Neural systems mediating recognition of changes in statistical regularities

Michael J. Tobia¹, Vittorio Iacovella¹, Ben Davis¹, Uri Hasson¹,²,§

¹ Center for Mind/Brain Sciences (CIMeC), The University of Trento, Italy
² Department of Psychology and Cognitive Sciences, The University of Trento, Italy
§ Corresponding author. Email address: uri.hasson [at] unitn.it (U. Hasson)

Abstract

Neuroimaging research has identified several brain systems sensitive to statistical regularities within environmental input. However, the continuous input impinging on sensory organs is rarely stationary and its degree of regularity may itself change over time. The goals of the current fMRI study were to identify systems sensitive to changes in statistical regularities within an ongoing stimulus, and determine to what extent sensitivity to such changes depends on intentional monitoring of order. We predicted that changes in regularity would be coded for in systems previously associated with statistical coding (hippocampus and middle frontal regions) or event segmentation (posterior medial regions). Participants listened to a rapid train of four different tones whose order levels fluctuated over time. In an active task, participants monitored the tones and indicated when they perceived a change in regularity; in a passive task, they performed a concurrent visuo-motor task and could ignore the auditory input. Behavioral responses in the active task were used to define points of consensus between participants regarding changes in regularity. Activity in 7.5 sec epochs that preceded these order-change points was contrasted with activity during matched-length epochs where no participant indicated a change in order. We found that brain regions differentiating these two types of epochs matched those identified in prior research as mediating event segmentation in narratives and movies. These consisted mainly of medial posterior parietal and occipital regions, with limited involvement of temporal and lateral frontal cortices and no hippocampal involvement. In both tasks, order-change epochs were associated with a higher BOLD response than stable-order epochs, but the specific regions showing this pattern varied across tasks. We suggest that partitioning an input stream on the basis of statistical shifts constitutes a basic neural function underlying the ability to segment both semantic and non-semantic inputs. We further discuss the implications of these findings for neurobiological theories of statistical coding and event segmentation.

Introduction

Coding for Statistical Regularities and its Benefits

Our perception of the external environment derives not only from neural coding of its instantaneous or nearly-instantaneous physical features, but also from an appreciation of more temporally extended macro-scale environmental features such as the types of events it contains, their relative frequency, and the sorts of constraints that hold between these events. Indeed, sensitivity to statistical features of the external environment is a capacity that is well developed in humans (see e.g., Smithson, 1997) and is also shared by less developed species (Herry et al., 2007). From a psychological perspective, sensitivity to statistical regularities could indicate coding the statistical constraints resulting from the signal generating process, or awareness of particular non-random features of the input independent of a representation of potential input sources.

Several separate lines of theoretical and experimental research suggest that sensitivity to statistical regularities (order-sensitivity henceforth) may serve a myriad of functions, including optimization of online perceptual processing due to item predictability (Bendixen, Schroger, & Winkler, 2009; Brodersen et al., 2008), and the ability to represent input in a compressed manner (Buiatti, Peña, & Dehaene-Lambertz, 2009). However, natural environments are marked by the fact that their order features change over time; that is, the environmental constraints themselves change in a non-stationary manner. This can be seen, for example, in the dynamics of traffic patterns, weather phenomena, and within human behavior (Renaud, Chartier, & Albert, 2009). Even the simplest non-linear system can produce local dynamics that are frequently changing, e.g., between strongly and weakly fluctuating local contexts. Thus, rather than assuming that an environment is stationary with non-changing temporal regularities, it is likely that humans are highly tuned to the possibility that environmental regularities themselves change (Stephen & Dixon, 2011).

From a psychological perspective, tracking changes in statistical regularities within a streaming signal entails the accumulation of evidence indicating that statistical features are not stationary. The ability to recognize a change in regularity may be fundamental to partitioning a continuous input into meaningful units (e.g., event segmentation) even before semantic...
event categories are established. Several brain regions, including lateral and medial prefrontal cortex (Behrens, Woolrich, Walton, & Rushworth, 2007; Huettel, Mack, & McCarthy, 2002), hippocampus (Harrison, Duggins, & Friston, 2006; Strange, Duggins, Penny, Dolan, & Friston, 2005), and lateral temporal regions (Bischoff-Grethe, Proper, Mao, Daniels, & Berns, 2000) have all been suggested as coding for inputs’ statistical features. In contrast, event segmentation is typically associated with a different system including mainly posterior midline areas with more modest frontal involvement (Speer, Zacks, & Reynolds, 2007; Whitney et al., 2009; Zacks et al., 2001).

Brain systems sensitive to non-stationary aspects of statistical order may play an important function mediating between systems coding for statistical features in stationary contexts, and those mediating the segmentation of continuous inputs on the basis of pre-established event categories. The overall goal of the current study was to identify systems sensitive to changes in statistical regularities (i.e., perceived changes in statistical features) and understanding how they code for change. Because formal parameterizations of input order do not necessarily match subjective perceptions of order (Falk & Konold, 1997) the current study was designed to investigate neural systems where activity correlates with subjective changes in perceived regularity, under two sorts of perceptual contexts; one where participants passively attended to the stimuli whose regularity was manipulated, and one where they were asked to indicate their conscious perception of changes in regularity.

**Systems that May Mediate the Perception of Order Changes**

Four lines of prior work have identified systems mediating processes that could be related to order-sensitivity. These have focused on (a) the hippocampus as an entropy-coding system, (b) pre-frontal cortices as coding statistical features in rapidly changing environments, (c) anterior cingulate (ACC) as sensitive to the degree of input volatility, and (d) an extended network for event-boundary detection including posterior midline and frontal regions.

Several studies have linked the hippocampus to the coding of environmental statistics. Two studies (Harrison et al., 2006; Strange et al., 2005) have shown that hippocampal responses to ongoing stimuli can be modeled as computations of a Bayesian observer sensitive to the degree of input disorder (entropy). Strange et al. (2005) found that hippocampal activity was related to the degree of diversity in an input, as quantified via Shannon's Entropy. Shannon's entropy quantifies the degree of input diversity within a stream; it is maximal when all tokens are equally frequent (drawn from a uniform distribution) and is reduced for less uniform sampling distributions. Harrison et al. (2006) found a relation between hippocampal activity and the Mutual Information within items in an input stream, which is a measure capturing the amount of information given by each item regarding the next one that would appear. Sensitivity to mutual information could be related to the region’s sensitivity to the degree of cue validity (Turk-Browne, Scholl, Johnson, & Chun, 2010), because valid cues can only exist in ordered series. The potential involvement of frontal regions in coding for order derives from work by Huettel et al. (2002). This work linked prefrontal regions to violations of a repeating pattern, and importantly, found that responses to violations scaled with the length of the pattern violated. This suggests that the frontal cortex generates predictions about the next stimulus or is involved in the representation of one’s certainty of environmental statistics (010101 provides greater evidence than 0101 regarding what the next stimulus is likely to be).

The aforementioned works examining sensitivity to cue validity and pattern-length effects on response violations are related to studies directly examining decision-making in environments differing in volatility. Simply put, in volatile environments the more recent input may be more diagnostic of the future than distant input, whereas in less volatile ones, future predictions are best based on considering distant inputs as well. Behrens et al. (2007) showed that a focal region of the ACC appears to represent the state of input volatility in a paradigm where participants made predictive judgments in the context of volatile or stable inputs, and were given feedback about their decisions. These data are relevant to the current study in that changes in order define volatile local environments, and so may be monitored by the ACC. However, the experimental paradigm used by Behrens et al. is a decision making one where optimal decision making could be achieved by coding for a volatility parameter, whereas our current paradigm does not necessitate a response to each item and includes a passive condition devoid of any attention to the stimuli whose order is manipulated.

