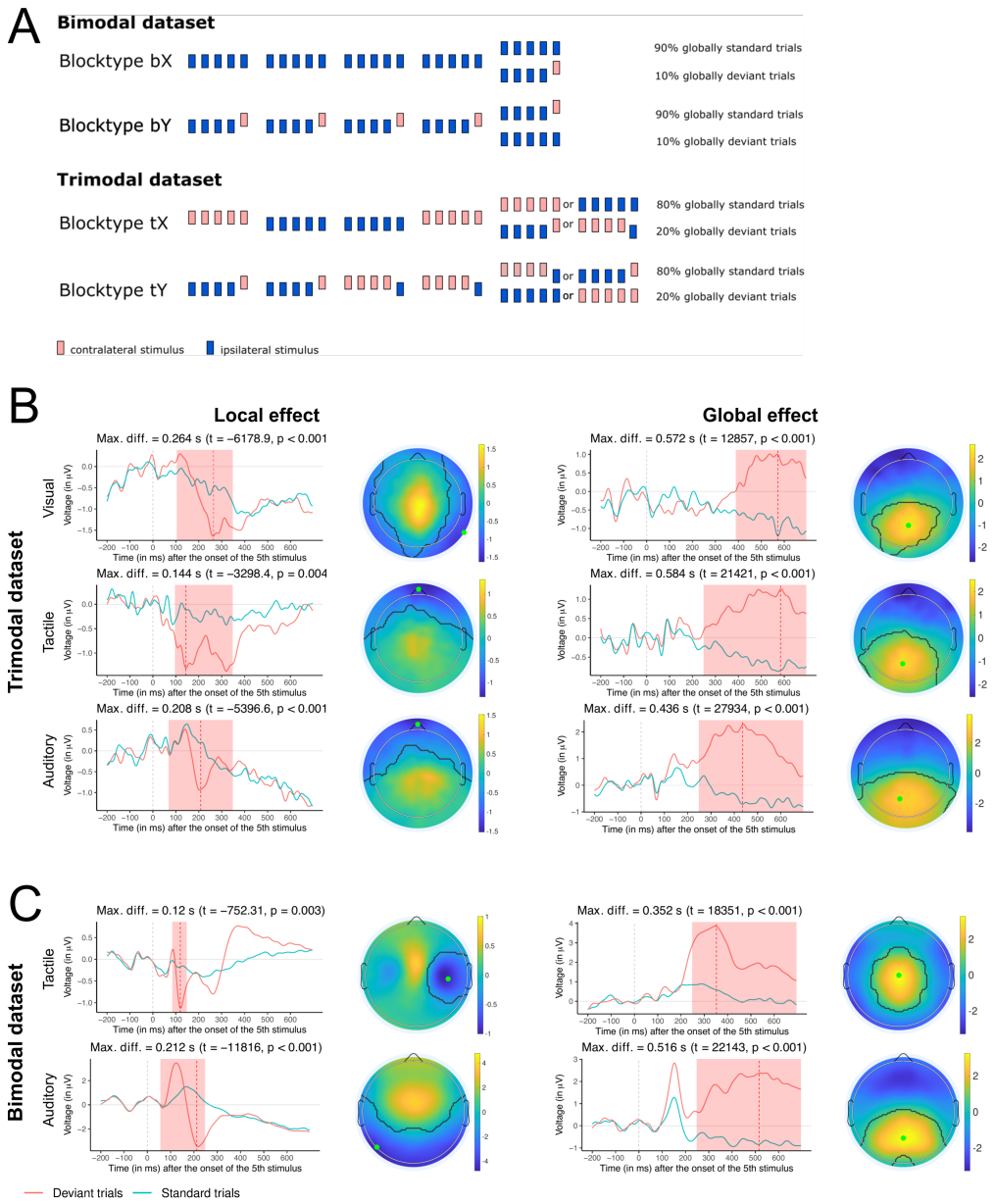

Figure 1. **Experimental design and ERP results.** Block type design for the local-global paradigm used in the bimodal and trimodal study (A). Cluster-based permutation test results for ERP amplitude differences showing that a local and global effect can be obtained in different sensory modalities for the trimodal (B) and the bimodal study (C). On the left, each panel shows ERP amplitude time courses of the corresponding deviant-standard condition pair. Next to the ERP voltage time course plot, the corresponding topographical map is shown. Time periods in which a cluster-based permutation test identified a difference between both conditions are highlighted in red in the ERP time course plot and delineated with a black line on the topographical map. The time point at which the difference between both conditions is maximal is delineated with a dotted red line in the ERP amplitude time course plot. The electrode at which this difference was obtained is marked with an orange dot on the topographical map.

remaining time points. This leads to a temporal generalisation matrix of classification performance scores. The shape of the temporal generalisation matrix offers insights into the temporal dynamic of cognitive operations and their cortical generators (Dehaene & King, 2016).

We observed that local effects could be decoded along the diagonal in a mid-range time window for each sensory modality (Figure 2). Across different contrasts, local effects were found to decay quickly. This finding is mostly consistent with a serial activation of different cortices dedicated to the sensory modality in which the local effect was applied (King, Gramfort, Schurger, Naccache, & Dehaene, 2014). At a local level, the visual local effect was maintained briefly between 200-400 ms (mean AUC = 0.511 ± 0.029, max. AUC = 0.61 at 268 ms training time and 268 ms testing time, mean cluster $t = 3.327$, $p < 0.05$). In the trimodal study, the somatosensory local effect (mean AUC = 0.511 ± 0.024, max. AUC = 0.564 at 316 ms training time and 312 ms testing time, mean cluster $t = 2.91$, $p < 0.05$) and the auditory local effect (mean AUC = 0.509 ± 0.028, max. AUC = 0.65 at 212 ms training time and 212 ms testing time, mean cluster $t = 2.599$, $p < 0.05$) were maintained for ~100 ms from ~200 ms. In the bimodal study, the somatosensory effect was best decoded between 200-300 ms (mean AUC = 0.516 ± 0.026, max. AUC = 0.629 at 208 ms training time and 208 ms testing time, mean cluster $t = 4.472 \pm 7.53$, $p < 0.05$). In this study, temporal decoding revealed a classification score matrix consistent with two distinct processes underpinning the auditory local effect. From ~100 ms, the auditory local effect can be decoded along the diagonal which suggests a serial propagation of cortical activity along the auditory cortical hierarchy. However, cortical activity is sustained for ~150 ms from ~200 ms (mean AUC = 0.507 ± 0.04, max. AUC = 0.714 at 188 ms training time and 188 ms testing time, mean cluster $t = 2.11 \pm 13.151$, $p < 0.05$). Although classification scores for the auditory and somatosensory local effect differed from chance across an extended time window, classifiers performed only slightly better than chance from ~350 ms for both effects.

