A partially nested cortical hierarchy of neural states underlies event segmentation in the human brain

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Abstract

A fundamental aspect of human experience is that it is segmented into discrete events. This may be underpinned by transitions between distinct neural states. Using an innovative data-driven state segmentation method, we investigate how neural states are organized across the cortical hierarchy and where in the cortex neural state boundaries and perceived event boundaries overlap. Our results show that neural state boundaries are organized in a temporal cortical hierarchy, with short states in primary sensory regions, and long states in lateral and medial prefrontal cortex. State boundaries are shared within and between groups of brain regions that resemble well-known functional networks. Perceived event boundaries overlap with neural state boundaries across large parts of the cortical hierarchy, particularly when those state boundaries demarcate a strong transition or are shared between brain regions. Taken together, these findings suggest that a partially nested cortical hierarchy of neural states forms the basis of event segmentation.

Introduction

Segmentation of information into meaningful units is a fundamental feature of our conscious experience in real life contexts. Spatial information processing is characterized by chunking spatial regions into objects (e.g. DiCarlo and Cox, 2007). In a similar way, temporal information processing is characterized by segmenting our ongoing experience into separate events (Kurby and Zacks, 2008; Newtson et al., 1977). Segmentation improves our understanding of ongoing perceptual input (Zacks et al., 2001a) and allows us to recall distinct events from our past (Flores et al., 2017; Sargent et al., 2013; Zacks et al., 2006). Recent work has shown that the end of an event triggers an evoked response in the hippocampus (Baldassano et al., 2017; Ben-Yakov and Henson, 2018), suggesting that events form the basis of long-term memory representations. Events that are identified in movie or auditory narratives are often very similar across individuals and can be segmented hierarchically on different timescales (Newtson and Rindner, 1979; Zacks et al., 2001a). According to event segmentation theory (EST), perceptual systems spontaneously segment activity into meaningful events as a side-effect of predicting future information (Zacks et al., 2007). That is, event boundaries are perceived when predictions become less accurate, which can be due to a change in motion or features of the situation such as characters, causes, goals and spatial location (Zacks et al., 2009). However, event boundaries are observed even when a change is predictable, suggesting that other mechanisms play a role (Pettijohn and Radvansky, 2016). One proposal is that experiences are grouped into categories (or event types), which we have learned previously. When a new event type is detected, an event boundary occurs (Shin and DuBrow, 2021).

While much is known about temporal event segmentation at a behavioral level, less is known about its neural underpinnings. A number of studies have investigated which brain regions show evoked responses around event boundaries. Although the exact regions vary across studies, commonly identified regions include the precuneus and medial visual cortex, as well as area V5 and the intraparietal sulcus (Kurby and Zacks, 2018; Speer et al., 2007; Zacks et al., 2001b; Zacks et al., 2010). Increased brain responses at event boundaries in these regions likely reflect updating processes that occur when shifting to a new event model (Ezzyat and Davachi, 2011). Recently a different approach has been introduced to investigate the neural underpinnings of event segmentation (Baldassano et al., 2017). These authors applied a data-driven method, based on Hidden Markov Models (HMMs) to functional magnetic resonance imaging (fMRI) data obtained during movie watching to identify time points where brain activity in a particular region transitioned from one temporarily stable activity pattern to a different pattern. We refer to these periods of relative stability as neural states to distinguish them from subjectively perceived events (Geerligs et al., 2021; Zacks et al., 2007).

These neural states occur on different timescales across the cortical hierarchy, with short lived states in early sensory regions and long lasting states in the precuneus and angular gyrus (Baldassano et al., 2017), in line with previous observations of a temporal hierarchy of information processing in the brain (Hasson et al., 2008; Honey et al., 2012; Lerner et al., 2011; Stephens et al., 2013). Interestingly, for a set of four brain regions, Baldassano and colleagues (2017) showed that neural state boundaries overlapped across different regions and with subjectively experienced event boundaries. These results suggest that neural state segmentation could be the source of perceived event boundaries and that states may be organized in a nested cortical hierarchy, such that the boundaries of faster states in regions lower in the cortical hierarchy are nested within the boundaries of slower regions higher up in the hierarchy. The idea is that each brain region integrates information within discretized neural states

that may align with sensory units in the external environment (e.g., phonemes, words, sentences) and provide its output to the brain regions higher in the cortical hierarchy (Nelson et al., 2017), until neural states at the highest level of the hierarchy align with subjectively experienced events. This way information traveling up the hierarchy is gradually integrated into complex and long-lasting multimodal representations (Hasson et al., 2015). Although this is an intriguing hypothesis, the evidence for it is limited, as it has only been investigated in one previous study using four pre-defined regions of interest (Baldassano et al., 2017). In addition, it remains unknown which brain regions show neural state boundaries that align with perceived event boundaries and what the temporal hierarchy of state segmentation is across large parts of the cortex that remain unexplored.

The aim of the current study was to investigate whether event segmentation is indeed underpinned by neural state segmentation occurring in a nested cortical hierarchy and to characterize the temporal hierarchy of neural state segmentation across the entire cortex. If the brain segments ongoing input in a nested hierarchical fashion, we would expect to find especially long lasting neural states in the frontal cortex, which is often considered the top of the cortical hierarchy (Fuster, 2001). We would also expect to find overlap between neural state boundaries and event boundaries across all levels of the cortical hierarchy, although this overlap should be most consistent for areas at higher levels of the hierarchy where the timescales of neural state segmentation should closely match the experienced timescale of events. Finally, we would expect that state boundaries are most strongly shared between groups of brain regions involved in similar cognitive functions (i.e. networks) and to a lesser extent between more distinct sets of brain areas.

To test these hypotheses we used a novel data-driven state segmentation method, that was specifically designed to reliably detect boundaries between distinct neural states (Geerligs et al., 2021). By using a large movie fMRI dataset from the Cam-CAN project (Shafto et al., 2014) that shows reliable stimulus-driven activity (i.e., significant inter-subject correlations) over nearly all cortical brain regions (Campbell et al., 2015; Geerligs et al., 2018), we were able to study neural state segmentation across the entire cortex for the first time. In comparison to previous work, we address the question of state segmentation in a more focused and extensive way, by identifying the degree of change moving from neural state to the next (i.e. boundary strength), and examining relationships between neural boundaries across functional networks.

Results

To identify neural state boundaries, we applied an improved version of the greedy state boundary search (Geerligs et al., 2021) to a large fMRI dataset in which 265 participants (aged 18-50 years) viewed an 8-minute Alfred Hitchcock movie (Shafto et al., 2014). After hyperaligning the data (Guntupalli et al., 2016) and hemodynamic deconvolution, GSBS was applied to multi-voxel brain activity time courses from overlapping spherical searchlights covering the entire cortex. GSBS provides a set of neural state boundaries for each searchlight and for different numbers of states (*k*). The t-distance metric was used to identify the optimal number of state boundaries in each searchlight (Geerligs et al., 2021). This metric identifies the optimal number of state boundaries such that the Pearson correlations (across voxels) of time points within a state are maximized and correlations of time points in consecutive states are minimized. To optimize the validity and reliability of the neural states detected by GSBS, we improved the algorithm in several ways as shown in the supplementary methods section. Searchlights in which we were unable to identify reliable neural state boundaries were excluded from further analysis (see figure S5). Searchlight-level results were projected to the voxel level by averaging results across overlapping searchlights.

The median duration of neural states differed greatly between brain regions, ranging from 4.5 seconds in the voxels with fastest transitions up to 27.2 seconds in the slowest voxels (see figure 1A). Most voxels showed median state durations between 5.1 and 18.5 seconds per state. To determine whether regional differences in state duration were reliable, neural state boundaries were identified in two independent groups of participants. At the voxel-level, there was a very high Pearson correlation between the median state durations of the two groups (r=0.85; see figure 1A). This correlation was lower when we computed it at the level of searchlights (i.e., before projecting to the voxel level; r=0.62). This suggests that regional differences in neural state timescales are highly reliable across participant groups and that the variability present in specific searchlights can be reduced substantially by averaging across overlapping searchlights. The timing of neural state boundaries was not associated with head motion (see supplementary results).

Figure 1A shows that there were particularly fast transitions between stable activity patterns in visual cortex, early auditory cortex and somatosensory cortex. State transitions were slower in areas further up cortical hierarchy, such as the angular gyrus, areas in posterior middle/inferior temporal cortex, precuneus, the anterior temporal pole and anterior insula. Particularly slow state transitions were observed in high-level regions such as the medial prefrontal gyrus and anterior portions of the lateral prefrontal cortex, particularly in the left hemisphere.

We also investigated how the variability of state durations differed across the cortex. Because variability of state duration, as measured by the interquartile range (IQR), tends to increase as the median state duration increases, we used a nonparametric alternative to the coefficient of variation (IQR divided by the median). We found very pronounced variability in state durations in the middle and superior temporal gyri and the anterior insula, while the variability was consistently lower in all other cortical areas. This effect was highly reliable across the two independent groups of participants (r=0.84 at voxel level; r=0.54 at the searchlight level).