Finally, work by Zacks and colleagues has examined neural responses to event transitions in natural stimuli consisting of both movies and written narratives (Speer et al., 2007; Zacks et al., 2001). In representative work (Speer et al., 2007) BOLD data were recorded while participants read narratives, and were modeled as a function of participants’ off-line parcellation of the narratives. Changes in location, time and several other narrative elements were associated with increased activity in a network encompassing the precuneus, bilaterally, extending into the posterior cingulate cortex (PCC). Additional regions on the right included anterior MTG, posterior superior temporal gyrus (STG) and the middle frontal gyrus (MFG). Interestingly, most of the differences were found in posterior regions, with the exception of small clusters in the left subcallosal gyrus and right MFG. This network of regions was taken to be sensitive to structural changes in narratives, and more generally, to updating mental models of
encountered information. In another study where movies of ongoing actions were presented (Zacks et al., 2001), event boundaries again correlated with BOLD activity in regions that largely excluded frontal ones, with the main clusters in posterior inferior temporal sulcus and fusiform gyrus bilaterally, and one frontal cluster in the precentral sulcus found only during intentional segmentation. In related work, Whitney et al. (2009) quantified narrative shifts via a formal analysis of text features and examined BOLD correlates of shifts between narrative propositions. Greater activity for narrative shifts vs. sentence endings not associated with a narrative shift revealed three activation loci; in the left middle and posterior cingulate cortex and the right precuneus. These activity patterns were interpreted in terms of encoding and maintenance of knowledge, as well as integration of ongoing input with prior input. These studies indicate that changes in input arrangements trigger concomitant activity in diverse regions that may depend on input domain (narrative vs. movies), but importantly, with relatively limited involvement of frontal regions and no evidence for hippocampal involvement. To the extent that the functions mediated by these regions reflect a basic updating mechanism not linked to semantic content, they may also signal gradual shifts in input order.

With the exception of the work of Zacks et al. and Whitney et al., the studies reviewed above are grounded in decision-making frameworks and learning paradigms where stimuli are presented slowly, participants are asked to respond to each stimulus, a correct response is defined, and optimal performance can be gained by monitoring for regularity or volatility. Nonetheless, such studies form a useful framework for examining cortical responses to order-sensitivity and we evaluate the results of the current study against the systems identified in these lines of research.

**Aims of Current Work**

This study was designed to investigate the neural mechanisms by which individuals track regularities within a temporally extended input, and whether the neural correlates of subjective recognition of changes in regularities during conscious monitoring overlap with those mediating spontaneous recognition of changes in order. We used an experimental paradigm in which participants listened to a continuous auditory stream several minutes in duration that consisted of rapidly presented tones (3.3 Hz) whose statistical regularities shifted over time according to pre-computed profiles. This allowed participants to indicate their subjective recognition of a change in the statistical regularities over a time interval by simply pressing a button.

Our first goal was to identify brain regions that differentiate between input segments where order was perceived as changing vs. segments where input was perceived as stable. During an fMRI scan, participants pressed a key whenever they thought that a change in order had occurred in the auditory series (see Methods). Subjective Order Change (SOC) epochs were defined as extended temporal periods occurring prior to time points in the auditory stream where participants showed consensus in their indication of order change. Thus, these segments capture intervals where evidence towards a change of order is being accumulated. Conversely, Subjectively Stable Order (SSO) epochs were defined as extended temporal periods during the auditory stream where none of the participants indicated a perceived change in order. These latter segments capture intervals where evidence for change in statistical structure is lacking. Using BOLD fMRI we could identify brain regions discriminating these two types of epochs.

The second goal was to understand if the perception of order-changes depends on conscious, strategic monitoring of input order or occurs spontaneously. Prior EEG and fMRI work has shown that that even very simple regularities can go unnoticed if subjects are not made explicitly aware of, or at least orientated towards the regularities. For instance, Bekinschtein et al. (2009) showed that a regular auditory pattern corresponding to 11110_11110, in which a "0" always follows four "1"s, was hardly noticed when participants were not oriented towards the stimuli, and was undetected when performing an unrelated visual task. Kimura et al. (2010) documented similar results for series of visual regularities. Therefore, to understand if order monitoring is only carried out under strategic contexts, we evaluated BOLD responses to order changes in absence of any explicit orientation to the input. The exact same auditory streams that were subjectively segmented by one group of participants (active monitoring condition), were presented to other participants while they were engaged in a simple incidental visual-monitoring task and passively listened to these inputs (passive exposure condition). As for the participants in the active group, we evaluated neural responses in the passive listening condition during the SOC and SSO epochs (as determined by participants in the active condition performing the order-monitoring task). Finding brain activity patterns that differentiate the SOC and SSO epochs in the passive condition would indicate recognition of order-change in absence of any specific demands. This design is similar to one used by Zacks et al. (2001) which asked participants to passively observe a film or segment it based on subjective event structure, and then analyzed BOLD responses to event-shifts as defined in the active task, during both passive and active viewing.

Finally, it is important to note how this investigation departs from previous work studying the brain’s response to single-item deviant stimuli. First, the inputs in the current work were never deterministic (i.e., not rule based), and order fluctuations were implemented by gradual waxing and waning of the relative strength of transition constraints between items. As such, the process we target in our study is not the response to contextually
novel items that depart from a rule-based context, but the response to novel contexts – i.e. ones whose joint statistical features differ from prior ones. Second, by examining BOLD responses during epochs that preceded participants’ subjective perception of order change, we could identify systems monitoring changes in regularity by accumulating evidence over a subjectively determined time-window. These two features of our experimental design differentiate it from work studying responses to single deviant items, which are defined as stimuli that are infrequent (e.g., as in paradigms studying visual or auditory mismatch negativity effects; Kimura et al., 2010), violate a highly diagnostic orienting cue (Vossel, Thié, & Fink, 2006; Vossel, Weidner, Thié, & Fink, 2009) or that violate an inter-stimulus association established by previous pattern (e.g., 101010 → 0; Bubic, Cramon, & Schubotz, 2011).

Materials and methods

Participants

Sixteen healthy, right-handed participants (8 F, Mean age 25.23, SD 3.49) with normal or corrected to normal vision were recruited from the University of Trento community to participate in the experiment. Participants were interviewed by medical staff prior to beginning the study and were screened for history of psychiatric or neurological disorders, substance abuse, or use of psychoactive medications. The protocol was approved by the University of Trento's Ethics Committee and all participants provided written informed consent. Data from one participant were excluded from the analysis due to excessive head motion.