At a global level, we found that classifiers trained to distinguish deviant and standard trials from ~200 ms generalised across other time samples in the remaining trial window regardless of which sensory modality was tested (Figure 2). This decoding procedure led to a rectangular classification score matrix for each global contrast. In line with earlier ERP time course comparison results (Figure 1), the visual global effect manifested relatively late from ~400 ms (mean AUC = 0.512 ± 0.06, max. AUC = 0.656 at 516 ms training time and 520 ms testing time, mean cluster t = 3.19, $p < 0.05$). In the trimodal study, the somatosensory global effect appeared from ~350 ms ((mean AUC = 0.52 ± 0.048, max. AUC = 0.644 at 512 ms training time and 508 ms testing time, mean cluster t = 5.561, $p < 0.05$)) and the auditory global effect from ~200 ms (mean AUC = 0.544 ± 0.069, max. AUC = 0.69 at 532 ms training time and 524 ms testing time, mean cluster t = 12.502, $p < 0.05$). In the bimodal study, temporal generalisation was found relatively early from ~150 ms for both the somatosensory (mean AUC = 0.56 ± 0.057, max. AUC = 0.697 at 372 ms training time and 344 ms testing time, mean cluster t = 19.317 ± 19.074, $p < 0.05$) and auditory global effect (mean AUC = 0.599 ± 0.048, max. AUC = 0.695 at 432 ms training time and 428 ms testing time, mean cluster t = 33.062 ± 17.556, $p < 0.05$). Cluster-based permutation tests comparing differences in classification scores between the local and global effect show that the global effect generalises in a late time window whereas the local effect does not (Figure 2). Collectively, our results indicate that cortical activation associated with the global effect starts no earlier than ~150 ms after onset of the last stimulus in a trial and is sustained over time until the trial ends. However, we observed some shifts in the onset latency between different global effects with the visual global effect not appearing before 400 ms. Despite these shifts, this pattern suggests that a single cortical system is active in that time window (King & Dehaene, 2014). This finding leaves the question open whether this system is dedicated to a specific sensory modality or shared between different senses.