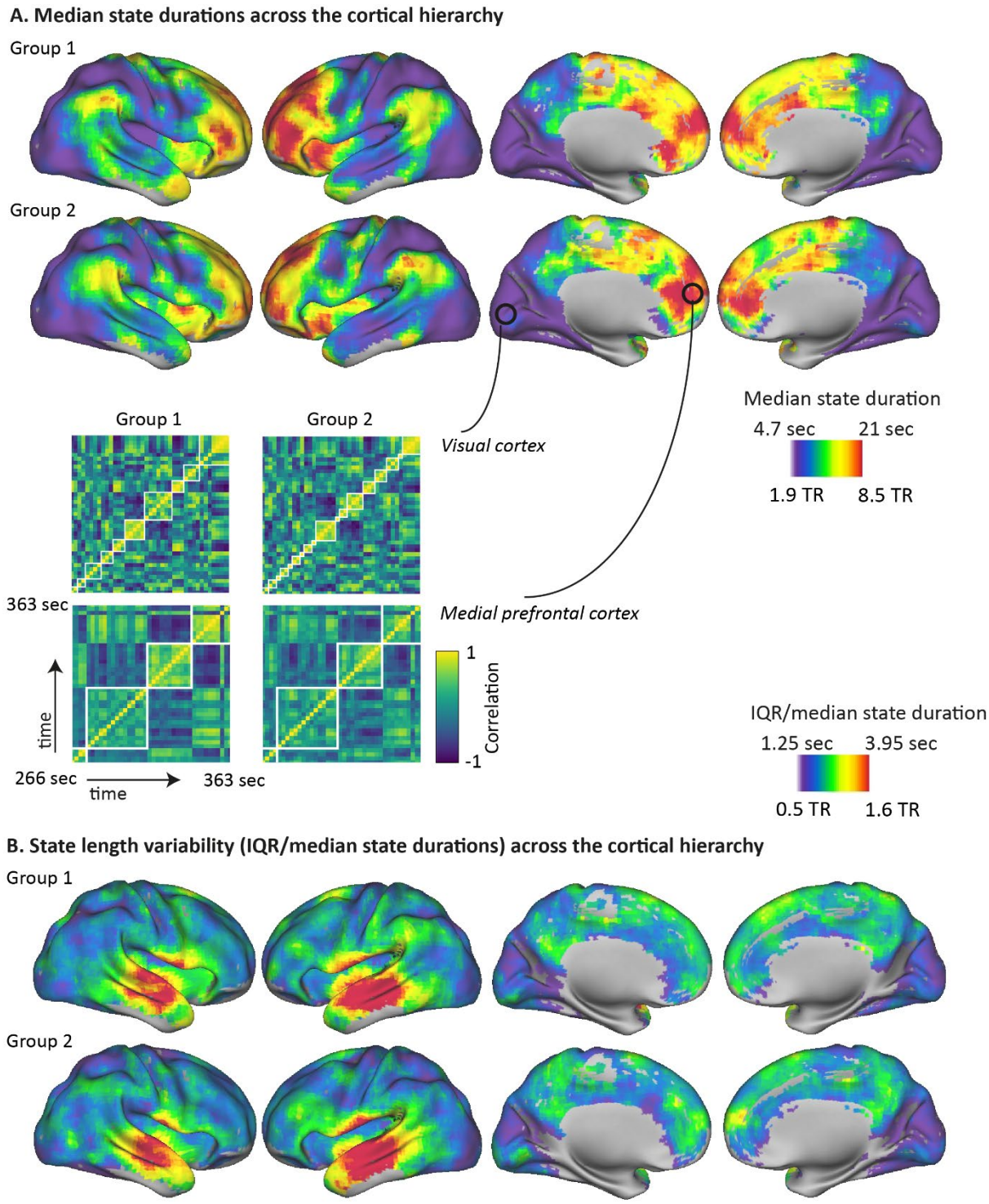

Figure 1A. The optimal number of states varied greatly across regions, with many shorter states in the primary visual, auditory and sensorimotor cortices and few longer states in the association cortex, such as the medial and lateral prefrontal gyrus. These results are highly consistent across two independent groups of participants. Parts of the correlation matrices for two selected searchlights are shown in the insets for each of the groups, representing approximately 1.6 minutes of the movie. The white lines in these insets are the neural state boundaries that are detected by GSBS. B. The variability in state durations, as quantified by the IQR/median state duration, was particularly high in the middle and superior temporal gyri and the anterior insula.

Neural states and perceived event boundaries

If neural states are organized in a nested cortical hierarchy, with some of the state boundaries at lower levels reoccurring throughout the hierarchy and reaching conscious awareness, we would expect state boundaries to align with perceived event boundaries across all of the different levels of the hierarchy. The most consistent alignment would be expected in higher level cortical areas where the number of states should more closely align with the number of perceived events. Event boundaries were determined by asking participants to indicate when they felt one event (meaningful unit) ended and another began (Ben-Yakov and Henson, 2018). To determine the similarity between neural state boundaries and perceived event boundaries, we computed the absolute boundary overlap. This is defined as the number of timepoints where neural state and perceived event boundaries overlapped, scaled such that the measure is one when all neural state boundaries align with a perceived event boundary and zero when the overlap is equal to the overlap that would be expected given the number of boundaries.

We found that a large number of brain regions, throughout the cortical hierarchy, showed significant absolute boundary overlap between neural state and perceived event boundaries after false-discovery-rate (FDR) correction for multiple comparisons (see figure 2A). In particular, we observed that the anterior cingulate cortex, dorsal medial prefrontal cortex, left superior and middle frontal gyrus and anterior insula show the strongest absolute overlap between neural state boundaries and perceived boundaries. This suggests that neural state boundaries in these regions are most likely to underlie the experience of an event boundary.

The absolute boundary overlap is partly driven by regional differences in the number of neural state boundaries. However, our hypothesis of a nested cortical hierarchy suggests that regions in early stages of the cortical hierarchy, with many neural state boundaries, should also show overlap between neural state and perceived event boundaries. To correct for regional differences in the opportunity for overlap, we computed the relative boundary overlap, which is scaled by the maximum possible overlap given the number of state and event boundaries. It is one when all perceived event boundaries coincide with a neural state boundary (even if there are many more neural states than events) or when all neural state boundaries coincide with an event boundary. A value of zero indicates that the overlap is equal to the expected overlap. This metric gives a different pattern of results, showing that regions across different levels of the cortical hierarchy (early and late) have strong overlap between neural states and perceived event boundaries (see figure 2B). Regions early in the cortical hierarchy, such as the medial visual cortex, the medial and superior temporal gyri and the postcentral gyrus show strong relative overlap. The same is true for regions later in the hierarchy, including the anterior insula, most areas of the default mode network (DMN), including the medial frontal gyrus, anterior parts of the precuneus and the angular gyrus and large parts of the lateral frontal cortex. These results suggest that there is overlap between event and neural state boundaries throughout the cortical hierarchy.

To determine what dissociates neural state boundaries that are not associated with an event boundary from those that are, we investigated the degree of neural state change at each boundary. Specifically, we define boundary strength as the Pearson correlation distance between the neural activity patterns of consecutive neural states. We found that stronger boundaries, so boundaries that coincided with a larger shift in brain activity patterns, were more often associated with an experienced event boundary, particularly in the middle and superior temporal gyri, extending into the inferior frontal gyrus (see figure 2C), but also in the precuneus and medial prefrontal cortex.

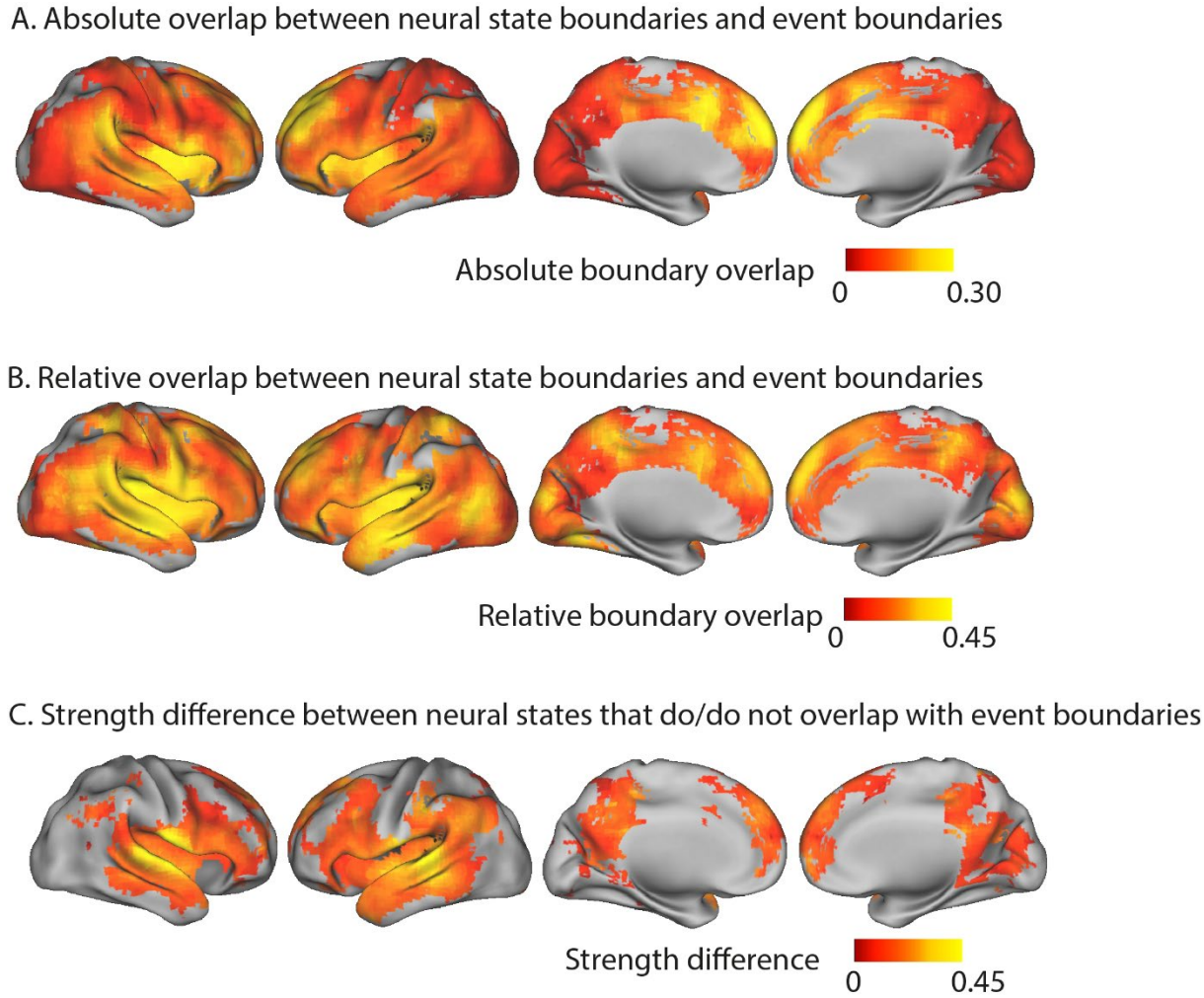

Figure 2A. Absolute boundary overlap between neural state boundaries the perceived event boundaries identified by a different group of participants outside the scanner. The metric is scaled between zero (expected overlap) and one (all neural state boundaries overlap with an event boundary). The medial prefrontal cortex, anterior insula, anterior cingulate cortex and left superior and middle frontal gyrus show the strongest alignment between neural state boundaries and perceived event boundaries. B. Relative overlap between neural state boundaries and perceived event boundaries (scaled w.r.t. the maximal possible overlap given the number of neural state boundaries). Regions in different parts of the cortical hierarchy (early and late) show a significant association between the neural state boundaries and perceived event boundaries C. Association between the strength of the neural state boundaries and perceived event boundaries. Regions with strong neural state boundaries (i.e., a large change between successive states) were more likely to overlap with perceived event boundaries than weak boundaries. Statistical analyses for panels A-C were based on data from 15 independent groups of participants, the depicted difference/overlap values were based on data in which all 265 participants were averaged together. All of the colored regions showed a significant association after FDR correction for multiple comparisons.

Neural state networks

If neural state boundaries are organized in a nested cortical hierarchy, different brain regions would be expected to show substantial overlap in their neural state boundaries. Therefore, we investigated for each pair of searchlights whether the relative neural state boundary overlap was larger than would be expected by chance, given the number of boundaries in these regions. We observed that the overlap was significantly larger than chance for 85% of all pairs of searchlights, suggesting that neural state boundaries are indeed shared across large parts of the cortical hierarchy (see figure 3A). Although the overlap was highly significant for the majority of searchlight pairs, we did not observe a perfectly nested architecture. If that were the case, the relative boundary overlap between searchlights would have been one.

To investigate the overlap between regions in more detail, we identified networks of brain regions that shared state boundaries, by computing the relative boundary overlap between each pair of searchlights and using consensus partitioning based on Louvain modularity maximization to identify networks (Blondel et al., 2008; Lancichinetti and Fortunato, 2012). We found that state boundaries were shared within long-range networks. Some of these networks resembled canonical networks typically identified based on (resting state) timeseries correlations (see figure 3B). To quantify this, we computed the proportion of searchlights overlapping with each of the networks defined by Power et al. (2011, see table S1). We identified an auditory network, that extended into regions involved in language processing in the left inferior frontal gyrus, a fronto-parietal control network (FPCN), a cingulo-opercular network (CON) and a motor network. The default mode network (DMN) we identified was fractionated into anterior, superior and posterior components. Similarly, the sensorimotor network (SMN) we identified was split into a lateral and medial component. We also identified a network overlapping with the dorsal attention network (DAN), although the network we identified only covered posterior parts of the DAN but not the frontal eye fields. While the visual network is typically identified as a single network in functional connectivity studies, we observed two networks, roughly corresponding to different levels of the visual hierarchy (early and late). Figure 3 visualizes for each voxel, which functional network label occurs most frequently for the searchlights overlapping that voxel. In contrast, the full extent of each of the functional networks can be seen in figure 4.