Stimuli and Tasks

Auditory stimulation consisted of four separate 5-minute trains. Each 5 min train consisted of four alternating tones presented at a rapid rate (3.3Hz). Presentation order was pre-computed so that transition probabilities in the 15 tones presented within the recent 4.5 seconds changed continuously, but with slower dynamics than would be expected in a random series. The construction of each series was implemented as follows. The first 30 tones were generated from the random matrix where all cells were reversed, returning the matrix towards the random state (all cells generated after each increase. At that point, the process was repeated, returning the matrix towards the random state (all cells generated after each increase. The pre-computed drift profile was set up to ensure gradual changes in statistical regularities over time with smoother fluctuations than would be expected by sampling from a random stationary distribution, and with a wider range of levels of statistical regularities (when calculated over 10sec sliding windows; see Tobia et al., 2012 for details regarding construction of series from a non-stationary Markov process). Tones were 300 ms duration with 50 ms inter-stimulus interval. PsychToolbox (Brainard, 1997; Pelli, 1997) for MATLAB was used to present stimuli and collect behavioral data. There were four functional runs in the study, with each run consisting of one 5-min auditory series followed by a 5 min silence interval (10 min in total per run). During the 5 min silent interval participants either monitored and responded to changes in a central fixation cross or simply fixated the cross and rested. Functional data acquired during the silent intervals are not reported here.

During the presentation of the four auditory sequences, participants performed one of two tasks (active, passive task), in a within-participant design. During both tasks, participants watched a visual fixation stimulus that rotated 45 degrees at random intervals (mean interval =30 sec, with different timings for each participant). In the passive task, participants were instructed to press a button with their right index finger when the visual fixation stimulus changed from “+” to “x” or vice versa. Thus, this task did not necessitate attention or monitoring of the auditory input. In the active task participants were instructed to press a button with their right index finger to indicate a perceived change in the order/complexity in the tone sequence. The same button and finger were used in both tasks. Participants performed each task twice, for two different tone sequences, thus being exposed to a total of four tone sequences; two in the context of the active task and two in the passive. The assignment of task to each of the four auditory sequences was counterbalanced across subjects so that each sequence was assigned to each task equally often. This allowed for the use of behavioral data from participants performing the active task for analyzing neuroimaging data collected from participants that heard the same auditory stimulation while performing the passive task, as explained in detail below.

Image Acquisition

A 4T Bruker/Siemens scanner was used to acquire a single 3D, T1-weighted MPRAGE (TR/TE=2700/4 ms, 1mm3 voxel, matrix 256x224x176), and 415 BOLD EPI images for each task run of the experiment (TR/TE=1500/34 ms, matrix 64x64, with 25 AC-PC parallel slices, voxel size 4 x 4 x 4 mm with .8 mm gap). Cardiac and respiratory data were recorded using a
photoplethysmograph from the left index finger and a pneumatic belt strapped around the upper abdomen, both sampled at 50 Hz to obtain paired time-series for each fMRI dataset.

**Analysis of Behavioral Data**

Participants' key presses in the active task indicated their perception of changes in order throughout the series. Simulations (N=1000) were used to identify times during the series when there was above-chance agreement among participants regarding a perception of order change, as well as an above-chance agreement regarding no change in order. A single simulation was conducted as follows. The 5 min (300 sec) presentation time was split into three hundred 1 sec bins. For each participant, the key-press timings of that participant were permuted to obtain a random distribution of key press events coded as a 1, with no key press events coded as a 0. By summing the permuted series of all participants, we could establish the frequency of cases where 0, 1, 2 or more participants clicked within the same bin. These simulations indicated that given the number of responses provided by the participants, the chance occurrence that 2 or more participants would click simultaneously within the same bin is lower than 5% (p < .03). These simulations also indicated that a streak of 5 time bins where none of the participants responded was similarly unlikely (p < .05).

The simulations thus allowed defining points of above-chance agreement in key-presses and no-key-presses. We used this information for defining two sorts of epochs. Temporal windows before key presses were defined as portions of the fMRI time series extending 7.5 seconds (5 functional volumes) prior to the consensus-defined group key press, effectively creating an epoch preceding the indication of order change (Subjective Order Change epochs [SOC]). When two agreement bins were identified in close temporal proximity, e.g. if two participants clicked at time point T, and three others clicked at time points T+2 or T+1, then the time bins were combined into a single instance of agreement that was assigned to the mean time point in the streak. In addition, from the simulation described above, we determined that epochs where subjectively perceived order was stable (Subjectively Stable Order [SSO] epochs) required unanimous agreement across participants for runs of 5 consecutive time bins where no participant performed a key press (7.5 sec). We thus extracted fMRI data for SSO epochs in a manner similar to that of the SOC epochs. Consecutive runs of SSO epochs (i.e., 10 consecutive time bins where no participants clicked) were divided into separate SSO epochs (length of 5 bins each).

To evaluate whether participants’ responses in the active order monitoring task could be modeled by changes in marginal frequencies of the four tokens or their joint distribution we conducted a model-fitting procedure for each participant’s data. The first procedure evaluated whether changes in marginal frequencies were related to participants’ key presses. In this analysis, relative to each time point t, we quantified (a) the marginal frequency of the 4 tones in a window of n tones in recent past (recent-past window: t . . . t-n) and (b) the marginal frequency of the four tones in the immediately preceding same-sized window (less-recent window: t-n . . . t-2n). Differences between these marginal distributions were quantified using Kullback-Leibler (KL) divergence (Kullback & Leibler, 1951), resulting in a time series of KL values describing changes in successive distributions over scale n. For instance, for n=10, the first point in this series would be the KL-divergence of the two sets of items [{1: 10}, {5: 15}], the second point would be the KL-divergence of the two sets [{5:15}, {10: 20}] and so on (the sliding window was always 5 items independent of n). For n = 20 the first two sets compared would be [{1: 20}, {5: 25}], the second set compared would be {5:25}, {10: 30}] and so forth. The parameter n can be taken to reflect the integration window in working memory over which distribution features are calculated and is allowed to vary across participants. For each value of n, we examined the correlation (beta of a linear model) between the KL-divergence time series and the key presses timing using the robust correlation lmrob function in the R statistical package. These models were fit separately for each participant, and the slope of the best fitting model propagated to a second-level group analysis testing differences of Beta from 0. One such analysis was performed for the marginal frequencies within each window as described above, and another analysis was performed for the joint-probability distributions within each window.

**Preprocessing of fMRI Data**

Data preprocessing was conducted using AFNI (Cox, 1996) and custom MATLAB code. Anatomical images were aligned to functional EPI data. The raw time-series were corrected for physiological noise effects following the image-based method for retrospective correction of physiological effects [RETOICOR: Glover, Li, & Ress, 2000]. The first 15 volumes of each run were removed to allow for magnetization equilibration prior to subsequent analyses.

The first 200 volumes of each run corresponded to the task conditions and were the ones underlying all subsequent analyses. Preprocessing of functional images included correction for slice acquisition time, volume registration to the first image in the scanning session, and despiking to suppress outliers. Variance associated with the six head motion parameters derived during volume registration was removed via linear regression. Variance introduced by key presses was removed via a Finite Impulse Response model. Data were then smoothed with a 6mm (FWHM) Gaussian smoothing kernel. The preprocessed time
series were then projected to 2-dimensional cortical surface space using SUMA/FreeSurfer (Fischl, Sereno, & Dale, 1999).

**BOLD fMRI Data Analysis**

On the basis of the simulations we identified time bins that included key presses by 2 or more participants and extracted the BOLD signal within 7.5sec windows prior to these points since it was within this window that the change in order occurred prior to the key press. Similarly, 7.5sec epochs characterized by unanimous no-key-press epochs on the group level were extracted from the time series. Technically, this analysis is identical to a slow event-related fMRI design, where the epochs of interest are defined on the basis of subjective indicators, rather than by exogenous stimulus events arranged by the experimenters (see Zacks et al., 2001, 2007 for similar designs).