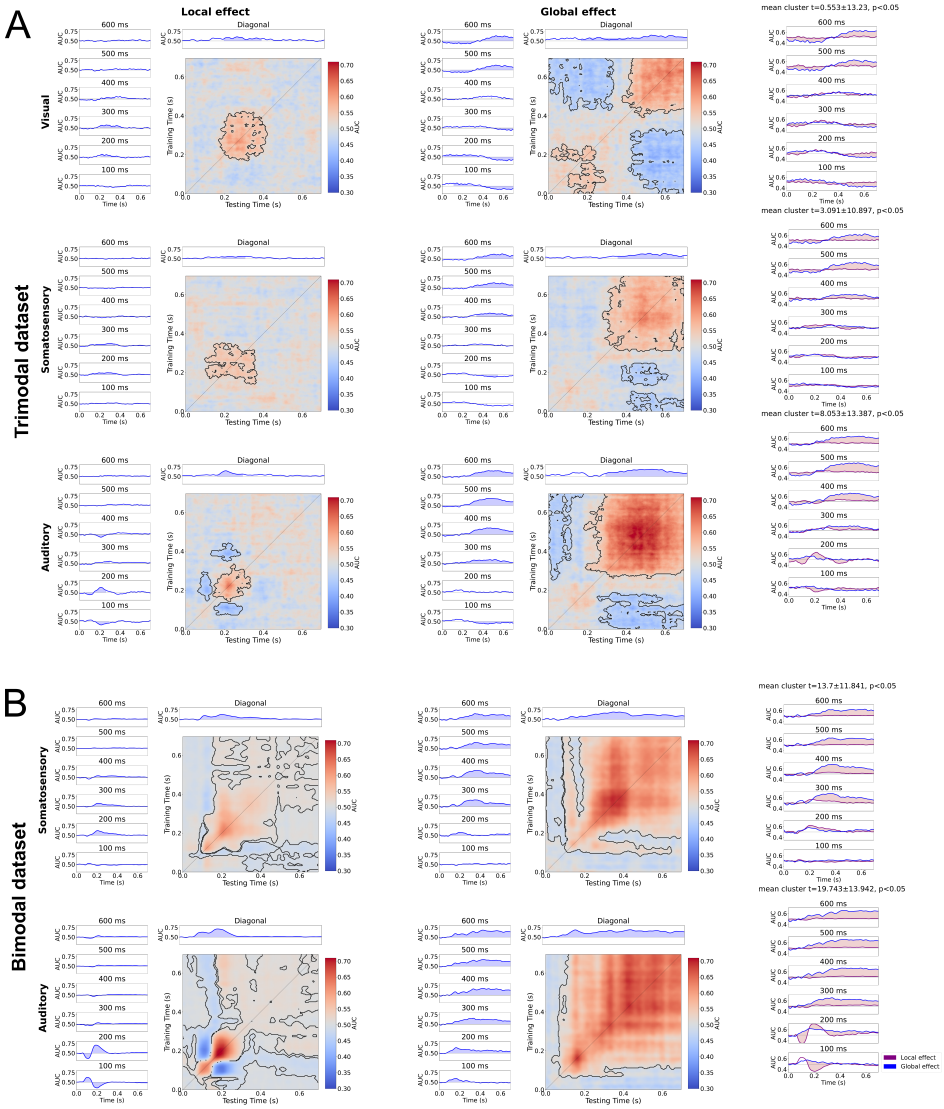

Figure 2. **Temporal generalisation analysis within sensory modalities.** Panels display temporal generalisation results for the local (left) and global effect (right) in the trimodal (A) and bimodal dataset (B). Each panel shows results of a temporal generalisation analysis in which a classifier is trained to distinguish deviant and standard trials at each time point and then tested on all remaining time points in a trial. Classification scores are displayed on a red-to-blue gradient. On top of each matrix, adjacent classification scores different from chance (0.5) in a cluster-based permutation test are highlighted with a black line. Next to each matrix, we show a series of time courses of classification scores produced by classifiers trained at the specified time point. On top of each matrix, we plotted the classification score time course for a decoding procedure in which a classifier is trained and tested on deviant-standard pairs at the same time point (corresponding to the matrix diagonal). Classification scores different from chance are highlighted with a blue shade. On the right side, we show results of a cluster-based permutation test contrasting classification score matrices of the corresponding local and global effect. Each subplot shows the classification score time courses of a classifier trained to separate global deviant-standard pairs at the specified time point and tested across the remaining time window, and its local counterpart. Time periods in which local and global effect classification time courses differ are highlighted in red shade.

A supramodal cortical signature sustained in time supports global but not local effects

Here we provide evidence for the hypothesis that cortical hierarchies dedicated to each sense are organised along a gradient of supramodality. Building up on our finding that global effects are associated with a sustained late cortical activation pattern, we further demonstrate that this sustained pattern is shared between different sensory modalities. We also show that local effects in different sensory modalities rely on few, if any, common cortical signatures in comparison to global effects.

Temporal decoding was employed to examine whether cortical responses share neural dynamics between sensory modalities. To identify common activity patterns linked to evoked responses, temporal generalisation analysis can be applied in two ways: Classifiers can be trained to separate a deviant-standard condition pair in a target sensory modality at a time point t and tested on deviant-standard condition pairs in a different sensory modality across all time points in a trial. Alternatively, a classifier can be trained to separate deviant-standard condition pairs when they are pooled across all sensory modalities separately at a global and a local level. We used a 5-fold stratified cross-validation approach in which classifiers were trained on 4/5 of the data and tested on the remaining 1/5 for both analyses (see Methods for details).

We initially trained a classifier to separate globally deviant from standard trials when trials for each condition pair are pooled across sensory modalities. This procedure revealed temporal generalisation in a late time window across different global contrast in both datasets (Figure 3). We provide evidence for shared activity supporting the auditory and visual global effect from ~400 ms regardless of whether classifiers were trained on the visual and tested on the auditory contrast (mean AUC = 0.517 ± 0.065, max. AUC = 0.663 at 452 ms training time and 572 ms testing time, mean cluster t = 4.622, $p < 0.05$) or vice versa (mean AUC = 0.508 ± 0.06, max. AUC = 0.653 at 676 ms training time and 496 ms

testing time, mean cluster t = 3.37, $p < 0.05$). A similar pattern was found for somatosensory and visual effects when classifiers were trained on visual and tested on somatosensory deviant-standard pairs (mean AUC = 0.51 ± 0.053, max. AUC = 0.636 at 540 ms training time and 464 ms testing time, mean cluster t = 3.202, $p < 0.05$) or vice versa (mean AUC = 0.51 ± 0.067, max. AUC = 0.675 at 580 ms training time and 540 ms testing time, mean cluster t = 2.945, $p < 0.05$). Shared activity between the auditory and somatosensory global effect was found from ~350 ms when classifiers were trained on the auditory and tested on the somatosensory contrast (mean AUC = 0.531 ± 0.046, max. AUC = 0.644 at 424 ms training time and 580 ms testing time, mean cluster t = 10.207, $p < 0.05$) or vice versa (mean AUC = 0.532 ± 0.064, max. AUC = 0.688 at 576 ms training time and 432 ms testing time, mean cluster t = 10.256, $p < 0.05$). This finding was replicated in the bimodal dataset in a more extensive time window from ~150 ms when classifiers were trained on the somatosensory and tested on the auditory effect (mean AUC = 0.568 ± 0.059, max. AUC = 0.674 at 188 ms training time and 160 ms testing time, mean cluster t = 22.265 ± 19.849, $p < 0.05$) and vice versa (mean AUC = 0.572 ± 0.049, max. AUC = 0.663 at 292 ms training time and 348 ms testing time, mean cluster t = 24.748 ± 17.699, $p < 0.05$). Taken together, these findings show that there is shared activation between global effects regardless of which sensory modality is used for training and testing. The global effect consistently manifests in a rectangular classification score matrix which suggests that common activation is maintained in cortical networks (with some temporal shifts in onset times).

Interestingly, temporal decoding of local effects revealed short-lived temporal generalisation around ~200 ms in both datasets. In the trimodal dataset, short-lived shared representations from ~200-350 ms were found to be associated with local effects across all comparisons: auditory to somatosensory (mean AUC = 0.511 ± 0.024, max. AUC = 0.587 at 208 ms training time and 304 ms testing time, mean cluster t = 4.07, $p < 0.05$), somatosensory to auditory (mean AUC = 0.509 ± 0.033, max. AUC = 0.612 at 296 ms

training time and 208 ms testing time, mean cluster t = 2.952, $p < 0.05$), auditory to visual (mean AUC = 0.506 ± 0.029, max. AUC = 0.615 at 196 ms training time and 268 ms testing time, mean cluster t = 2.075, $p < 0.05$), visual to auditory (mean AUC = 0.52 ± 0.017, max. AUC = 0.588 at 264 ms training time and 196 ms testing time, mean cluster t = 6.587, $p < 0.05$), somatosensory to visual (mean AUC = 0.506 ± 0.027, max. AUC = 0.597 at 284 ms training time and 272 ms testing time, mean cluster t = 1.812, $p < 0.05$) and visual to somatosensory (mean AUC = 0.497 ± 0.018, max. AUC = 0.546 at 256 ms training time and 216 ms testing time, mean cluster t = -0.897, $p < 0.05$)). In the bimodal dataset, we found evidence for shared representations from ~200 ms when classifiers were trained on somatosensory and tested on auditory deviant-standard pairs (mean AUC = 0.515 ± 0.03, max. AUC = 0.677 at 208 ms training time and 176 ms testing time, mean cluster t = 4.905 ± 9.025, $p < 0.05$) and vice versa (mean AUC = 0.508 ± 0.024, max. AUC = 0.639 at 172 ms training time and 208 ms testing time, mean cluster t = 2.991 ± 8.745, $p < 0.05$).