Figure 3C shows the average timescale within each of these functional networks. The networks with the longest durations were the anterior DMN and the FPCN, while the early visual network, lateral SMN and DAN had particularly short state durations. Although regions within functional networks tended to operate on a similar temporal scale, we also observed a lot of variability in state duration within networks, particularly in the auditory network (see figure 3C). Many networks also showed a clear within-network gradient of timescales, such as the auditory network, the sensorimotor networks, the posterior DMN and the FPCN (see figure 4). These results suggests that the relative boundary overlap between regions is not simply driven by a similarity in the number of states, but rather by a similarity in the state boundary timings. This is also supported by the results in figure S6, showing that the relative boundary overlap was highly distinct from the absolute pairwise differences in median state duration (r=-0.05).

Although the networks we identified show overlap with functional networks previously identified in resting state, they clearly diverged for some networks (e.g., the visual network). This divergence was supported by the overall limited similarity with the previously identified networks by Power et al.

(2011; adjusted mutual information = 0.39), as well as the differences between the correlation matrix that was computed based on the mean activity time courses in each searchlight and the relative boundary overlap between each pair of searchlights (figure S6; r=0.31). Interestingly, regions with strongly negatively correlated mean activity time courses typically showed overlap that was similar to or larger than the overlap expected by chance. Indeed, the relative boundary overlap between each pair of searchlights was more similar to the absolute Pearson correlation coefficient between searchlights (r=0.39) than when the sign of the correlation coefficient was preserved (r=0.31). This suggests that pairs of regions that show negatively correlated BOLD activity still tend to show neural state boundaries at the same time.

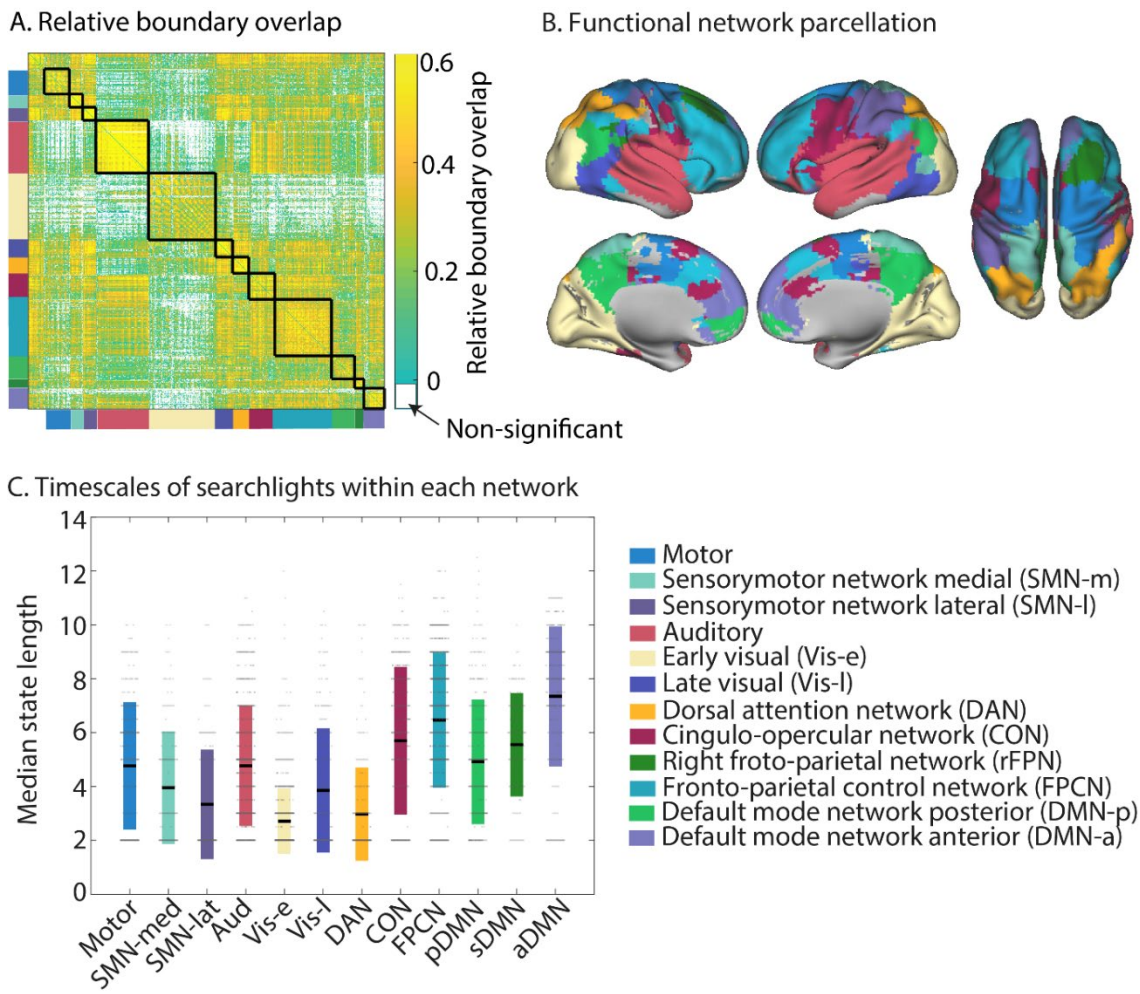

Figure 3. Neural state boundaries are shared within and across distinct functional networks that span the cortical hierarchy. A. The relative boundary overlap between each pair of searchlights, ordered according the functional networks they are in. The black lines show the boundaries between functional networks. Searchlight pairs shown in white did not have significant relative boundary overlap after FDR correction for multiple comparisons. B. Visualization of the detected functional networks. The network label at each voxel is determined by the functional network that occurs most often in all the searchlights that overlap with that voxel. C. Visualization of the neural state durations within each network. Each searchlight is shown as a dot. The colored bars show the mean and one standard deviation around the mean for each network. The data shown in panels A-C are based on data averaged across all participants. The test for statistical significance in panel A were performed with data of 15 independent groups of participants.

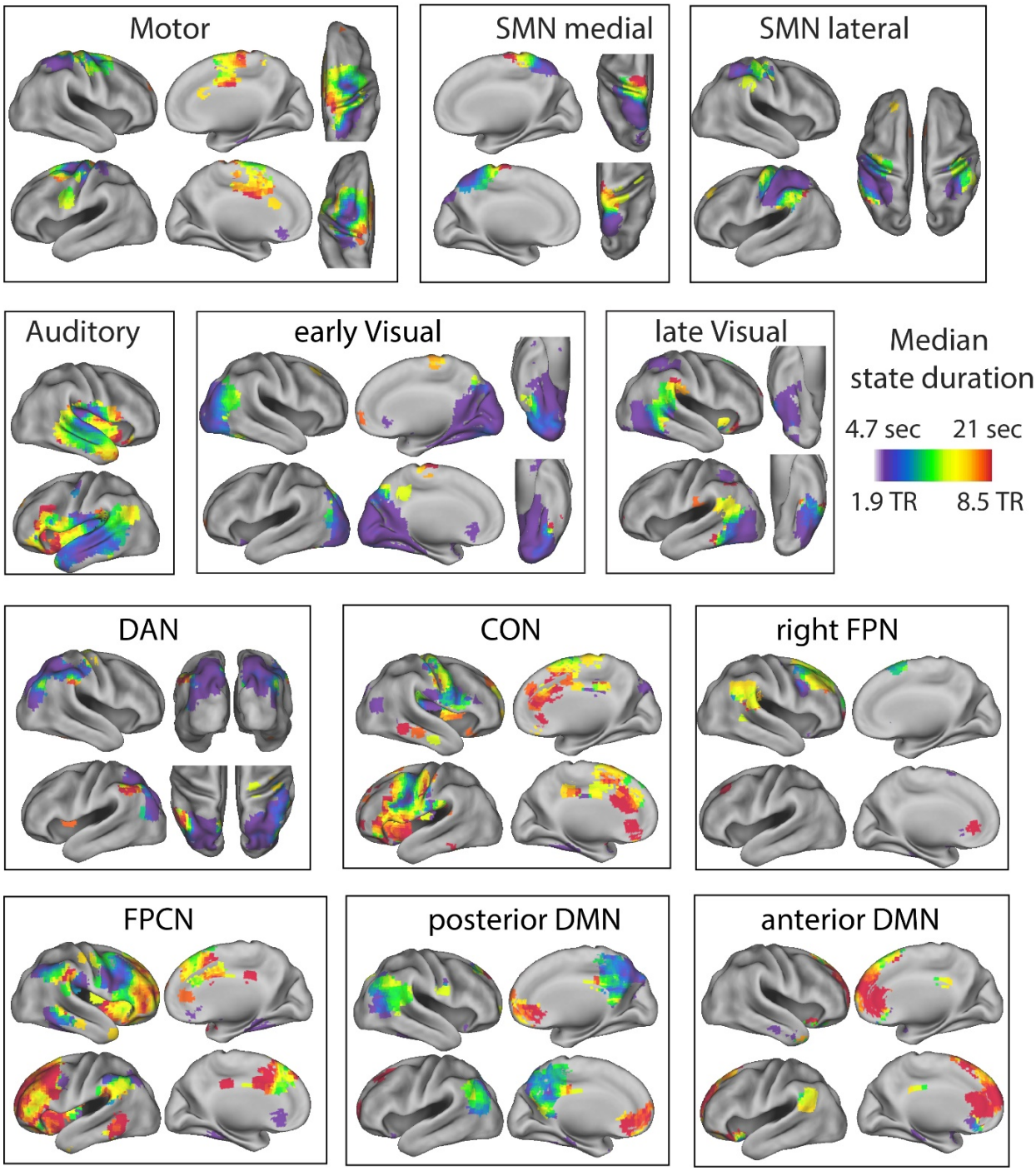

Figure 4: Separate visualizations for each of the identified functional networks, showing the median state duration for each of the searchlights within the functional network. SMN=sensorimotor network, DMN=default mode network, FPCN=fronto-parietal control network, CON=cingulo-opercular network, DAN=dorsal attention network. The figure shows the median state duration estimates across all 15 groups of participants.

It should be noted that although the overlap in neural state boundaries was strongest for the searchlights that were part of the same functional networks, we also found a lot of evidence for the idea that boundaries are shared across different levels of the cortical hierarchy (see figure 3A). Overlap

was particularly strong between all higher-order networks (DAN, CON, FPCN and the DMNs), as well as between the motor and sensorimotor networks. The sensorimotor, motor and auditory networks also showed highly significant overlap with the higher order networks. Lower levels of overlap were observed between the early-visual network and all other networks (except the DAN), as well as between the auditory and the sensorimotor networks.

If state boundaries form a nested cortical hierarchy, we expect that boundaries that are shared within functional networks, and particularly those that are shared across networks, will be more frequently associated with the perception of an event boundary. To investigate this, we computed the percentage of searchlights that showed a state boundary within each of the networks for each timepoint. Next, we used a logistic regression model per network to compute how much of the variance in the occurrence of perceived event boundaries (boundary absent or present) could be explained by the boundary co-occurrence within each network as well as across the whole cortex.