**BOLD fMRI Data Analysis**

The fMRI data in the SOC and SSO epochs were examined for differences in mean level of activation. For each voxel, the BOLD signal in each epoch was averaged over the five functional volumes. Epochs were then averaged together for each of the 4 auditory series. Because two auditory series were assigned to the passive and active task, we further averaged across the two instances of each task. This procedure ultimately produced 4 values for each voxel: SSO activity in passive task, SOC activity in passive task, SSO activity in active task and SOC activity in active task. In a whole-brain analysis, these epoch-averaged data were submitted to paired t-tests with alpha set to .005 (two-tailed uncorrected) at the single voxel level and controlled for family wise error using cluster-extent thresholding (p < .05) to examine differences in the magnitude of the average BOLD signal between SOC and SSO epochs, and to identify differences attributable to task condition (active monitoring vs. passive listening). All analyses were conducted on a whole-brain level.

For time series plots, in clusters differentiating the SOC and SSO epochs, we extracted the mean time series of these two epoch types for each participant, and then averaged these time series across participants.

**Conjunction analysis identifying regions showing reliable effects for individual participants**

It has been shown that group-level results may be poor indicators of what are statistically significant results at the single-participant level (Heller et al., 2007). To identify regions showing statistically significant differences between SOC and SSO-epochs at the single-participant level we used the same event markers used in the group analysis to model the SOC vs. SSO contrast for each participant: this was done via a T-test comparing BOLD signal values in SOC and SSO-epochs for each voxel on the single-participant level, thereby obtaining a statistical map showing voxels discriminating SSO from SOC epochs for that participant. We then implemented a conjunction analysis similar to that reported by Heller et al. (2007) to identify brain regions where the SSO vs. SOC contrast was reliable (p < .05 single voxel level) for more than 4 participants (p < .004 on binomial test). The analysis identifies the degree to which individual response patterns were similar. The analysis was controlled for multiple-comparisons using cluster extent thresholding.

**Hippocampus region of interest analysis**

The first part of this analysis examined BOLD signal during the SOC and SSO epochs, for the passive and active task, in the hippocampus. It was conducted in the same manner as the whole-brain analysis, but the BOLD values in the four conditions were averaged across all voxels separately for the left and right hippocampus. The region was anatomically defined using FreeSurfer's parcellation procedure (Fischl et al., 2004) and verified manually.

The second part of this analysis examined functional connectivity of the hippocampus on a whole-brain level and identified regions showing reliable connectivity with the hippocampus during the active task, the passive task, as well as regions where the correlation with the hippocampus varied as function of task. We first partialled out several nuisance factors from each voxel’s time series via linear regression, including the 6 movement parameters as well as time series derived from white matter regions, cerebral spinal fluid, and a region outside the brain. The residuals of this analysis served as the input for the functional connectivity. To construct a seed time series for the hippocampus we performed the following steps using custom code in Matlab (R). The time series of all voxels in the left and right hippocampus were combined to a single matrix M with n voxels (rows) and y time points (columns). Rather than averaging across voxels, we aimed to find components that accounted for the majority of the hippocampal activation, bilaterally, without loading specifically on the left or right hippocampus. This was done so that connectivity results would not be biased by a potential laterality effect. To this end the time series were Z-scored, and a singular value decomposition (SVD) applied to the M matrix. From the SVD results we retained as many components that contributed a significant amount of variance determined by an incremental F-test (standard for testing the significance associated with R-squared change for each variable in multiple regression). We verified that none of these loaded more strongly on voxels in the left or right hippocampus, indicating they reflected common activity bilaterally. This procedure usually resulted in returning 1 component, but in one case returned as many as 3. A hippocampal seed time series was then reconstructed from these significant eigenvectors. The correlation analysis returned 4 functional connectivity maps per participant: 2
for the auditory series presented in the context of the active task, and 2 for the auditory series presented in the context of the passive visual orientation task. Each of the map-pairs was averaged to create one map per task condition per participant.

**BOLD activity related with key presses during the active and passive task**

To evaluate key-press related activity in the order monitoring and visual perception tasks we used the activity estimates for key-presses (see section 2.5). The FIR model returned the estimated HRF in each voxel. We averaged time points 1.5 sec-7.5 sec from key-press onset, reflecting the dominant parts of the response and used that as a measure of key-press related activity. A paired-sample T-test on the group level contrasted the two conditions to identify potential differences, and in addition, T-tests against baseline (0) were performed as a validity check as these should identify strong motor-related activity. Single-participant results were registered to a common Talairach template using FLIRT (FSL, Jenkinson et al., 2002) and group-level tests were conducted in that space. In addition, we used the BrodmannArea template from MRIcron (Drury et al., 1999) to obtain mappings of Brodmann areas 44 and 45 and cross-referenced those against the functional findings.

**Results**

**Behavioral Data: Heart-Rate during Tasks**

Because the order-monitoring resulted in purely subjective measures, it was important to attempt to objectively determine whether participants were engaged in the task. For this reason, we calculated for each participant the mean heart rate (Beat Per Minute) during the order monitoring task, visual orientation task, and during the rest period that followed those tasks. As would be expected if participants were engaged in order monitoring, heart rate was significantly higher during order monitoring (M = 72.2 BPM, SE = 0.77) than during the visual orientation task (M = 69.5 BPM, SE=0.48), t(14) = 2.25, p = .043, or the resting period after the tasks (M = 69.3 BPM, SE = 0.48), t(14) = 2.53, p = .024.

In the order-monitoring task there was also a marginally significant positive correlation between heart rate and the number of transitions identified (robust correlation, τ(14) = 1.934, p = .065). These data indicate that participants were involved in the order monitoring task and indeed showed a higher arousal level during that task than during
Behavioral Data: Monitoring of Changes during the Visual Orientation Task

As a measure of visuomotor task engagement during the passive listening condition we computed the accuracy and reaction time (RT) of participants’ responses to the intermittent change in the orientation of the fixation stimulus. Data indicate that participants were indeed engaged with the task as evidenced by accurate and rapid responding. The mean accuracy across participants was 89.4% (SD=3.7%), and the mean RT was 556 ms (SD=119 ms). Two participants responded only when the fixation cross changed from “+” to “x” and were consistent in this pattern.

Behavioral Data: Key-press Data during Active Monitoring of Order

Time points with above-chance agreement with respect to perceived order change were identified in the four auditory series and used to define SOC epochs. These epochs were extracted for the four versions of the tone sequence. Agreement in any given time bin ranged between 0 to n where n reflects the number of participants monitoring the particular auditory input in the active task (n = 6, 7 or 8). On the basis of the simulations, agreement was defined as a time point where at least two participants noted a change of order, but several bins demonstrated stronger agreement (with a maximum of 5 of 6 participants [83%] responding in the same bin). A total of 10, 9, 11 and 16 SOC epochs were defined with this procedure. The SSO epochs were similarly identified as explained in the Methods section, yielding a total of 8, 13, 11 and 4 SSO epochs for the four auditory series. Figure 1 demonstrates the distribution of agreement in one of the four auditory series (see also Supplementary Video for temporal depiction).

On average, participants responded every 16.4 sec (SD = 4.9 sec). The distribution of response intervals is shown in Supplementary Materials Figure S1, indicating that while most of the responses were made within 20 sec of the prior one, there were many cases of 30-50 sec intervals.