Our result demonstrates that local effects are supported by supramodal transient activation patterns starting from ~200 ms. Although our finding is compatible with the idea that local effects are processed in cortical hierarchies dedicated to the sensory modality in which the stimulation is applied, we provide evidence for some overlap in higher-order or associative regions between these hierarchies. In sum, these results support the hypothesis that global effects share sustained neural activation patterns between the senses while local effects share fewer, if any, activity (Figure 3)

To corroborate these findings, we use temporal decoding to examine the temporal evolution of cortical activity when global deviant-standard pairs and local deviant-standard pairs are each pooled across sensory modalities. Our results show that the local effect is associated with some temporal generalisation from ~180-250 ms in both the bimodal (mean AUC = 0.508 ± 0.025, max. AUC = 0.649 at 204 ms training time and 204 ms testing time, mean cluster t = 2.747 ± 8.431, $p < 0.05$)and the trimodal dataset (mean AUC =

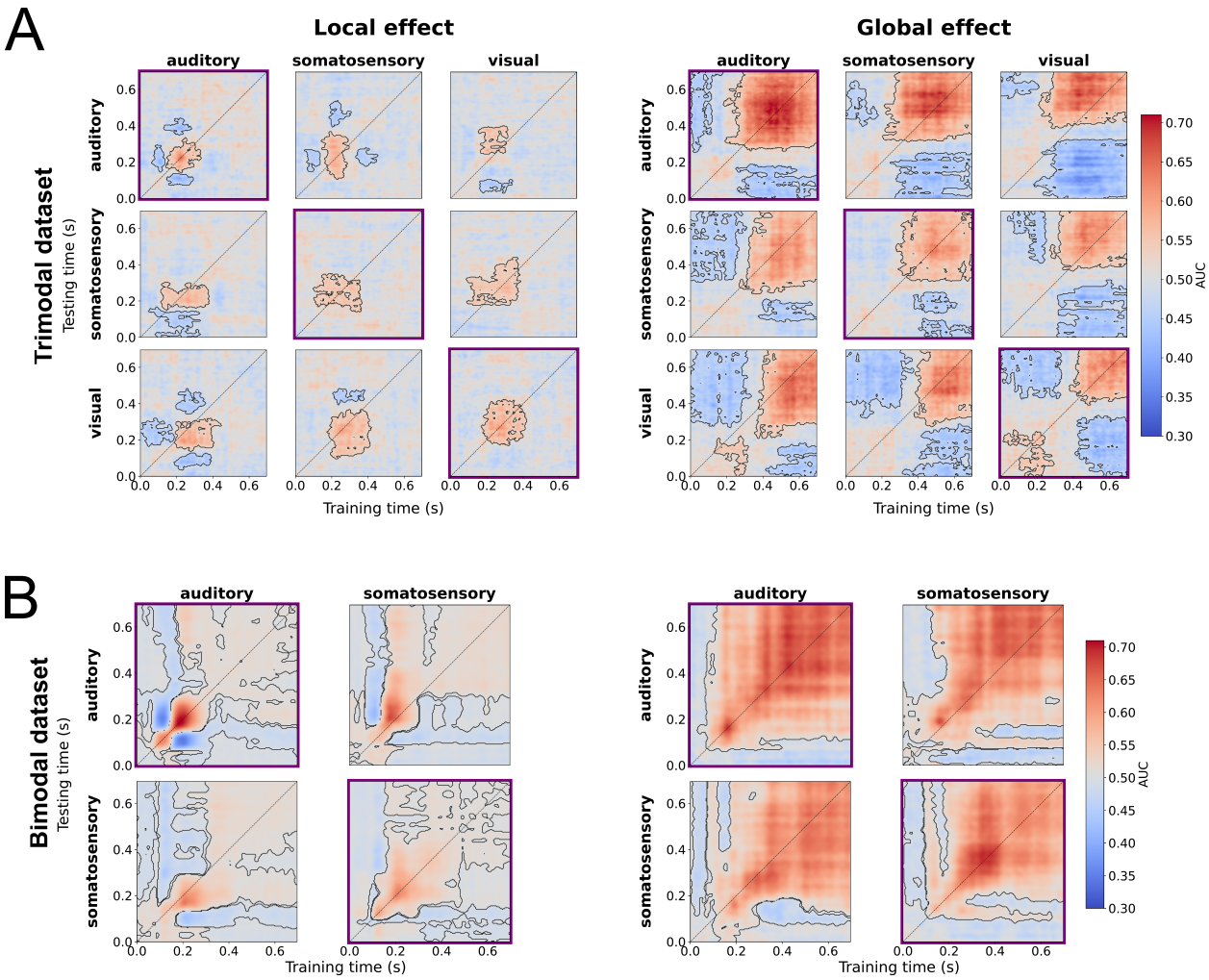

Figure 3. **Temporal generalisation analysis within and between sensory modalities.** Each panel shows results from a series of temporal generalisation analyses decoding the local effect (left) and the global effect (right) in the trimodal dataset (A) and bimodal dataset (B). Each matrix shows results of a temporal generalisation analysis in which a classifier is trained to distinguish deviant and standard trials at each time point in the training modality and then tested on all remaining time points in a trial in the testing modality. For each experiment, this leads to an n-by-n matrix with n being the number of sensory modalities tested in a study (3 for the trimodal and 2 for the bimodal study). Temporal generalisation matrices placed along the diagonal of a panel show results from a decoding analysis performed within a sensory modality and are highlighted with a purple frame. The remaining temporal generalisation matrices show results from a decoding procedure in which a classifier is trained to distinguish deviant and standard trials corresponding to the sensory modality indicated next to each row and tested on the sensory modality corresponding to the column label. AUC-ROC classification scores are shown on a red-to-blue gradient. Classification score clusters which were found to be different from chance in a cluster-based permutation test are delineated with a black line. 0 ms describes the onset of the last stimulus in a trial.