We found that perceived boundaries were significantly predicted by boundary co-occurrence in each of the functional networks (see figure 5A). The networks that explained the most variance were the aDMN, sDMN, FPCN and auditory network, followed by the CON and pDMN. The DAN, visual, motor and SMN networks explained the least variance. These results show that boundary co-occurrence within specific networks is associated with perceived event boundaries. Interestingly, boundary co-occurrence across the whole cortex (all searchlights) showed an even stronger association with perceived event boundaries than the aDMN, suggesting that boundaries shared more broadly across the cortical hierarchy are more likely to coincide with the experience of an event.

To investigate the role of boundary co-occurrence across networks in more detail, we investigated for each pair of searchlights whether boundaries that are shared have a stronger association with perceived event boundaries as compared to boundaries that are unique to one of the two searchlights. We found that boundary sharing had a positive impact on overlap with perceived boundaries, particularly for searchlights in the auditory network and the aDMN (see figure 5B and C). In particular, we saw that boundaries that were shared within the auditory network or between the auditory and the early and late visual networks, the CON and aDMN were more likely to be associated with a perceived boundary than non-shared boundaries. The same was true for boundaries shared between the aDMN and the lateral and medial SMN network, the DAN and the pDMN.

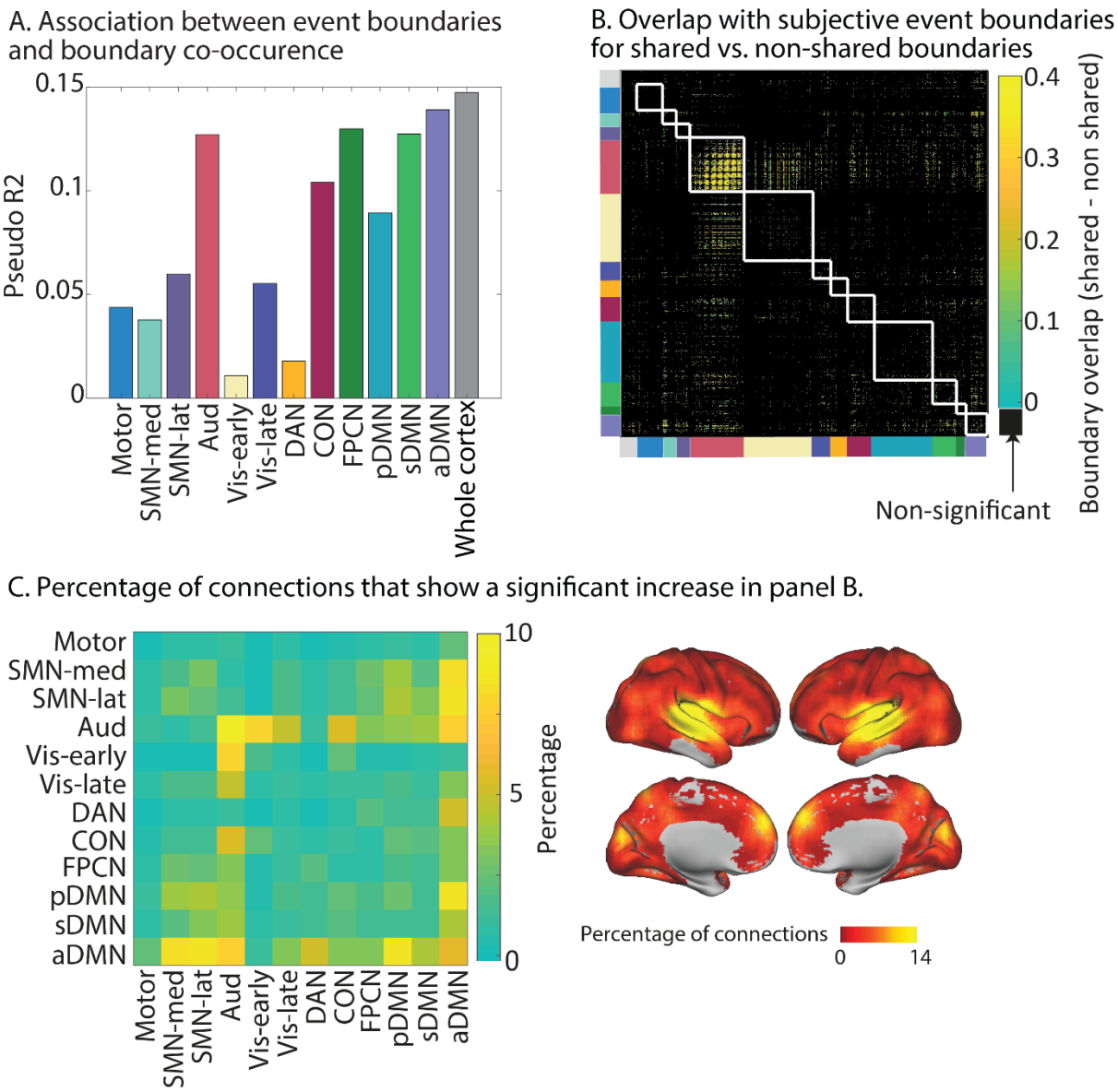

Figure 5A. For each network, we show the Nagelkerke pseudo R^2 that is obtained when using a logistic regression model to explain perceived event boundaries with neural state boundary co-occurrence within each network, as well as across the whole cortex. Each of the networks shows a significantly positive association with perceived boundaries. B. For each pair of searchlights we compare the relative boundary overlap between neural state boundaries between boundaries that are shared and boundaries that are not shared. In particular, for each pair, the searchlight with the highest relative boundary overlap with events is used as the reference in the comparison. The white lines show the boundaries between functional networks. C. Shows the percentage of connections in panel B that show a significant increase in relative boundary overlap with events for shared vs. non-shared neural state boundaries. Here, the data are summarized to a network-by-network matrix for ease of interpretation. It should be noted that the color scale in C does not reflect the full range of the data because there was an outlying value in the auditory network, where 32% of connections showed an increase in overlap for shared vs. non shared boundaries.

Discussion

While event segmentation is a critical aspect of our ongoing experience, the neural mechanisms that underlie this ability are not yet clear. The aim of this paper was to investigate the cortical organization of neural states that may underlie our experience of distinct events. By combining an innovative data-driven state segmentation method, with a movie dataset of many participants, we were able to identify neural states across the entire cortical hierarchy for the first time. We observed particularly fast states in primary sensory regions and long periods of information integration in the left middle frontal gyrus and medial prefrontal cortex. Across the entire cortical hierarchy, we observed associations between neural state and perceived event boundaries and our findings demonstrate that neural state boundaries are shared within long-range functional networks as well as across the temporal hierarchy between distinct functional networks.

A partially nested cortical hierarchy of neural states

Previous findings have suggested that neural states may be organized in a nested cortical hierarchy (Baldassano et al., 2017). In line with this hypothesis, we observed that neural state boundaries throughout the entire hierarchy overlap with perceived event boundaries, but this overlap is particularly strong for transmodal regions such as the dorsal medial prefrontal cortex, anterior cingulate cortex, left superior and middle frontal gyrus and anterior insula. In line with event segmentation theory, the strong alignment in the anterior cingulate cortex suggest that the disparity between predicted and perceived sensory input may play a role in the experience of an event boundary (Holroyd and Coles, 2002; Kurby and Zacks, 2008), while the involvement of the dorsal medial prefrontal cortex is in line with previous studies linking this region to representations of specific events (Baldassano et al., 2018; Krueger et al., 2009; Liu et al., 2021).

Once we accounted for the maximal possible overlap given the number of neural states in a particular brain region, we also found strong overlap in unimodal areas such as the visual, auditory and somatosensory cortices. This finding suggests that some of the neural state boundaries that can be identified in early sensory regions are represented throughout the cortical hierarchy until they are eventually reflected in conscious experience. Which of the boundaries in lower-level areas propagate to higher-order cortical areas may be moderated by attentional mechanisms, which are known to alter cortical information processing through long-range signals (Buschman and Miller, 2007; Gregoriou et al., 2009). In the extreme case when participants are not attending the sensory input (i.e., during daydreaming) there may be much lower correspondence between neural state boundaries in higher and lower-level regions.

So, what do these neural states represent? Recent work by Chien and Honey (2020) has shown that neural activity around an artificially introduced event boundary can be effectively modeled by ongoing information integration, which is reset by a gating mechanism, very much in line with the mechanism proposed to underlie event segmentation (Kurby and Zacks, 2008). Similarly, neural states may represent information integration about a particular stable feature of the environment, which is reset when that feature undergoes a substantial change (Bromis et al., 2022). This suggests that neural states in early visual cortex may represent short-lived visual features of the external environment, while

states in anterior temporal cortex may contain high-level semantic representations related to the ongoing narrative (Clarke and Tyler, 2015). For transmodal regions such as the medial prefrontal cortex, or middle frontal gyrus, that have been associated with many different high level cognitive processes (e.g. Duncan, 2010; van Kesteren et al., 2012; Simony et al., 2016), it is not yet clear what a distinct neural state might represent. Just as perceived event boundaries can be related to changes in one or multiple situational dimensions, such as changes in goals or locations (Clewett et al., 2019; Zacks et al., 2009), neural state boundaries in transmodal cortical areas may not necessarily reflect one particular type of change. State boundaries in these regions are likely also dependent on the goals of the viewer (Wen et al., 2020).

We also investigated the factors that distinguish neural state boundaries that traverse the hierarchy from those that do not. It has previously been shown that changes across multiple aspects of the narrative are more likely to result in an experienced event boundary (Zacks et al., 2010). In line with this, we observed that boundaries that were represented in more brain regions at the same time were also more likely to be associated with the experience of an event boundary. The strength of the neural state boundary, as measured by the amount of change in neural activity patterns, was also identified as a factor that can to some degree distinguish neural states that appear in subjective experience from the neural states that do not, particularly in temporal cortex, inferior frontal gyrus, precuneus and medial prefrontal gyrus. This suggest that a neural state boundary is not an all or none occurrence. Instead, the reset of representations at neural state boundaries (Chien and Honey, 2020) may differ based on what is happening in other brain regions, on the current attentional focus or based on the degree of change in the representations of the environment in that particular brain region.

More evidence for the idea of a nested cortical hierarchy of neural state boundaries comes from our connectivity analyses, which show that neural state boundaries are shared both within and across groups of regions that partly resemble well known functional brain networks. This sharing of boundaries across different cortical areas may suggest that neural states in higher level cortical regions represent an overarching representation that corresponds to many distinct states in lower-level cortical areas, which all represent different features of that overarching representation (e.g., words spoken, characters on screen or locations within a particular situation). This is in line with previous conceptualizations of events as partonomic hierarchies (Zacks et al., 2001a) and with other models of hierarchical neural representations, such as the hub-and-spokes model for semantic representations, which proposes that semantic knowledge is represented by the interaction between modality-specific brain regions and a transmodal semantic representational hub in the anterior temporal lobe (Lambon Ralph et al., 2010; Rogers et al., 2004). It is also in line with a recently proposed hierarchical representation of episodic memories, in which items that are linked within small-scale events are in turn linked within large-scale episodic narratives (Andermane et al., 2021).

Timescales of information processing across the cortex

While previous studies have been able to show regional differences in the time scale of information processing across parts of the cortex (Baldassano et al., 2017; Hasson et al., 2008; Honey et al., 2012; Lerner et al., 2011; Stephens et al., 2013), here we were able to reveal neural state timescales across the entire cortex for the first time. The validity of our results is supported by extensive validations using simulations (see supplementary materials and Geerligs et al., 2021) and the reliability of our

observations across independent groups of participants. It is also supported by the similarity between our results and previous findings based on very different approaches, such as experiments with movies and auditory narratives that have been scrambled at different timescales (Hasson et al., 2008; Honey et al., 2012; Lerner et al., 2011), or resting-state fluctuations in electrocorticography (Honey et al., 2012) and functional MRI data (Stephens et al., 2013).