To evaluate whether subjective order-change indications can be accounted for by relatively straightforward models of objective order-change, we conducted a model-fitting procedure examining if each participant’s key presses could be accounted for changes in marginal frequencies of the 4 tokens (tones) over time, or changes in their joint probability distribution. The analysis (see Methods) quantified changes in marginal or joint probability distributions within successive windows consisting of n items, and calculated the difference between these successive distributions using the Kullback-Leibler divergence measure. The slope of the linear model where KL-divergence values best accounted for each...
participant's responses was propagated to a second-level group analysis where these slopes, which could be positive or negative, were tested against 0. Neither the marginal frequency model nor the joint-frequency model revealed statistically significant results. We note that participants' subjective responses could be driven by numerous statistical parameters that may have changed over time, e.g., the fractal complexity of the subsequences, their auto-correlation, the number of self-repetitions within subsequences, etc. Furthermore, individuals may be sensitive to all these and so their responses could reflect a blend of sensitivity to multiple features, whose weights may themselves change over time.

**BOLD-signal Differences Between SOC and SSO epochs**

For each task we identified cortical regions differentiating between SOC and SSO epochs. Recall that these epochs were defined as a function of participants' responses in the active auditory monitoring task, and when applied to the visual orientation (passive listening) task capture order-related differences devoid of a decision component. In both tasks, the modal pattern was for greater activity for the SOC epochs relative to the SSO ones.

For the active task, BOLD signal in the SOC epochs was greater than that found during SSO epochs (see Figure 2, Table 1). These were identified bilaterally in the middle frontal gyrus and parahippocampal gyrus, and additionally in posterior midline and occipital regions including the posterior cingulate, lingual gyrus and precuneus. Figure 2 also shows, for each of the clusters, the time series in the voxel showing maximal effect. As the figure shows, while in some cases the difference appeared to be driven by increased activity in the SOC epochs maximizing shortly before the key press, in several regions including the posterior cingulate and precuneus it was driven by a relatively steady activity in the SOC periods but a gradual decline in activity during the SSO periods.

To understand whether activity in these regions during the SOC periods scaled with inter-individual differences in perception of order changes we conducted a Brain:Behavior correlation. For each of these 12 clusters we used robust regression (see Wager, 2005) to study the relation between participants' mean BOLD signal in the SOC and SSO epochs and the frequency of key presses during the active task. For the SOC epochs, a reliable correlation was only found for the left parahippocampal gyrus. A stronger pattern was found for the SSO epochs: Of the 12 clusters, 4 showed reliable correlations between BOLD activity in these epochs and response frequency, and these correlations were positive in all cases (see Table 1 for Beta values for the correlation). These included posterior regions bilaterally.

Examining differential activity for these behaviorally-defined epochs, but within data collected during passive listening revealed greater activity for SOC than SSO epochs, but in somewhat different regions than those identified in the active task. (see Figure 3, Table 2) including the ACC and STG.

Given that the analyses did not reveal sensitivity to order changes in the inferior frontal gyrus and sulcus or the insula, regions previously associated with violations of streaks (Huettel et
al., 2002), we lowered the single voxel threshold to a liberal extent (p < .05) and examined whether there was any effect in those regions (see Supplementary Figure S2). Even at that threshold there was no indication for the involvement of these systems.

To establish the magnitude of these effects on the single-participant level and identify inter-individual differences we conducted an additional analysis for data acquired during the active task, which quantified the statistical significance of the SOC vs. SSO contrast, for each voxel, on the single-participant level. We then determined the extent of overlap of these regions across the entire participant group (see Methods section 2.6.2; Heller et al., 2007 for motivations to consider conjunction as additional measure). This analysis (see Supplementary Figure S3) showed strong overlap of SOC > SSO patterns in posterior STS and posterior midline regions (of the latter, some were identified in the typical group analysis). Interestingly, the analysis also revealed orbito-frontal regions that showed greater activity for SSO epochs, a pattern not evident in the more typical group analysis. These findings suggest considerable inter-individual differences in order monitoring processes, whereby some individuals show strong effects in posterior STS and orbitofrontal regions. However, this pattern was not shared across participants, and consequently, this finding is not evident in the typical analysis.

**BOLD-signal Differences Between the Active and Passive Tasks**

To evaluate the degree to which the areas identified by the contrasts in the active and passive task were exclusive to each task, we defined clusters identified in the SOC vs. SSO contrast in the active task as functional ROIs and examined their activation profile during the passive task, and vice versa. This constitutes a conservative analysis for potential similarities in sensitivity across tasks as it uses regions demonstrated to be highly sensitive to the SOC vs. SSO contrast in one task (p < .005 at group level) to probe for potential sensitivity in the other task. Of the regions differentiating the two epochs in the active task, none differentiated the two in the passive task. The converse analysis found that of the regions identified in the passive task, only the STG cluster showed a similar differentiation pattern in the active task.

We then directly compared activity between the two tasks, for the SOC and SSO epochs separately, on a whole-brain level. A direct contrast of the SOC periods showed two regions that differentiated the two epochs in the active task, none differentiating the two in the passive task. The converse analysis identified one region differing between the two tasks in the right temporal-parietal junction (posterior STS, Angular Gyrus, see Figure 4B, Table 3), which showed a stronger BOLD signal during change in the passive task.

**Hippocampal Analysis**

We computed the mean BOLD signal in the SOC and SSO epochs for both left and right hippocampus, per participant. Left and right hippocampal seed regions were included as separate levels in the analysis. A 2 (task: order monitoring, visual orientation) x 2 (epoch: SOC, SSO) x 2 (hemisphere: left, right) revealed no main effects or interactions that approached significance. These data suggest that the hippocampus was not specifically sensitive to changes in order. However, it could still be that the region was more generally implicated in the tracking of order, without being particularly sensitive to order changes. To evaluate this issue, we examined whether the hippocampus
showed stronger functional connectivity, with any brain region, during the order monitoring task relative to the visual orientation task. Connectivity maps (Figure 5) indicated strong connectivity in both tasks, with a distribution of regions that very precisely matched prior analyses of hippocampal connectivity obtained during rest (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). There were no reliable differences in connectivity between the tasks.

### Activity Related to Key-Presses in Active and Passive tasks

Our analyses to this point focused on activity preceding key presses (vs. matched condition). However, it is possible that the key-press action itself carried additional important information about order-sensitive systems. This question could be addressed by contrasting BOLD activity during key-presses that indicated order-change with BOLD activity during key-presses that were a response to simple visual change detection. It was particularly important to know whether the former would show increased activity in systems previously implicated in the monitoring of event boundaries. Figure 6 summarizes the findings of this analysis. As would be expected, key-presses in both tasks revealed strong motor-related activity, mainly on the left (given the right-handed key press). Additionally, there was stronger activity in visual areas for key-presses made in response to visual change, as these presses were made during and ongoing visual event. Both these initial results validate the analysis.

More important, this analysis identified a single region where key-press activity for order change was stronger than that for visual change; the left IFG. We cross-referenced the areas showing this pattern (blue cluster in Figure 6C) against anatomical information, separately evaluating activity in posterior IFG (BA44) and more anterior IFG (BA45). We found greater activity for key presses in the order-monitoring task for both sub-regions. In both, activity in the order-monitoring task differed significantly from baseline (BA45: $T(15) = 4.14$, $p = .0005$; BA44: $T(15) = 6.08$, $p < .0001$), whereas activity in the visual task did not. Increased activity in left IFG has been generally related to increased task difficulty (Binder et al., 2004). Because the current cluster encompassed both posterior and central aspects of the regions, a parsimonious explanation is that increased difficulty during the order-monitoring task (corroborated by the higher heart rate) is related to increased activity during the decision itself. However, this left IFG activation may reflect the processing of our acoustic tone stimuli musically, with presses indicating a violation in perceived musical syntax (Sammler, Koelsch and Friederici, 2011). These findings suggest that in the current paradigm, the core processes related to order monitoring may have concluded by the time of the key press, with relatively little order-related higher-level activity occurring during the key press itself.