0.513 ± 0.026, max. AUC = 0.574 at 220 ms training time and 220 ms testing time, mean cluster t = 3.874, $p < 0.05$). For local effects, our result is most consistent with the involvement of a series of modality-specific neural generators in early levels of the cortical hierarchy and a contribution of supramodal regions in later stages. Again, temporal decoding revealed sustained shared activation starting from ~150 ms until trial end for the global effect in the bimodal dataset (mean AUC = 0.579 ± 0.057, max. AUC = 0.667 at 340 ms training time and 336 ms testing time). In the trimodal dataset, shared activation between global effects extended across the complete time window. We found evidence for sustained activity from ~350 until trial end. Our results also reveal a rectangular classification score cluster which differs slightly but significantly from chance from the onset of the last stimulus in a trial to ~250 ms (mean AUC = 0.524 ± 0.057, max. AUC = 0.657 at 520 ms training time and 544 ms testing time, mean cluster t = 7.354, $p < 0.05$). Based on work by King et al. (King & Dehaene, 2014), these temporal generalisation results suggest that there is a common generator for global effects in different sensory modalities. In contrast, multiple neural generators support the local effect. For the local effect, our evidence shows that these generators are modality-specific in early stages and supramodal in later stages of cortical processing (Figure 4). Ultimately, we assessed whether there are differences in decoding strength between the local and global effect in a comparison of maximum classification scores in a cluster drawn from all 14 temporal decoding analyses. Peak decoding performance was found to differ between local and global effects using a Mann-Whitney U test (U = 31, $p < 0.001$).

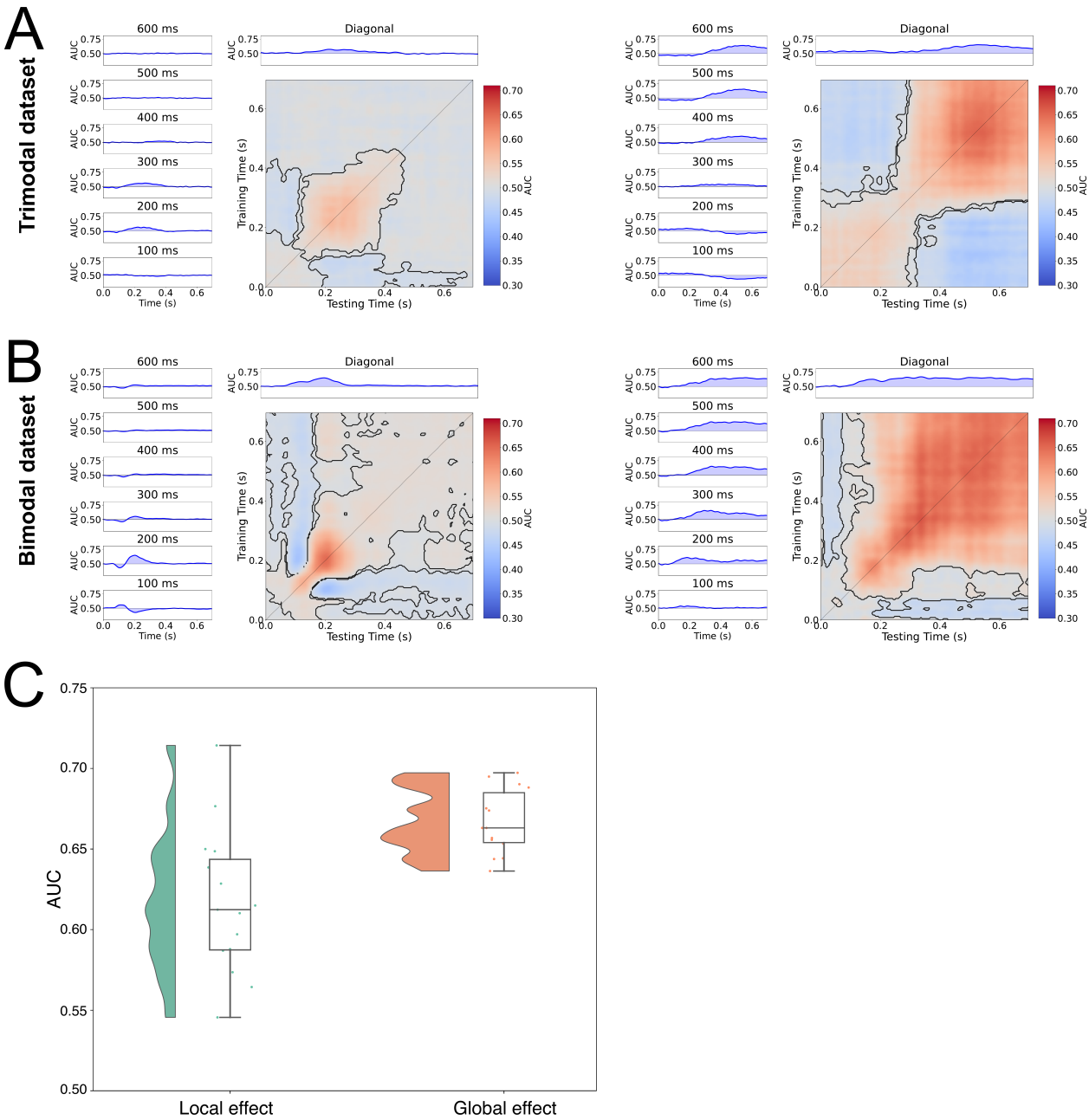

Figure 4. **Temporal decoding of combined sensory modalities.** In a temporal decoding analysis, we pooled deviant trials and standard trials regardless of sensory modality and tested whether a classifier trained to discriminate deviant and standard trials at a specific time point might generalise to the remaining time points. Each panel shows the resulting matrix of AUC-ROC classification scores for the global (A) and local effect (B). In each panel, results for the global effect are shown on the right and results for the local effect are displayed on the left. In conditions in which cluster-based permutation was performed, clusters which differ from chance are highlighted with a purple horizontal line for classification performance in intervals of 100 ms and green for diagonal classification performance. 0 ms marks the onset of the last stimulus in a trial. Clusters of AUC-ROC scores which differed from chance were delineated with a dotted line. Each rain cloud plot shows the distribution of maximum classification scores in a cluster drawn from all 14 temporal decoding analyses for the local and global effect as well as corresponding box-and-whisker plots. Significant differences assessed with a Mann-Whitney U Test are highlighted with an asterisk (C).