Although we characterized brain areas based on their median state length, we observed that neural states within a region were not of equal duration, suggesting that regional timescales may change dynamically based on the features of the stimulus. This is also in line with the observed correspondence between neural state and perceived event boundaries. Event boundaries have previously been shown to align with changes in features of the narrative, such as characters, causes, goals and spatial locations (Zacks et al., 2009). Therefore, the overlap between state boundaries and perceived event boundaries across the cortex also suggest that characteristics of the sensory input are driving the occurrence of neural state boundaries. Together, these findings show that the timescale of information processing in particular brain regions are not only driven by stable differences in the rate of temporal integration of information, that may be associated with interregional interactions in the neural circuitry (Honey et al., 2012), but also by the properties of the input that is received from the environment. Our results show that some of the areas that were not covered in previous investigations (Baldassano et al., 2017; Hasson et al., 2008; Honey et al., 2012; Lerner et al., 2011; Stephens et al., 2013), such as the medial prefrontal cortex and middle frontal gyrus, have the longest timescales of information processing. This suggests these regions at the top of the cortical hierarchy (Clarke and Tyler, 2015; Fuster, 2001) also have the slowest timescales of information processing, in line with expectations based on the hierarchical process memory framework (Hasson et al., 2015).

Functional networks of neural state boundaries

In line with previous work (Baldassano et al, 2017) we found that neural state boundaries are shared across brain regions. Our results show for the first time that these boundaries are shared within distinct functional networks. Interestingly, the networks we identify partially resemble the functional networks that are typically found using regular functional connectivity analyses (c.f. Power et al., 2011; Yeo et al., 2011), though there are some differences. For instance, the visual network was segregated into two smaller subnetworks and for other networks, the topographies sometimes deviated somewhat from those observed in prior work.

Our results show that functional networks defined by state boundaries differ in their timescales of information processing. While some networks have a particular temporal mode of information processing, other networks show a within-network gradient of neural state timescales. For the DMN we observed a split into posterior, superior and anterior subnetworks with markedly different timescales. The anterior and posterior subnetworks closely resemble previously observed posterior and anterior DMN subnetworks (Andrews-Hanna et al., 2010; Campbell et al., 2013; Lei et al., 2014), while the superior subnetwork resembles the right dorsal lateral DMN subnetwork (Gordon et al., 2020). The posterior/fast DMN is particularly prominent in the precuneus and angular gyri, which are thought to engage in episodic memory retrieval through connectivity with the hippocampal formation (Andrews-Hanna et al., 2010). The posterior DMN has also been proposed to be involved in forming mental scenes or situation models (Ranganath and Ritchey, 2012). Thus, neural states in this

subnetwork may reflect the construction of mental scenes of the movie and/or retrieval of related episodic memories. The superior DMN (or right dorsal lateral DMN) showed timescales of neural states that were in between those of the anterior and posterior DMN. This network has previously been suggested to be a connector hub within the DMN, through which the FPCN exerts top-down control over the DMN. This is line with the strong state boundary overlap we observed between searchlights in the sDMN and the FPCN. The anterior/slow DMN is particularly prominent in the medial prefrontal cortex which has been related to self-referential thought, affective processing, and integrating current information with prior knowledge (Benoit et al., 2014; Gilboa and Marlatte, 2017; Van Kesteren et al., 2012; Northoff et al., 2006). The current results suggest that these processes require integration of information over longer timescales.

Real life experience

Although event segmentation is thought to be a pivotal aspect of how information is processed in real life (Zacks et al., 2007), it is often not considered in experimental settings, where events are predetermined by the trial or block structure. This study and previous work (Baldassano et al., 2017) shows that we are now able to investigate brain activity as it unfolds over time without asking participants to perform a task. This allows us to study brain function in a way that is much more similar to our daily life experience than typical cognitive neuroscience experiments (Hamilton and Huth, 2020; Lee et al., 2020; Willems et al., 2020). This opens the door for investigations of neural differences during narrative comprehension between groups of participants, such as participants with autism who may have trouble distinguishing events that require them to infer the state of mind of others (Baron-Cohen, 2000; Hasson et al., 2009), or participants with Alzheimer's disease, who may have trouble with segmenting and encoding events in memory (Zacks et al., 2006).

It should be noted that this more naturalistic way of investigating brain activity comes at a cost of reduced experimental control (Willems et al., 2020). For example, some of the differences in brain activity that we observe over time may be associated with eye movements. Preparation of eye movements may cause activity changes in the frontal-eye-fields (Vernet et al., 2014), while execution of eye movements may alter the input in early sensory regions (Lu et al., 2016; Son et al., 2020). However, in a related study (Davis et al., 2021), we found no age difference in eye movement synchrony while viewing the same movie, despite our previous observation of reduced synchrony with age in several areas (particularly the hippocampus, medial PFC, and FPCN; Geerligs et al., 2018), suggesting a disconnect between eye movements and neural activity in higher-order areas. In addition, reducing this potential confound by asking participants to fixate leads to an unnatural mode of information processing which could arguably bias the results in different ways by requiring participants to perform a double task (monitoring eye movements in addition to watching the movie).

Conclusion

Here, we demonstrate that event segmentation is underpinned by neural state boundaries that occur in a nested cortical hierarchy. This work also provides the first cortex-wide mapping of timescales of information processing and shows that the DMN fractionates into faster and slower subnetworks. Together, these findings provide new insights into the neural mechanisms that underlie event

segmentation, which in turn is a critical component of real-world perception, narrative comprehension, and episodic memory formation. What remains to be addressed is how timescales of different brain regions relate to the types of neural representations that are contained within these regions. For example, does the dissociation between the posterior and anterior default mode network reflect relatively fast construction of mental scenes and slow integration with existing knowledge, respectively? Studying brain function from this perspective provides us with a new view on the organizational principles of the human brain.

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Materials and Methods

Participants

This study included data from 265 adults (131 female) who were aged 18–50 (mean age 36.3, SD = 8.6) from the healthy, population-derived cohort tested in Stage II of the Cam-CAN project (Shafto et al., 2014; Taylor et al., 2017). Participants were native English-speakers, had normal or corrected-to-normal vision and hearing, and had no neurological disorders (Shafto et al., 2014). Ethical approval for the study was obtained from the Cambridgeshire 2 (now East of England - Cambridge Central) Research Ethics Committee. Participants gave written informed consent.

Movie

Participants watched a black and white television drama by Alfred Hitchcock called 'Bang! You're Dead' while they were scanned with fMRI. The full 25-minute episode was shortened to 8 minutes, preserving the narrative of the episode (Shafto et al., 2014). This shortened version of the movie has been shown to elicit robust brain activity, synchronized across participants (Campbell et al., 2015; Geerligs et al., 2018). Participants were instructed to watch, listen, and pay attention to the movie.

fMRI data acquisition

The details of the fMRI data acquisition are described in Geerligs et al. (2018). In short, 193 volumes of movie data were acquired with a 32-channel head-coil, using a multi-echo, T2*-weighted EPI sequence. Each volume contained 32 axial slices (acquired in descending order), with slice thickness of 3.7 mm and interslice gap of 20% (TR = 2470 ms; five echoes [TE = 9.4 ms, 21.2 ms, 33 ms, 45 ms, 57 ms]; flip angle = 78 degrees; FOV = 192mm x 192 mm; voxel-size = 3 mm x 3 mm x 4.44 mm), the acquisition time was 8 minutes and 13 seconds. High-resolution (1 mm x 1mm x 1 mm) T1 and T2-weighted images were also acquired.

Data pre-processing and hyperalignment

The initial steps of data preprocessing for the movie data were the same as in Geerligs et al. (2018) and are described there in detail. Briefly, the preprocessing steps included deobliquing of each TE, slice time correction and realignment of each TE to the first TE in the run, using AFNI (version AFNI_17.1.01; https://afni.nimh.nih.gov; Cox, 1996). To denoise the data for each participant, we used multi-echo independent component analysis (ME-ICA), which is a very promising method for removal of non-BOLD like components from the fMRI data, including effects of head motion (Kundu et al., 2012; Kundu et al., 2013). Co-registration followed by DARTEL intersubject alignment was used to align participants to MNI space using SPM12 software (http://www.fil.ion.ucl.ac.uk/spm).

To optimally align voxels across participants in the movie dataset, we subsequently used whole-brain searchlight hyperalignment as implemented in the PyMVPA toolbox (Guntupalli et al., 2016; Hanke et al., 2009). Hyperalignment is an important step in the pipeline because the neural state segmentation method relies on group-averaged voxel-level data. Hyperalignment uses Procrustes transformations to derive the optimal rotation parameters that minimize intersubject distances between responses to the same timepoints in the movie. The details of the procedure are identical to those in Geerligs et al.

(2021). After hyperalignment, the data were highpass-filtered with a cut-off of 0.008 Hz. For the analyses that included 2 or 15 independent groups of participants, we ran hyperalignment separately within each subgroup to make sure that datasets remained fully independent.

Data-driven detection of neural state boundaries

To identify neural state boundaries in the fMRI data, we used greedy state boundary search (GSBS) (Geerligs et al., 2021). GSBS performs an iterative search for state boundary locations that optimize the similarity between the average activity patterns in a neural state and the (original) brain activity at each corresponding time point. At each iteration of the algorithm, previous boundary locations are finetuned by shifting them by 1 TR (earlier or later) if this further improves the fit. To determine the optimal number of boundaries in each brain region, we used the t-distance metric. This metric identifies the optimal number of states, such that timepoints within a state have maximally similar brain activity patterns, while timepoints in consecutive states are maximally dissimilar. The validity of these methods has been tested extensively in previous work, with both simulated and empirical data (Geerligs et al., 2021). The input to the GSBS algorithm consists of a set of voxel time courses within a searchlight and a maximum value for the number of states, which we set to 100, roughly corresponding to half the number of TRs in our data (Geerligs et al., 2021).

Here we improved on the existing method in three ways to increase the validity and reliability of our results. First, GSBS previously placed one boundary in each iteration. We found that for some brain regions this resulted in late detection of important boundary locations, which led to an overestimation of the number of states (see figure S1A). We were able to address this issue by allowing the algorithm to place two boundaries at a time. A 2-D search is performed, which allows the algorithm to determine the location of a new state, rather than identifying a boundary between two states. A restriction to the search is that both boundaries must be placed within a single previously existing state. In some cases, it may be more optimal to place one new boundary than two, for example when an existing state should be split in two (rather than three) substates. To accommodate this, we allow the algorithm to determine whether one or two boundaries should be placed at a time, based on which of these options results in the highest t-distance.

As a consequence of this change in the fitting procedure, we also adjusted the boundary finetuning. While we previously finetuned boundaries in the order they were detected (i.e. first to last) we now perform the fine-tuning starting from the weakest boundary and ending with the strongest boundary. These changes to the algorithm are all evaluated extensively in the supplementary methods section. Code that implements the improved version of GSBS in Python is available in the StateSegmentation Python package (https://pypi.org/project/statesegmentation/).