### Discussion

There are good reasons to think that people are sensitive to changes in statistical features within their environment. Because these changes form boundaries in what is an otherwise continuous sensory input unfolding over time, noticing them and constructing a typology of temporal patterns can serve as a building block for forming new semantic or event categories. Statistical shifts within a continuous sensory stream can also signal highly meaningful changes such as shifts in weather pattern, an unwelcome change in the health of the car’s motor or a worrisome change in sleeping habits. It is therefore likely that people evolved mechanisms to
code for statistical changes, which would be consistent with behavioral work showing high sensitivity to statistical regularities within complex inputs (e.g., Smithson, 1997; Stephen & Dixon, 2011). Our findings indicate that the neocortical coding of changes in perceived order is mediated mainly via posterior structures previously associated with the coding of order and event structure, and the posterior middle frontal gyrus. The current findings revealed a consistent pattern of higher activity during temporal epochs that preceded subjective perceptions of order change (vs. epochs where no changes were noted) independent of whether order was explicitly monitored for. However, there was a clear spatial dissociation between areas that tracked order changes during active monitoring versus passive listening in the visual orientation task.

Monitoring for Order Change: The Role of Hippocampal, Frontal, and Posterior Midline Regions

Beyond the impact of task, which we discuss in detail below, the current work identifies several general principles by which order changes are coded. With respect to the location of regions sensitive to perceived order stability, the data highlight the importance of the posterior cingulate, fusiform, parahippocampal gyri, and the middle frontal gyrus in sensitivity to order changes. As outlined in the Introduction, prior work suggests that sensitivity to changes in regularity could be mediated by the hippocampus (Harrison et al., 2006; Strange et al., 2005), prefrontal cortex or ACC (Behrens et al., 2007; Harrison, Bestmann, Rosa, Penny, & Green, 2011; Huettel et al., 2002) or within a set of posterior midline regions (Speer et al., 2007; Whitney et al., 2009; Zacks et al., 2001). Our data offer little support for the first option, moderate support for the second and strong support for the third.

The hippocampus has been linked to the representation of short, fixed sequences and their violation (Kumaran & Maguire, 2006), the representation of cue validity of single elements (Turk-Browne et al., 2010), and the coding of high-level statistical features of inputs such as their degree of diversity (Shannon Entropy; Strange et al., 2005) or the mutual information between items (Harrison et al., 2006). However, in the current study the hippocampus did not differentiate between SOC and SSO epochs suggesting it does not mediate the perception of order changes. Because this was a null effect we studied whole-brain functional connectivity with a hippocampal seed region to determine if monitoring for order-changes induced different connectivity patterns than did passive listening. We postulated that if the hippocampus mediates a general function associated with the monitoring for order-change it would show stronger connectivity with certain regions when such monitoring is required. This functional connectivity analysis pointed to three conclusions. First, hippocampal connectivity patterns were highly robust during both tasks, a result that validated the analysis and indicated sufficient signal quality in the region. Second, these connectivity patterns did not differentiate between the two tasks. Third, connectivity patterns did not differentiate between the two tasks. Third, connectivity patterns were extremely similar to those previously documented for the hippocampus during rest (Vincent et al., 2008). To conclude, the hippocampus did not appear to play either a specific role in being sensitive for changing statistical regularities or a more general role in order monitoring temporal patterns. When taken together with the fact that these connectivity patterns were highly similar to ones documented during rest, our findings support recent work that has failed to link hippocampal function to the coding of associative novelty (Bubic et al., 2011) or statistical regularities (Tobia, Iacovella, & Hasson, 2012).
With respect to frontal activity, the analyses did not identify the extensive distribution documented in prior work (Huettel et al., 2002). In that work (examining only frontal activity) violations of streaks, which could be interpreted as order shifts, resulted in increased activity in a network including the MFG bilaterally, but also the inferior frontal gyrus and sulcus (bilaterally), the insula, and the ACC. The bilateral MFG region we identify as sensitive to order changes during active monitoring was located in spatial coordinates near those reported by Huettel et al., and somewhat more posteriorly during passive monitoring. However, we did not document similar sensitivity in the inferior frontal gyrus and sulcus or insula even at a very liberal threshold (p < .05 uncorrected).

In contrast, the distribution of regions documented in the current study was consistent with that identified in prior work on the neural correlates of event segmentation and narrative shifts (Speer et al., 2007; Whitney et al., 2009; Zacks et al., 2001). In that work, an ongoing action, e.g., doing dishes was defined as a sequence of events. Transitions between events have been associated with BOLD responses in a distributed set of largely posterior regions, notably excluding the insula and ACC, and with more limited frontal involvement. These responses to event transitions have been interpreted in terms of perceptual event segmentation for visually presented sequences (Zacks et al., 2001) or the segmentation of more abstract events when described via narratives (Speer et al., 2007; Whitney et al., 2009), possibly for consolidation as episodic memories (Ezzyat & Davachi, 2011). The activity centers we document in the middle occipital gyrus, precuneus and superior temporal and fusiform gyri closely match coordinates reported for event segmentation (Zacks et al., 2001) with remarkable commonalities and little divergence. The parallelism is notable since in prior work events had semantic content and were presented via movies or printed narratives, whereas the boundaries identified here were based on subjectively perceived statistical features.

It is important to note that the correlation between event boundaries and the BOLD response is typically one where there is a strong BOLD increase immediately after the boundary as if time locked to an event, whereas in the current study, the epochs examined were ones occurring prior to participants' indication of order changes; that is, during the stage where evidence was accumulated. However, even on this point there exist similarities with work on event perception (Zacks et al., 2001) that identified posterior and frontal regions where activity began changing 7-10 sec prior to points marked as event boundaries. This buildup of activity has been interpreted as suggesting that these regions play a role in the buildup of information that precedes the perception of an event change.

It is noteworthy that the regions identified in our analysis tended to show a gradual decrease in activity in sections where no order changes were indicated rather than an activity increase preceding a perceived change point. This could indicate that these regions are associated with a routine monitoring of order, with a decrease in activity occurring during rare periods of very high regularity. That is, rather than monitoring for changes, they could signal particularly constant inputs. A related interpretation for these time series patterns derives from work by Hesselmann et al. (2010). That work identified a number of regions were BOLD signal prior to presentation of a near-threshold stimulus discriminated between subsequent hits and subsequent false alarms. Crucially, activity preceding 'hits' remained at baseline for several seconds prior to stimulus presentation, whereas activity preceding 'false alarm' decisions was characterized by a gradual decrease in activity over the few seconds prior to stimulus presentation. The authors suggest this pattern indicates a brain system involved in generating precise prediction-error signals: stronger activity in this system would be associated with adequate error signals (leading to hits and correct rejections), whereas a gradual decrease in activity indicates a shunting of necessary error signals, leading to false alarms due to excessive influence of top-down predictions. This account fits well with our data and suggests that in SOC contexts where order is changing, error terms are continuously generated, leading to a 'change' responses, where in stable (SSO) contexts, the more stable nature of the statistical environment leads to greater reliance on top-down signals with a reduction in error terms, as manifested in reduced activity.