Discussion

Hierarchically nested sensory targets elicit local and global responses across sensory modalities

A long-standing debate in neuroscience revolves around which sensory and perceptual processes are supramodal or modality-specific (Cao, Summerfield, Park, Giordano, & Kayser, 2019; Driver & Noesselt, 2008; Faivre, Filevich, Solovey, Kühn, & Blanke, 2018; Walz et al., 2013). Inspired by the notion that perceptual systems in the cortex are hierarchically organised on a simple-to-complex axis (Dürschmid et al., 2016; Kiebel et al., 2008; C. Murray, 2004; Rao & Ballard, 1999), we investigated whether cortical responses to sensory targets implemented in successive levels of the cortical hierarchy are ordered along a gradient of supramodality. We examined whether cortical responses to sensory targets rely more on supramodal activation patterns when sensory targets are complex. Across a series of two experiments combining evidence from the somatosensory, visual and auditory modality, we first established that selective hierarchically nested divergences of sensory inputs can trigger a MMN-like effect at a local level and a P3b-like effect at a global level in different sensory modalities. We applied temporal decoding to show that complex rule-based targets elicit a sustained global response in each modality which relies on a single supramodal network in higher-order cortical networks. Our results demonstrate that the prolonged maintenance of cortical activation elicited by the global effect and the serial propagation of the local effect are principles of cortical function found across sensory modalities. Extending earlier temporal decoding results showing that the auditory global effect is maintained in higher-order cortical networks while cortical activity representing the auditory local effect is serially propagated along cortical areas (King et al., 2014), we demonstrate that cortical hierarchies implement target detection processes which track sensory irregularities in hierarchically nested different timescales at successive cortical processing stages for each sense. Crucially, our finding that the P3b-like global effect relies

on sustained supramodal cortical signatures while the local effect elicits short-lived responses with few commonalities between the senses supports the notion of a gradient of supramodality underpinning cortical hierarchies but also refutes the idea that early cortical processes are strictly unimodal.

Rule-based sensory targets elicit supramodal and sustained responses in the cortex

Our finding that the P3-like global effect as a response to complex sensory targets is supported by sustained common supramodal activation patterns contributes to a debate around its putative supramodal underpinnings. Some studies investigating cortical activation linked to the auditory and visual P3 suggest a common network including the insula and frontoparietal areas between these senses (Linden et al., 1999; Walz et al., 2013). However, other studies highlight a contribution of higher-order regions in modality-specific cortical hierarchies to the P300 (Bledowski et al., 2004). Our results support the notion that the P3 is partially supported by a supramodal network while at the same time not ruling out contributions of modality-specific processes.

In the recent decade, the global effect has been proposed to be a cortical signal reflecting the conscious processing of incoming sensory stimulation (Bekinschtein et al., 2009). By this view, the global effect reflects recurrent information flow in a global neuronal workspace which maintains cortical signatures to become consciously accessible (Dehaene & Changeux, 2011). Sensory inputs from modality-specific cortices are fed forward to the global neuronal workspace which broadcasts integrated multisensory information from the top down to the levels below (Mashour, Roelfsema, Changeux, & Dehaene, 2020). Our observation that the cortical signatures supporting the global effect are supramodal are consistent with the theory that the global effect marks a supramodal top-down-driven process in which sensory information is amplified for conscious access via allocated attention (Chennu et al., 2013).

Local responses to sensory targets are linked to short-lived modality-specific activation

We discovered a short-lived supramodal contribution to the MMN-like local effect which refutes a classic view according to which the MMN relies on modality-specific mechanisms (Nyman et al., 1990; Pazo-Alvarez, Cadaveira, & Amenedo, 2003). In our study, temporal cross-decoding analyses uncovered short-lived supramodal signatures for the local effect starting from ~200 ms after onset of the last stimulus in a trial. Previous studies demonstrate that local effects are supported by a temporofrontal network in which neuronal messages are propagated forward to the inferior frontal gyrus after initial processing in primary sensory areas which raises the possibility that frontal contributions to the MMN might host supramodal signatures. Both the visual and auditory MMN were found to consist of an earlier component in modality-specific early sensory cortices followed by an attention-modulated late frontal component from ~200 ms after oddball onset (Deouell, 2007; Hedge et al., 2015). Similarly, studies of effective connectivity underpinning the MMN show that the potential is likely supported by a network spanning primary and secondary sensory cortices as well as frontal regions in different sensory modalities (Auksztulewicz & Friston, 2015; Chennu et al., 2016; Fardo et al., 2017; Garrido et al., 2009; Ostwald et al., 2012). Finally, the temporal characteristics of supramodal signatures supporting the local effect are congruent with a contribution of frontal areas linked to attention and target detection (Garrido, Kilner, Stephan, & Friston, 2009). Combined with earlier results, our results suggest that the MMN-like local effect might consist of a modality-specific and a supramodal component. Our result is consistent with the idea that successive layers in the cortical hierarchy might support increasingly supramodal processes.