The final change compared to our previous work entails the use of deconvolved data. We observed that the algorithm was often unable to differentiate short states from transitions between longer states due to the slow nature of the hemodynamic response. This issue can be resolved by first deconvolving the data. Simulations and empirical results demonstrate that these changes resulted in stark increases in the reliability of our results (see supplementary methods). The data were deconvolved using Wiener deconvolution as implemented in the rsHRF toolbox (version 1.5.8), based the canonical hemodynamic response function (HRF; Wu et al., 2021). Importantly, we did not use the iterative Wiener filter algorithm, as we noticed that this blurred the boundaries between neural states.

We also investigated the effects of estimating the HRF shape, instead of using the canonical HRF and found that this did not have a marked impact on the results (see supplementary methods).

Whole-brain search for neural state boundaries

We applied GSBS in a searchlight to the hyperaligned movie data. Spherical searchlights were scanned within the Harvard-Oxford cortical mask with a step size of two voxels and a radius of three voxels (Desikan et al., 2006). This resulted in searchlights with an average size of 97 voxels (max: 123, IQR: 82-115), this variation in searchlight size was due to the exclusion of out-of-brain voxels. Only searchlights with more than 15 voxels were included in the analysis.

Previous analyses have shown that neural state boundaries cannot be identified reliably in single-subject data. Instead data should be averaged across a group of at least ~17 participants, to eliminate sources of noise from the data (Geerligs et al., 2021). As the group size increases, the reliability of the results also increases. Therefore, all the results reported here are with the maximal possible group size. To illustrate the reliability of the cortical hierarchy of state durations, we randomly divided the data into two independent samples of ~135 participants each before identifying the optimal number of states. In all other analyses the figures in the results section are derived from data with all participants averaged in one big group. Statistical testing to determine statistical significance of these results is done with data in which participants were grouped in 15 smaller independent subgroups of 17/18 randomly selected participants per group.

Comparison of neural state boundaries to event boundaries

Event boundaries in the Cam-CAN movie dataset were identified by Ben-Yakov and Henson (2018) based on data from sixteen observers. These participants watched the movie outside the scanner and indicated with a keypress when they felt “one event (meaningful unit) ended and another began”. Participants were not able to rewind the movie. Ben-Yakov and Henson (2018) referred to the number of observers that identified a boundary at the same time as the boundary salience. In line with their approach, we only included boundaries identified by at least five observers. This resulted in a total of 19 boundaries separated by 6.5–93.7 s, with a salience varying from 5-16 observers (mean=10).

To compare the neural state boundaries across regions to the event boundaries, we computed two overlap metrics; the absolute and relative boundary overlap. Both overlap measures were scales with respect to the expected number of overlapping boundaries. To compute these values, we first define the probability that a given TR overlaps with an event boundary $P(event) = Ne/n$ and the probability that a given TR contains a neural state boundary in a given searchlight $P(state) = Ns/n$, where Ne is the number of event boundaries, Ns is the number of state boundaries in a particular searchlight and n is the number of TRs. If we assume that there is no association between the occurrence of event boundaries and state boundaries, the expected number of overlaps is defined as $P(event) \times P(state) \times n$. The absolute overlap was scaled such that it was zero when it was equal to the expected overlap and one all neural state boundaries overlapped with an event boundary. Instead, the relative overlap takes the number of state boundaries into account, it is one when it is equal to the maximal possible overlap, defined as $\min\{Ne, Ns\}$. For each searchlight we tested whether the boundary overlap was significantly different from zero across the 15 independent samples.

In addition to investigating the overlap between the event boundaries and the state boundaries, we also investigated the effect of boundary strength. Specifically, we investigated the difference in the strengths between the neural state boundaries that overlap with event boundaries and those than do not overlap within each searchlight.

Quantification of boundary overlap between searchlights

In order to quantify whether the overlap between neural state boundaries between different brain regions was larger than expected based on the number of state boundaries, we compared relative boundary overlap as described above. The relative boundary overlap allows us to quantify the degree to which state boundaries are nested. For each pair of searchlights, the expected overlap between neural state boundaries was quantified as $E = \frac{Bi}{N} \times \frac{Bj}{N} \times N$ with *N* the number of timepoints, B_i the number of state boundaries in searchlight *I* and B_j the number of boundaries in searchlight *j* (as in Zacks et al., 2001a). The maximal possible overlap is defined as $\min\{Bi, Bj\}$. The relative boundary overlap metric was scaled such that it was zero when it was equal to the expected overlap and one when it was equal to the maximal possible overlap. For each pair of searchlights, we tested whether the boundary overlap was significantly different from zero across the 15 independent samples.

Identification of functional networks

In order to identify networks of regions that contained the same neural state boundaries, we computed the boundary overlap between each pair of searchlights as described above. We used the data in which all 265 participants were averaged. Based on the boundary overlap between all searchlight pairs, functional networks were detected using a consensus partitioning algorithm (Lancichinetti and Fortunato, 2012), as implemented in the Brain Connectivity Toolbox (Rubinov and Sporns, 2010). The aim of the partitioning was to identify networks (groups) of searchlights with high boundary overlap between searchlights within each network and low(er) overlap between searchlights in different networks. Specifically, an initial partition into functional networks was created using the Louvain modularity algorithm (Blondel et al., 2008), which was refined using a modularity fine-tuning algorithm (Sun et al., 2009) to optimize the modularity. The fit of the partitioning was quantified using an asymmetric measure of modularity that assigns a lower importance to negative weights than positive weights (Rubinov and Sporns, 2011).

Because the modularity maximization is stochastic, we repeated the partitioning 100 times. Subsequently, all 100 repetitions for all of the groups were combined into a consensus matrix. Each element in the consensus matrix indicates the proportion of repetitions and groups in which the corresponding two searchlights were assigned to the same network. The consensus matrix was thresholded such that values less than those expected by chance were set to zero (Bassett et al., 2013). The values expected by chance were computed by randomly assigning module labels to each searchlight. This thresholded consensus matrix was used as the input for a new partitioning, using the same method described above, until the algorithm converged to a single partition (such that the final consensus matrix consisted only of ones and zeroes).

The procedure described above was applied for different values of the resolution parameter *γ* (varying γ between 1 and 3; Reichardt and Bornholdt, 2006). Increasing the value of *γ* allows for the detection of smaller networks. We used the same values for *γ* across the initial and consensus partitioning. We selected the partition with the highest similarity to a previous whole brain network partition (Power et al., 2011), as measured by adjusted mutual information (aMI; Xuan Vinh et al., 2010). We specifically chose the parcellation by Power et al. (2011) as a reference as it proved functional network labels per voxel, rather than regional of interest, making it more similar to our searchlight analyses. To compare our network labels for each searchlight to the voxelwise Power networks, we labeled each searchlight according to the Power network label that occurred most frequently in the searchlight voxels. The highest similarity was observed for gamma=1.8 (aMI=0.39). We named each functional network we identified in accordance with the Power network that it overlapped most with, in addition to a descriptive term about the network location (e.g., ventral, posterior) or function (early, late).

Co-occurrence of neural state boundaries and events

On the level of functional networks, we investigated the association between neural boundary co-occurrence and event boundaries. To do this, we averaged all neural state boundary time series across all searchlights within a specific functional network. These neural state boundary time series contained zeros when there was no change in state and ones when there was a transition to a different state. This results in a time series in which each time point indicates the percentage of searchlights within a network (or across the cortex) that have a co-occurring neural state boundary.

We used logistic regression to determine how much variance in the presence or absence of event boundaries could be explained by each of these network average boundary timeseries. To approximate a measure of explained variance with logistic regression, we used the Nagelkerke pseudo R^2 (Nagelkerke, 1991). To test whether the association between neural state boundary co-occurrence and event boundaries was significant, we looked at whether the regression coefficients were significantly larger than zero across the 15 independent samples of participants.

To look at more detail at how boundaries that are shared vs. boundaries that are not shared are associated with the occurrence of an event boundary, we performed an additional analysis at the level of searchlights. In particular, for a pair of searchlights *I* and *j*, we investigated the boundary overlap between event boundaries and neural state boundaries for boundaries that were shared between *I* and *j* (Oij), as well as for boundaries that were unique to *I* (Oi) or unique to *j* (Oj). The overlap was computed as described in the section 'Comparison of neural state boundaries to event boundaries'. Then we tested whether the overlap for the shared boundaries was larger than the overlap for non-shared boundaries, using searchlight that showed the largest overlap in their unique boundaries as the baseline: $Oij > \max\{Oi, Oj\}$.

Statistical testing and data visualization

The results reported in the paper are based on analyses in which data were averaged over all 265 participants (or two groups of ~127 participants for the results in figure 1). To investigate the statistical significance of the associations within each searchlight, network or network pair, we also ran separate analyses within 15 independent samples of participants. For each metric of interest, we obtained a p-

value for each searchlight, by testing whether this metric differed significantly from zero across all 15 independent samples using a Wilcoxon signed rank test (Wilcoxon, 1945). P-values were corrected for multiple comparisons using FDR correction (Benjamini and Hochberg, 1995). Results in which the sign of the effect in the one group analysis did not match the sign of the average effect across the 15 independent subgroups were considered non-significant.

For all searchlight-based analyses, p-values from the searchlights were projected to the voxel level and averaged across the searchlights that overlapped each voxel before they were thresholded using the FDR-corrected critical p-value (Benjamini and Hochberg, 1995). When projecting the results of the analyses to the voxel-level, we excluded voxels for which less than half of the searchlights that covered that voxel were included in the analysis. These excluded searchlights had too few in-brain voxels (see section 'Whole-brain search for neural state boundaries'). Data were projected to the surface for visualization, using the Caret toolbox (Van Essen et al., 2001).

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Supplementary Methods

Detecting states

Since the publication of our paper describing the greedy state boundary search (GSBS) algorithm, we discovered some issues which have resulted in several improvements to the algorithm. First, we discovered that for specific brain regions the original GSBS algorithm performed sub-optimally; the placement of one new boundary at a late stage in the fitting process resulted in a large increase in the t-distances (our measure of fit; see figure S1A). To deal with this problem, we adapted the algorithm, such that it can place two boundaries at the same time, essentially demarcating the location of a new 'substate' within a previously defined state (as described in the methods). In the following, we refer to this adapted version as states-GSBS. This change in the fitting procedure remedied the issues we experienced before (see figure S1B) and resulted in more robust fitting behaviour, which we observed across many brain regions. It also resulted in a change in the approach we used to finetune boundary locations; while we previously finetuned boundary locations based on their order of detection, the order is now determined by the strength of the boundaries (weakest – strongest). To investigate how these changes to GSBS impacted reliability, we split the data in two independent groups of participants and looked at the percentage of overlapping boundaries between the groups for each searchlight. To make sure differences in number of states between methods did not impact our results, we fixed the number of state boundaries to 18 or 19. Because the states-GSBS algorithm can place one or two boundaries at a time, we cannot fix the number of state boundaries exactly, which is why is can be either 18 or 19. We also investigated the reliability of regional differences in states duration, by computing the correlations in median state duration across all searchlights between the two independent groups. Both metrics of reliability increased substantially for states-GSBS, compared to the original GSBS implementation and also compared to the GSBS implementation with altered finetuning (see figure S2).