The similarity between the current findings and those documented in studies of event perception and narrative shifts (Whitney et al., 2009) suggests that regions previously linked to event segmentation may also mediate lower-level functions related to the coding of statistical changes in streams that lack semantic content. We propose that the ability to integrate information over time and notice changes in statistical patterns is a stepping-stone towards representing and segmenting event sequences. Though the current work does not address event perception, at least some event transitions are fuzzy or vague (Zacks, Speer, Swallow, Braver, & Reynolds, 2007) rather than clear-cut (e.g., the end of a work shift). Noting fuzzy transitions may depend on the accumulation of evidence over time. If so, regions coding for statistical changes could be well positioned to bootstrap such higher-level functions. We note however, that the analogy between statistical segmentation and event segmentation has its limits: some events are perceived as such because of purely physical changes, e.g., changes in the amount of movement over time, or because they are related to achievement or failure of high level goals (Zacks et al., 2007). Event boundaries in such domains result in activity in different brain areas and may represent the characteristics of the event, rather than a boundary per se.
Several of the posterior clusters identified during the active task, extending from the posterior cingulate to the cuneus, and including the fusiform, showed a correlation between participants' sensitivity to order changes (clicks/minute) and activity in SSO epochs, suggesting that the activity range within these regions is sensitive to variations in subjective order perception. Identifying regions tracking sensitivity to order shifts is important since increased sensitivity to variation, e.g., within a rudimentary control system, could indicate (a) integration of information over shorter time windows leading to less stability that stems from more frequent updating, (b) increased noise in the coding of order leading to a less stable representation of input statistics or (c) a lower threshold for determining what constitutes a meaningful change. All of these are interesting processes that could be fleshed out in future work. The involvement of posterior regions in the coding of order is consistent with prior work (Tobia et al., 2012) that documented sensitivity to fluctuations in order while passively listening to a stimulus set similar to the one used here. Specifically, posterior medial cortical regions were sensitive to deflections in the contextual sequence, consistent with the possibility of being sensitive to statistically defined boundaries. The account we offer here for activity in the posterior regions is similar to that offered by Whitney et al. (2009), who interpreted their sensitivity to narrative changes as an updating function. A parsimonious explanation for the current and prior work is that these regions mediate a low-level boundary detection function in multiple domains.

**Similarities and Differences Across Active Monitoring and Passive Perception**

The specific pattern of activity associated with the detection of order-changes depended to some extent on whether these were explicitly monitored. Nonetheless, there were also important similarities across tasks, namely that in both tasks BOLD signal in SOC epochs was consistently higher than that in SSO epochs. The particular profile of BOLD responses in these epochs also held across tasks, and in most cases was one where the differences between SOC and SSO epochs did not derive from greater activity during the SOC epochs.

Beyond these similar activation patterns, the data also point to important task-related differences. First, differential activity during SOC and SSO epochs was found in separate clusters within each task. When we considered regions that differentiated the two epochs as functional ROIs and applied them to data collected in the other task we found that none of the regions identified in the active task showed a statistically significant differentiation between SOC and SSO epochs in the passive task, and of the regions identified in the passive task, only one, the STG, showed a similar pattern in the active task. Thus, regions highly sensitive to the SOC vs. SSO contrast in each task did not extend this sensitivity to the other task. In addition, a direct contrast between the two tasks identified three regions with statistically significant task differences. During SOC epochs, intentional monitoring was associated with a stronger response in the left MTG, and weaker response in the orbitofrontal cortex as compared to passive listening. For the SSO epochs, activity in the angular gyrus was significantly reduced during intentional monitoring than passive listening. These data indicate that the explicit monitoring for order not only changes activation patterns during periods associated with such changes, but also during periods where no changes are perceived.

These data are consistent with prior work showing that the coding of statistical features within temporally extended inputs depends on whether one’s attention is oriented towards the stimulus whose order is manipulated. For instance, in absence of explicit monitoring, only local violations in streaks are noticed, but regularities that depend on establishing longer-range relations between items go unnoticed (Bekinschtein et al., 2009; Kimura et al., 2010). Similarly, it has been shown that cortical responses to order depend on whether one is pre-informed of the nature of sequential regularity. Bischoff-Grethe et al. (2000) identified several areas where the magnitude of differential responses for random and deterministic sequences varied as function of conscious awareness of the sequential constraints. In our current work, an interesting exception to the task-dependent effects was documented in the left STG, in the vicinity of the lateral part of the transverse temporal gyrus, where we found greater activity for SOC epochs in both tasks. This finding is similar to data from Bischoff-Grethe et al., which documented sensitivity in this region to transition constraints independently of whether participants were aware of the order manipulation. This temporal region has also been linked to parsing random vs. sequential syllable sequences (McNealy et al., 2006).

Could the differences between the active monitoring task and passive task be the result of a decision-planning component that was part of the active monitoring task? It is impossible to rule out this possibility. However, two aspects of the current findings suggest that task-related differences were not related to decision-planning demands in the active task. Work on perceptual decision making in paradigms where response planning is based on evidence accumulation over time has led to two general conclusions (Heekren et al., 2008): areas mediating decision variables in contexts of perceptual decision-making include prefrontal, motor and premotor cortices – regions which in the current study do not show SOC-SSO effects in the active task, nor differentiate the active and passive task, and (b) that the pattern of activity associated with perceptual decision-making is one of a gradual increase in activity prior to decision, which remains elevated until a response is made. As detailed above, the pattern for the active task was the opposite – i.e. a gradual decrease in
activity for SSO epochs rather than a gradual increase in activity
prior to key presses. Thus, both the distribution of regions and
the time series in those regions do not strongly support to the
possibility that areas showing task differences do so because they
implement a decision-making component.

Relation to Input Non-Stationarity

The stimuli used in the current study were generated by a
simple algorithm whose purpose was to control gradual waxing
and waning of regularity over time, thus allowing a greater
opportunity for noticing changes in regularity than a stationary
generator. However, there is reason to suppose that participants' indications of order change do not necessarily reflect sensitivity to the non-stationary aspect of the input, and it may be that similarly frequent behavioral responses (and concomitant BOLD patterns) would have been found if a stationary distribution was used instead. Prior work suggests as much: Huettel et al. (2002) generated stimuli from a stationary random distribution and showed that participants were sensitive to very local changes in patterns (terminations of short streaks or alternations). In that study, participants demonstrated increased BOLD signal when these local patterns terminated, suggesting that they were parsing the input not as memory-unlimited Bayesian observers, but from a local perspective where more recent information was weighted more strongly. A similar point is made by recent work of Harrison et al. (2011) that showed that fluctuations in brain activity indicate stronger weighting of the most recently encountered information, even though stimuli were sampled from a stationary, random distribution. For these reasons it would be not surprising if results similar to the current findings were found for data sampled from a stationary distribution.

Summary

The main import of the current work is that the brain is
sensitive to changes in statistical features of incoming input, or
lack thereof, and that these responses are found in two different brain systems depending on how attention is directed to the stimuli. In both cases the responses are similar to those involved in the segmentation of perceptual events (Zacks et al., 2001) and encompass regions known to be sensitive to fluctuations in order over the recent past (Tobia et al., 2012), as well as regions that are sensitive to accruing information about increasingly long chains of regular sequences such as the MFG (Huettel et al., 2002). Our findings further show that the differentiation between contexts where order changes and those where order is static is marked by a pattern of decreased activity when order is static rather than a strong buildup of activity when it is volatile. This was the dominant pattern under both active and passive listening. As such, the systems identified here could be involved in a default monitoring of the environment for changes in order, possibly related to the generation of error terms in the context of the evaluation of continuous predictions.