A gradient of supramodality as a principle of cortical organisation

The canonical view of cortical function states that cortical hierarchies implement a strict unimodal-to-supramodal gradient. According to this view, supramodal processing is deferred to associative and frontal cortices (Felleman & Van Essen, 1991). Mounting evidence demonstrates that multisensory processes are ubiquitous in the cortical hierarchy and occur at all processing stages which refutes the idea that early cortices are strictly unimodal (Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006). Integrating both views, our findings support the view that the cortex is hierarchically organised along a gradient of supramodality. Feature-based sensory irregularities trigger quickly decaying and early modality-specific processes which dominate early stages of sensory processing. Finally, a sustained late response to rule-based sensory irregularities shared between sensory modalities might reflect a recurrent supramodal process in higher-order cortical areas. However, our finding that local responses evolve into short-lived supramodal activation patterns provide evidence for the notion that early cortical function is not strictly specific to a sensory modality.

Our results are compatible with a predictive coding view of cortical function. Predictive coding states that cortical responses to irregular sensory information reflect a prediction error resulting from a reconciliation of actual sensory inputs and their predictions (Clark, 2013; Friston, 2005; Hohwy, 2012; Rao & Ballard, 1999). From this perspective, local and global effects can be seen as manifestations of prediction errors located at temporally dissociable successive levels of a dedicated cortical hierarchy for each sense (Wacongne et al., 2011). A central idea in predictive coding is that higher-order levels of the cortical hierarchy converge information from different senses forwarded from the levels below to generate predictions about the sensory environment (Clark, 2013; de Lange et al., 2018; Friston, 2005; Hohwy, 2012). This aligns with our result that higher-order cortical responses share supramodal signatures between the senses while

lower-order responses largely rely on modality-specific activation patterns.

Most research on the MMN and P3b as cortical underpinnings of prediction error signals concentrates on the auditory or visual domain, and comparably less is known about the somatosensory P3b or MMN (Linden et al., 1999; Ostwald et al., 2012). Earlier studies employed the local-global paradigm to demonstrate that the MMN-like local effect is generated in the primary auditory cortex and the global effect relies on activity in frontoparietal regions (Bekinschtein et al., 2009; Chao et al., 2018; Chennu et al., 2013; El Karoui et al., 2015; Uhrig et al., 2014; Wacongne et al., 2011). Extending earlier work, we deliver an integrative framework for cortical responses to sensory targets tracking different timescales at successive levels of the cortical hierarchy across different sensory modalities.

Materials and methods

Participants

We developed two multisensory versions of the local-global paradigm. In the bimodal version, separate blocks of somatosensory or auditory expectation violations were presented. In addition to purely visual, somatosensory and auditory blocks, the trimodal version of the paradigm encompassed blocks in which trials combined inputs from two different sensory modalities which could either be visual, auditory or somatosensory. Only individuals with no history of neurological or psychiatric conditions and no tactile and auditory impairment were recruited into both studies. In addition, participants with visual impairments were excluded from participant in the trimodal study. All participants gave written and informed consent. Data for the bimodal local-global paradigm were collected at the University of Cambridge and obtained ethical approval from the Department of Psychology (CPREC 2014.25). For the bimodal study, we invited individuals aged 18-35 to participate through the SONA participant database at the Department of Psychology. We recruited 30 individuals (15/15 female/male, mean+-STD age is 24.5667(+-4.5157)) who

were paid £10 per hour for a duration of 3-3.5 hours. The trimodal task was performed at the Centre Nationale de la Recherche Scientifique (CNRS) in France. Participants for this study were invited through the CNRS RISC system. Only individuals aged 18-80 were asked to participate in the trimodal study. Of 54 participants (35 female, mean(±STD) age: 25.20(±4.1) years) who participated in the trimodal study, 7 were excluded due to a recording error. Participants in the trimodal study were paid €40 for their effort.

Materials

In the trimodal study, auditory stimulation was applied using Etymotic noise-isolating insert earphones. Eccentric Rotating Mass motors controlled by two Texas Instruments DRV2605 haptic drivers were employed to deliver vibrotactile stimulation to the wrist. Two independent 8x8 LED matrices implemented in virtual reality goggles were used to apply visual inputs isolating visual hemifields. The setup was controlled using an Arduino Zero board. The bimodal study used auditory inputs generated by mixing three sinusoidal signals of either 500, 1000, and 2000 Hz (tone type A) or 350, 700, and 1400 Hz (tone type B) in Matlab R2016 based on (Chennu et al., 2013) and applied using EARTONE 3A insert earphones. Tactile stimulation was delivered using a custom-made device which applies mechanical pins to the fingertip with a Saia-Burgess 12.7 mm stroke, 12 v, 4 W DC push-action solenoid with 0.3-0.6 N force, and no nominal delay after current onset) controlled by an Arduino Mega board.

Paradigm

In a series of two experiments. expectations about sensory inputs were violated either locally within trials or globally between trials. Trials were composed of five stimuli with a stimulus duration of 50 ms and a stimulus onset interval of 150 ms. Each trial consisted of four identical ipsilateral stimuli followed by a deviant contralateral stimulus (locally deviant trials) or another ipsilateral stimulus (locally standard trials). Contrasting locally

deviant and standard trials reveals a MMN-like amplitude difference referred to as local effect in a time window between 50-250 ms after onset of the last stimulus in a trial. Global expectation violations are achieved when a frequently presented trial type is occasionally interspersed with a different trial type. A comparison of frequent (globally standard) trials and rare (globally deviant) trials uncovers a global effect which manifests as a late distributed P3b-like positive wave (Bekinschtein et al., 2009; Chennu et al., 2013, 2016; Phillips et al., 2016; Sitt et al., 2014; Wacongne et al., 2011).

During each study, two block types were presented. The bimodal study consisted of 8 auditory and somatosensory blocks. Standard stimuli in 50% of blocks were presented on the left side and on the right side in the remaining blocks. Each block consisted of 78% globally standard trials and 22% globally deviant trials. In block type bX, locally standard trials were occasionally interrupted by 22 % locally deviant trials which could equally likely be a locally deviant trial in which only the laterality or both laterality and stimulus type were varied. In block type BY, a stream of locally deviant trials in which the last stimulus was applied to the contralateral body hemisphere was occasionally interrupted by locally standard trials or locally deviant trials in which the last stimulus differed in laterality and stimulus type. In the trimodal study, blocks were composed of 80% globally standard and 20% globally deviant trials. Trials randomly started on the left or right side within each block with 50% probability. In blocktype tX, locally standard trials consisting of five identical stimuli were interspersed with locally deviant trials in which the last stimulus was applied to the contralateral hemisphere. Blocktype bY consisted of a sequence of locally deviant trials occasionally interrupted by locally standard trials.