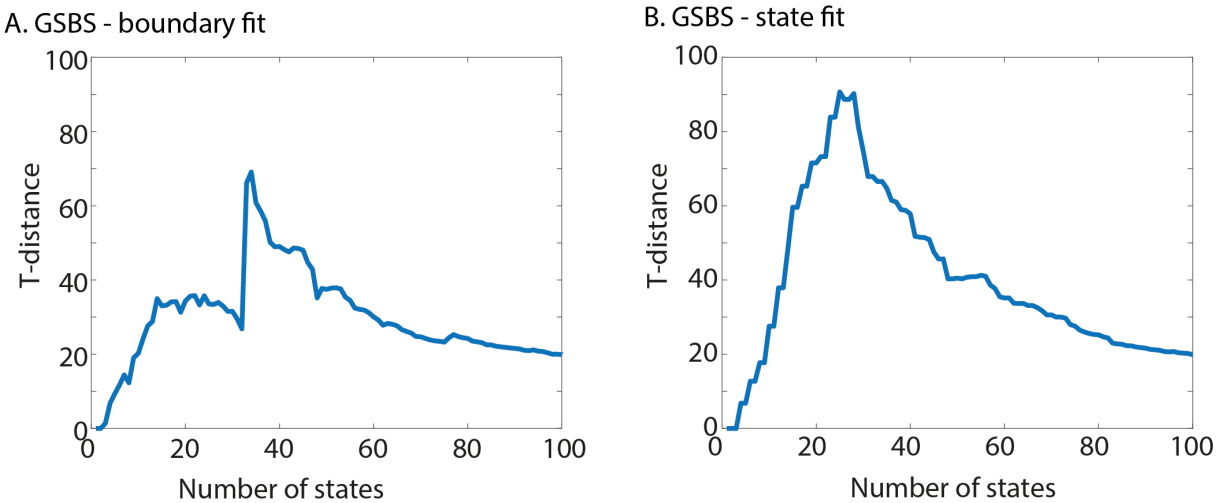


Figure S1: A. The t-distance curve for the original GSBS implementation for an example brain region. B. The t-distance curve for the same brain region with the new option for two placing boundaries in one iteration of the algorithm.

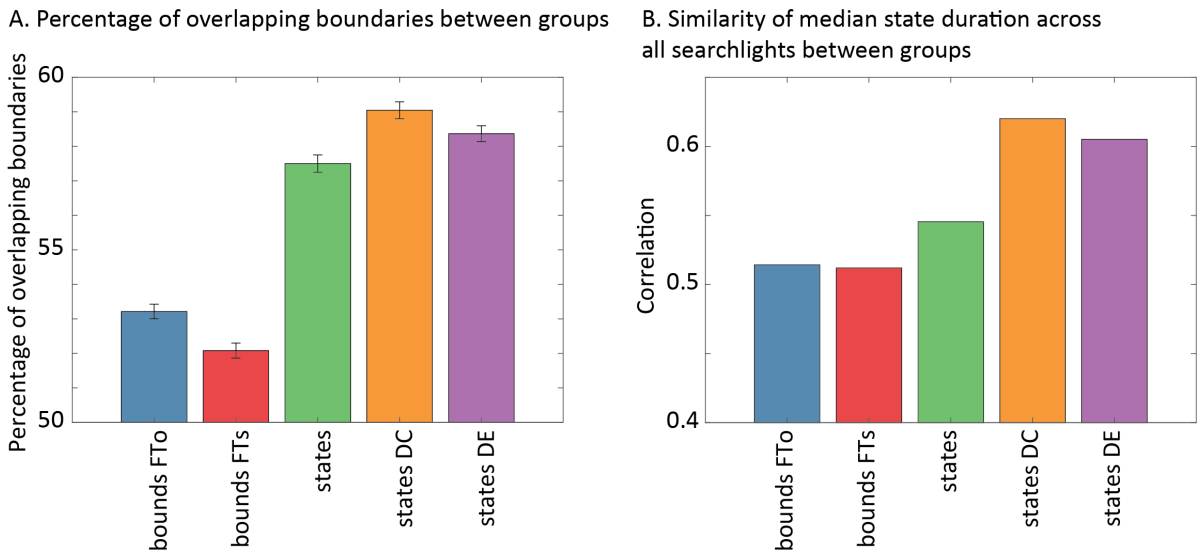


Figure S2: Comparing different implementations of the GSBS algorithm and different data pre-processing steps. A. The percentage of overlapping boundaries between two independent groups for each searchlight. The bar shows the mean across 5029 searchlights, while the error bar shows the standard error. B. The correlation between the estimated median state lengths over all searchlights between two independent groups (correlation computed across 5029 searchlights). Bounds FTo = the original GSBS implementation; bounds FTs = the GSBS implementation with strength-ordered finetuning; states = the states-GSBS implementation that can place two boundaries at a time; states DC = states-GSBS applied to data deconvolved with a canonical HRF; states DE = states-GSBS applied to data deconvolved with an estimated HRF.

Deconvolution

Another issue we discovered with GSBS is that it was unable to detect short states (of one or two TRs) in some cases. Specifically, we noticed that this happens when consecutive neural states are strongly anticorrelated. We observed such anti-correlated states in many of our searchlights. To investigate this issue, we simulated data with 15, 30 or 50 neural states within 200 TRs, using the same setup as our previous work (Geerligs et al., 2021). However, instead of randomly generating an activity pattern per state, we used one activity pattern which we inverted when there was a state boundary. This resulted in strongly anti-correlated states (see figure S3A). In this simulated setup, we found that as the number of states increased and there were more states with very short durations, the number of states was underestimated by states-GSBS. We hypothesized that this was due to the slow hemodynamic response, which obscures transitions between short states. Indeed, when we deconvolved the simulated data, the number of states was estimated correctly, even when there were 50 states (see figure S4B). Because we wanted to be able to identify states with both short and long durations, we choose to apply HRF deconvolution to our data before running states-GSBS, using a canonical HRF. We found that deconvolution resulted in a very large improvement in the reliability of regional differences in states duration and also substantially increased the boundary overlap between independent samples (see figure S2). However, it should also be noted that deconvolution may not be optimal for every study interested in neural states. It is particularly important for studies that are interested in accurately identifying the number of neural states in particular brain regions and for studies that are interested in short-lasting states. For studies that

are more interested in transitions between longer- lasting states the deconvolution may actually result in lower signal-to-noise. In particular because we also observed that deconvolution results in reduced similarity of timepoints within the same state as well as increased similarity of timepoints between states.

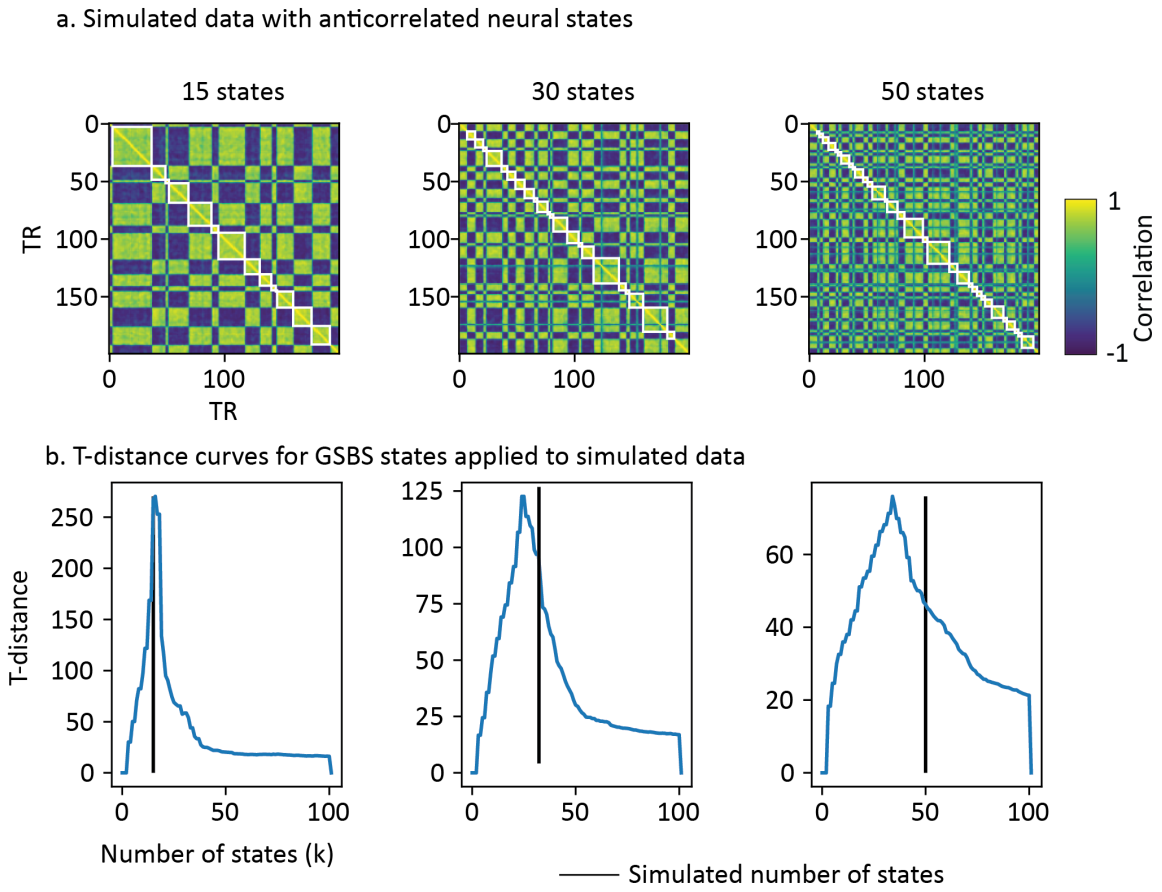


Figure S3. Performance of states-GSBS on simulated data with anticorrelated states and (from left to right) 15, 30 or 50 states. A. the correlation matrices with the detected neural state boundaries in white. B. the T-distance curves, where the black line indicates the simulated number of states. For k=30 and k=50, the t-distance peaks at a number of states that is below the simulated number of states, suggesting that some of the boundaries of short lasting neural states are not detected.

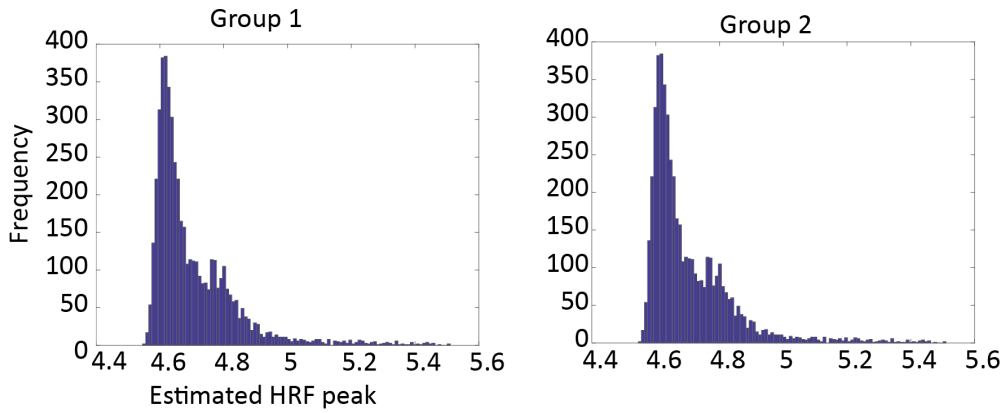
Regional differences in HRF

One concern with deconvolution is that there are known differences between regions in the timing of the HRF (Taylor et al., 2018). To investigate whether such differences might impact our results, we estimated the HRF for each participant and each searchlight, using the rsHRF toolbox that can estimate HRFs in resting state data (Wu et al., 2021). Because HRF estimation is applied to single subject data that contains many sources of noise, we performed some extra data denoising steps (as in Geerligs et al., 2018), which included regressing out signals from the CSF and white matter as well as head motion signals. This denoised data was used to run the HRF estimation for each participant and for each voxel within a searchlight. Subsequently, the HRF shape was averaged across all voxels in a searchlight and the data were deconvolved for each participant. Importantly, we used the same data as before (without the extra denoising steps) as the input for the deconvolution to make sure results were

comparable. Also we observed that data cleaning removed some of the signal of interest resulting in slightly decreased reliability of boundaries. After deconvolution, the data were again averaged within the two independent groups of participants and then we applied the states-GSBS algorithm.