Whereas the hippocampus is purportedly involved in coding for the order information of discrete events (Harrison, et al., 2006; 2011; Strange et al., 2005; Turk-Browne et al., 2010), our findings suggest it is not a central component of the system that codes for contextual order over a temporally extended series. To the contrary, hippocampal connectivity was similar to that previously documented during rest, for both tasks employed in our study. This suggests an important distinction that should be drawn between the novelty of a particular stimulus given recently encountered stimuli – a feature previously associated with hippocampal activity (Kamaran & Maguire, 2006) - and the novelty of a temporally extended context given recent contexts. The former refers to the stimulus that violates a structured sequence whereas the latter refers to a shift between statistical distributions. This distinction may explain why our findings do not identify a role for the episodic and source memory system anchored at the hippocampus, but rather identifies systems associated with transitions between narrative events or the perception of visual event boundaries.

The brain systems we identify play a basic role in partitioning input streams on the basis of changing input patterns. Taken together with prior reported findings regarding event segmentation and recognizing event transitions, the current findings suggest that these systems may play a fundamental role in the segmentation of both semantic and non-semantic input streams. The ability to segment inputs based on statistics alone could enable the construction of temporal categories and thus bootstrap the creation of semantically rich event types. The longitudinal process by which a newly identified temporal pattern accrues meaning is an interesting topic for future work.

References


**Acknowledgements**

This research has received funding from the European Research Council under the 7th framework starting grant program (ERC-STG #263318) to U.H.
### Table 1

Table 1. Findings from active order monitoring task. Clusters where activity during epochs preceding indications of order change exceeded activity during matched length epochs that did not precede indications of order change.

<table>
<thead>
<tr>
<th>Cluster</th>
<th>Talairach</th>
<th>BA</th>
<th>Anat. Label</th>
<th>Area (mm²)</th>
<th>T</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>-23 37</td>
<td>46</td>
<td>Parahippocampal Gyrus</td>
<td>364</td>
<td>4.876</td>
</tr>
<tr>
<td>2.</td>
<td>-31 31</td>
<td>9</td>
<td>Middle Frontal Gyrus</td>
<td>212</td>
<td>5.749</td>
</tr>
<tr>
<td>3.</td>
<td>-12 30</td>
<td>6</td>
<td>Posterior Cingulate</td>
<td>364</td>
<td>4.303</td>
</tr>
<tr>
<td>4.</td>
<td>-14 11</td>
<td>30</td>
<td>Posterior Cingulate</td>
<td>125</td>
<td>4.293</td>
</tr>
<tr>
<td>5.</td>
<td>-15 16</td>
<td>10</td>
<td>Posterior Cingulate</td>
<td>80</td>
<td>4.067</td>
</tr>
<tr>
<td>6.</td>
<td>-9 47</td>
<td>7</td>
<td>Precuneus</td>
<td>67</td>
<td>3.984</td>
</tr>
<tr>
<td>Right</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>31 23</td>
<td>9</td>
<td>Middle Frontal Gyrus</td>
<td>163</td>
<td>5.011</td>
</tr>
<tr>
<td>2.</td>
<td>37 9</td>
<td>19</td>
<td>Middle Occipital Gyrus</td>
<td>143</td>
<td>4.395</td>
</tr>
<tr>
<td>3.</td>
<td>26 7</td>
<td>19</td>
<td>Fusiform Gyrus</td>
<td>133</td>
<td>4.820</td>
</tr>
<tr>
<td>4.</td>
<td>12 14</td>
<td>18</td>
<td>Cuneus</td>
<td>81</td>
<td>4.831</td>
</tr>
<tr>
<td>5.</td>
<td>29 6</td>
<td>30</td>
<td>Parahippocampal Gyrus</td>
<td>72</td>
<td>3.087</td>
</tr>
<tr>
<td>6.</td>
<td>19 0</td>
<td>18</td>
<td>Lingual Gyrus</td>
<td>71</td>
<td>3.894</td>
</tr>
</tbody>
</table>

Note: Subscripts next to anatomical label indicate whether there was a relation between BOLD magnitude in the SOC (order change) and SSQ (stable order) epochs and the number of click model participants per minute. (a) correlation with activity during SSQ epochs. (b) correlation with activity during SOC epochs. No clusters showed a pattern where activity was greater in SSQ epochs. Clusters correspond to those shown in Figure 2.

### Table 2

Table 2. Findings from visual orientation task.

<table>
<thead>
<tr>
<th>Cluster</th>
<th>Talairach</th>
<th>BA</th>
<th>Anat. Label</th>
<th>Area (mm²)</th>
<th>T</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>-1 6 4</td>
<td>None</td>
<td>Hypothalamus/Mammillary Body</td>
<td>76</td>
<td>6.634</td>
</tr>
<tr>
<td>2.</td>
<td>-54 4 22</td>
<td>22</td>
<td>Superior Temporal Gyrus</td>
<td>69</td>
<td>5.544</td>
</tr>
<tr>
<td>3.</td>
<td>-21 44 6</td>
<td>6</td>
<td>Middle Frontal Gyrus</td>
<td>66</td>
<td>4.258</td>
</tr>
<tr>
<td>Right</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>20 47 24</td>
<td>24</td>
<td>Middle Frontal Gyrus</td>
<td>199</td>
<td>5.636</td>
</tr>
<tr>
<td>2.</td>
<td>11 -89 4</td>
<td>17</td>
<td>Lingual Gyrus</td>
<td>168</td>
<td>5.239</td>
</tr>
<tr>
<td>3.</td>
<td>-36 -14 20</td>
<td>20</td>
<td>Fusiform Gyrus</td>
<td>106</td>
<td>4.751</td>
</tr>
<tr>
<td>4.</td>
<td>-2 0 0</td>
<td>None</td>
<td>Anterior Cingulate/Thalamus</td>
<td>68</td>
<td>6.362</td>
</tr>
</tbody>
</table>

Note: In all clusters, SOC epochs showed greater activity than SSQ epochs. Clusters correspond to those shown in Figure 3.

### Table 3

Table 3. Areas where sensitivity to regularity patterns differed between the order monitoring and the visual orientation tasks.

<table>
<thead>
<tr>
<th>Cluster</th>
<th>Talairach</th>
<th>BA</th>
<th>Anat. Label</th>
<th>Area (mm²)</th>
<th>T</th>
</tr>
</thead>
<tbody>
<tr>
<td>Order Monitoring SOC – SSQ</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>-34 52 15</td>
<td>22</td>
<td>L. Superior/Middle Temporal Gyrus</td>
<td>130</td>
<td>5.033</td>
</tr>
<tr>
<td>2.</td>
<td>-17 -11 20</td>
<td>20</td>
<td>L. Subcallosal Gyrus</td>
<td>113</td>
<td>3.013</td>
</tr>
<tr>
<td>Visual Orientation SOC – SSQ</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>38 60 39</td>
<td>R. Angular Gyrus</td>
<td>321</td>
<td>3.013</td>
<td></td>
</tr>
</tbody>
</table>

Note: Clusters correspond to those shown in Figure 4A,B.