In the bimodal study, somatosensory locally standard trials consisted of five touches ipsilaterally applied to the index finger. We introduced two types of locally deviant trials in which the last stimulus in a trial was applied to the contralateral index finger or contralateral middle finger. In auditory blocks, locally standard trials presented as five identical sounds. Local deviations were introduced by varying either only the laterality of

the ear which received the last sound in a trial or both the laterality and pitch of the last sound in a trial. The latter locally deviant trial type was globally deviant type in each block type and the former locally deviant trial type was globally standard in block type Y and deviant in block type X. The bimodal study consisted of 8 auditory and 8 somatosensory blocks. The block order was pseudo-randomised so that the experiment started with somatosensory block type Y followed by somatosensory block type X, no more than two consecutive blocks were presented in the same sensory modality, and each half of the experiment contained equal proportions of somatosensory and auditory blocks. Each block consisted of 158-160 trials and lasted ~4.5 min. Inter-trial intervals were randomly sampled from a uniform distribution between 800-1000 ms in steps of 50 ms. In each block, 30-34 globally deviant trials were embedded in a sequence of 112 globally standard trials and both deviant types occurred in equal proportions. Each globally deviant trial was preceded either by 2, 3, 4 or 5 globally standard trials in equal proportions. Participants were exposed to white noise during somatosensory blocks to avoid auditory cues from the tactile stimulation device.

The trimodal study contained blocks with exclusively auditory, visual or somatosensory stimulation. Participants in this study also underwent multisensory blocks in which expectations violations require to converge inputs from two of these sensory modalities and which were not further analysed. Local deviations were introduced by varying the laterality of the last stimulus in a trial. 50% of trials applied standard stimuli to the left hemisphere (ear, visual hemifield, or wrist) and the last stimulus to the right hemisphere (and vice versa). Participants underwent three experimental sessions with a total duration of 20 min (4.5 min per session). The remaining two sessions applied crossmodal stimulation and analyses were not included in this paper. 16 participants were presented with somatosensory blocks, 15 participants with auditory blocks and 16 participants with visual blocks. Each block type was presented twice per session in a fixed order: X-Y-X-Y. 31 (~20%) trials included in each block were globally deviant. Each

globally deviant trial was preceded by 3, 4, or 5 globally standard trials.

EEG data analyses

EEG data acquisition was performed using a Net Amps 300 amplifier with an Electrical Geodesics 256-channel high density EEG net at the ICM in Paris for the bimodal study and a 128-channel high density EEG net at the Department of Psychology, University of Cambridge for the trimodal study. We performed EEG data preprocessing using EEGLAB 2019 in Matlab 2019b. In a first step, data were down-sampled to 250 Hz, filtered between 0.5-30 Hz and epoched with respect to the onset of the last stimulus in a trial. Habituation trials at the start of each block were removed. Having removed electrodes placed on the neck and cheek which record mostly muscle artefacts, we retained 91 electrodes in the bimodal data set and 175 electrodes in the trimodal data set for further analysis. We performed baseline removal using a window of 100 ms before epoch onset. Noisy trials (with a variance of >350) and channels (with a variance of >500) were temporarily removed using a semi-automated procedure. We removed artefacts resulting from sweat, eye and muscle movements using independent component analysis. Ultimately, we removed the remaining artefacts using trial-wise interpolation.

We performed cluster-based permutation analyses to test for differences in ERP amplitude time courses, We used the Common Average as a reference and performed a baseline correction in a time window of 100 ms before onset of the last stimulus in a trial. For each condition pair with unequal trial numbers, trials in the condition with a higher trial number were randomly deselected until the number of trials in both conditions was equal. Cluster-based permutation uses Monte Carlo partitioning to obtain a cluster-level t-statistic. To perform Monte Carlo partitioning, data are pooled and randomly divided into two new data sets of equal size. We performed two-sided t-tests on the subject averages time-channel pairs and retained only t-values with $p < 0.05$. Spatiotemporally adjacent t-values were summarised and the largest cluster-level summarised t-value was

identified. Having performed this procedure 3000 times, we determined the p-value corresponding to the proportion of maximal cluster-level t-values larger than the observed t-value in the original comparison. Conditions were deemed to be different if $p < 0.05$ (Oostenveld, Fries, Maris, & Schoffelen, 2011).

We applied temporal decoding to examine whether two contrasts rely on similar cortical signatures. Temporal decoding is a machine learning procedure which assesses whether a classifier trained to discriminate two trial types at one time point will generalise to the remaining time points in a sample. We applied a bootstrapping procedure in which 5 trials were randomly sampled from each dataset until we reached 540 epoch averages for each trial type (deviant/standard) respectively. This procedure was repeated 50 times. Classification performance was assessed on each of the resulting datasets. To perform temporal decoding within a sensory modality, we used a 5-fold stratified cross-validation procedure in which linear support vector machines were trained to optimally separate standard and deviant trials on 4/5 of the data set and tested on the remaining data. For temporal decoding between sensory modalities, we fitted classifiers using training and testing datasets from two different sensory modalities. For each condition pair, we trained and tested classifiers on every time point in a time window of 600 ms after onset of the last stimulus in a trial. Classification performance was assessed using the Area Under the Curve Receiver Operating Characteristic (AUC-ROC) which is a non-parametric criterion-free measure of separability. This procedure results in a training time vs testing time temporal generalisation matrix with AUC-ROC classification scores as cells. To identify adjacent AUC-ROC scores which differ from chance, we performed a Monte Carlo cluster-based permutation analysis with 1024 random partitions on classification score averages from each bootstrapped dataset and applied two-tailed paired t-tests to identify clusters of AUC-ROC values ($p < 0.05$) which differ from chance (King & Dehaene, 2014; King et al., 2014).

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