Figure 4A shows the estimated HRF peak delays for each brain region after averaging the estimated peaks across all participants within each of the two independent groups. The differences between searchlights in their estimated HRF delay (averaged across participants) were highly reliable across the two independent groups (r=0.87). The peak delays varied between 4.6 and 5.4 seconds, which is very similar to the delay of the canonical HRF (5 seconds). Estimating the HRF delays resulted in a slight decrease in the boundary overlap between independent samples and also slightly reduced the reliability of regional differences in states duration (see figure S2). Regional differences in state duration were highly similar when we compared the deconvolution with the canonical HRF and the deconvolution with the estimated HRF (r=0.92 and r=0.93 for the two groups at the voxel level and r=0.73 and r=0.76 at the level of searchlights). These results suggest regional differences in the HRF shape did not bias the estimated regional timescales.

A. Estimated HRF peak delay



B. Simulated data with different HRF peak delays (k=50)

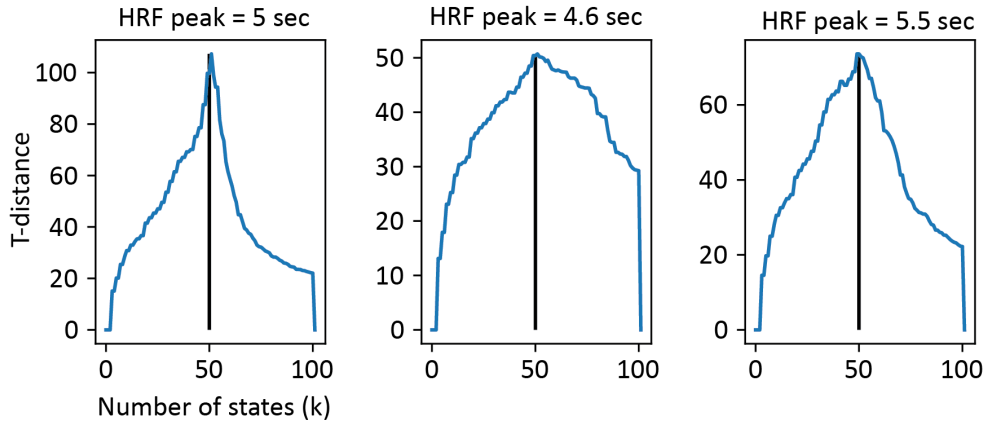


Figure S4. A. The estimates of the HRF peak delays for all searchlights are shown in a histogram. The values are averaged across all participants within each of the independent groups. The distribution is highly similar for both groups. B. T-distance curves are shown for simulated data with different HRF delays that are deconvolved with a canonical HRF. There is no systematic under- or overestimation of the number of states when the HRF peak delays are in the range of the empirical data.

To investigate this in more detail, we ran additional simulations to investigate the consequences of slight deviation in the HRF shape on the recovery of the state boundaries (see figure 4B). Simulated data with HRF delays between 4.6 and 5.4 seconds, which were deconvolved with a canonical HRF, did not show an under or overestimation in the number of states. Together these results show that the regional differences we observe in the duration of neural states when we use data that is deconvolved with a canonical HRF cannot be explained by regional differences in the HRF shape. Furthermore, it is not clear that the extra step of estimating the HRF shape results in more accurate or reliable results. That is why we opted for the simpler approach of canonical HRF estimation throughout the manuscript.

Sample size effects

To look at how replicable results are across samples and how this depends on the sample size, we computed the proportion of boundaries that was shared between each unique pair of participant groups. In line with our previous work, we observed that the boundary timecourses were a lot more consistent between different pairs of participant groups when the data were split into two independent groups of 127/128 participants per group (63% of boundaries shared on average) than when the data were split into fifteen groups of around 17/18 participants per group (49% of boundaries shared on average). That is why, throughout the paper, we report the results with the largest possible sample size. To make sure there were enough unique data points to perform tests for statistical significance to show the consistency of effects across samples, all statistical analyses are performed on the data split into fifteen independent groups.

Supplementary results

Reliability

As a first step, we determined in which searchlights neural state boundaries were sufficiently reliable for follow-up analyses when we looked at the smallest and therefore least reliable sample size (15 groups with 17/18 participants per group). Specifically, we investigated which searchlights showed a significantly positive Pearson correlation between state boundary time courses in each participant group and the average state boundary time courses across all other participant groups (similar to Geerligs et al., 2021). Reliable boundary timecourses were observed in 5029 out of 5061 searchlights. The 32 regions without reliable boundary timecourses were not included in any of the analyses reported in the manuscript or the supplementary methods or results (see figure S5A for a map of these regions). In these 5029 regions, the reliability was highest for searchlights around the visual and auditory cortex and lowest around the paracentral lobule and the posterior parts of the orbitofrontal cortex (see figure S5B).

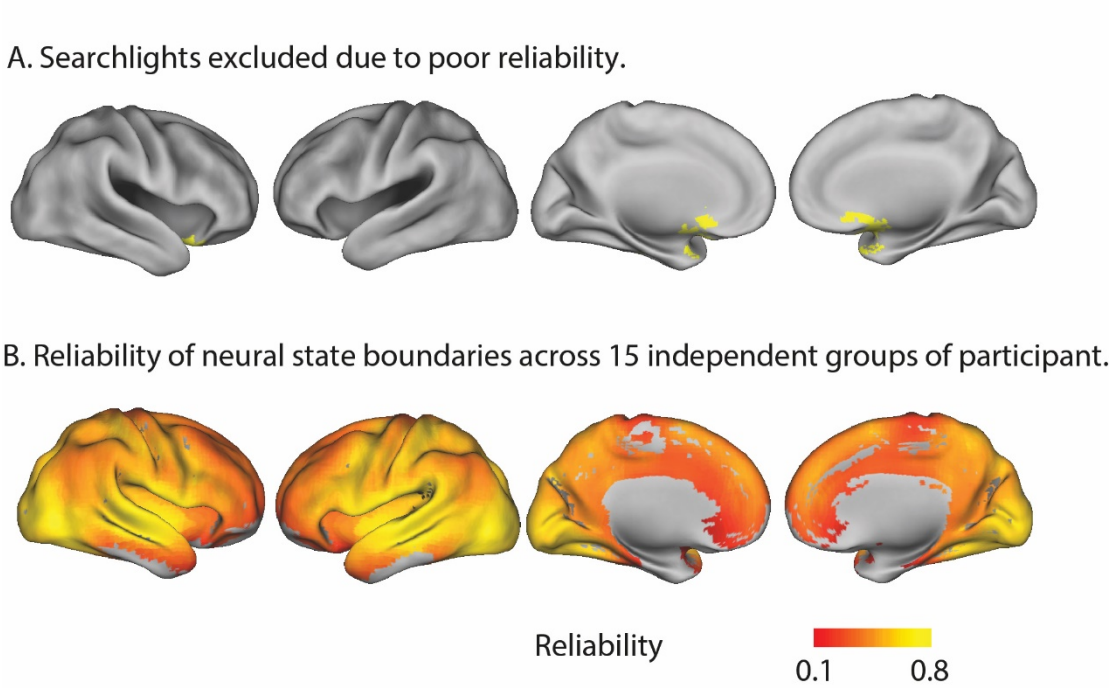


Figure S5: A. Searchlights that were excluded due to poor reliability. B. A map of the reliability of neural state boundaries across the cortex.

Head motion

Another quality check we performed was to investigate the association between neural state boundaries and head motion. First, we computed the average amount of head motion for each TR across all the participants in each of the 15 independent groups. Second, we computed Pearson correlations between the neural state boundary timecourses and the average head motion timecourses. We investigated whether there was a consistently positive or negative association between state boundaries and head motion across the 15 samples after FDR correlation for multiple comparisons. This was not the case for any of the searchlights.

Overlap between searchlights

To examine if boundary overlap is simply a proxy for 'regular' functional connectivity we compared it to the correlation between mean activity time courses in each searchlight (figure S6A&B). We found that these correlation patterns could only explain a small part of the regional differences in boundary overlap. To investigate whether the boundary overlap is simply a result of regional similarities in state length we compared the boundary overlap to regional differences in state duration (see figure S6A&C). We found that differences in state duration cannot explain the overlap patterns we observed.

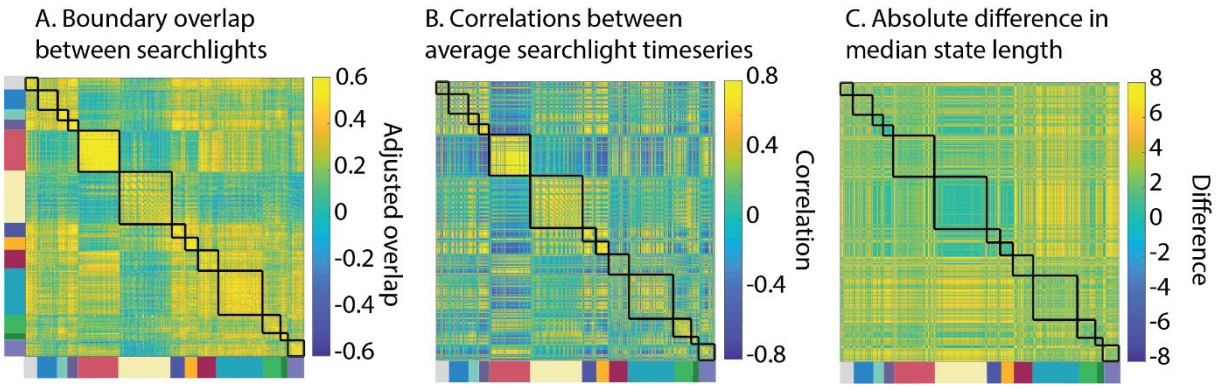


Figure S6. A. The neural state boundary overlap between each pair of searchlights. B. The correlation matrix based on the averaged brain activity timecourse in each searchlight (i.e., standard measure of functional connectivity). C. The difference between each pair of searchlights in median state length was markedly different from the boundary overlap (S6A), showing that the boundary overlap between different regions was not just due to regional differences in the optimal number of states.

Table S1: For each network, the table lists the network defined by Power et al (2011) that showed the highest overlap and the percentage of searchlights in the network that overlapped with that particular Power (2011) network.

Network name	**Power network**	**Percentage of searchlights**
Motor	Sensorimotor	49
Sensorimotor-medial	Sensorimotor	45
Sensorimotor-lateral	Sensorimotor	37
Auditory	Auditory	24
Visual early	Visual	58
Visual late	Visual	20
Dorsal Attention Network	Dorsal Attention Network	27
Cinglulo-Opercular Network	Cinglulo-Opercular Network	23
Fronto-parietal control network	Fronto-parietal task control	24
Posterior Default Mode Network	Default mode network	57
Superior Default Mode Network	Default mode network	24
Anterior Default Mode Network	Default mode network	68