# Neural mechanisms for integrating consecutive and interleaved natural events

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# Neural mechanisms for integrating consecutive and interleaved natural events

**Running title: Event integration**

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# Abstract

To understand temporally extended events, the human brain needs to accumulate information continuously across time. Interruptions that require switching of attention to other event sequences disrupt this process. To reveal neural mechanisms supporting integration of event information, we measured brain activity with functional magnetic resonance imaging (fMRI) from 18 participants during viewing of 6.5-minute excerpts from three movies i) consecutively and ii) as interleaved segments of approximately 50-s in duration. We measured inter-subject reliability of brain activity by calculating inter-subject correlations (ISC) of fMRI signals and analyzed activation timecourses with a general linear model (GLM). Interleaving decreased the ISC in posterior temporal lobes, medial prefrontal cortex, superior precuneus, medial occipital cortex and cerebellum. In the GLM analyses, posterior temporal lobes were activated more consistently by instances of speech when the movies were viewed consecutively than as interleaved segments. By contrast, low-level auditory and visual stimulus features and editing boundaries caused similar activity patterns in both conditions. In the medial occipital cortex, decreases in ISC were seen in short bursts throughout the movie clips. By contrast, the other areas showed longer-lasting differences in ISC during isolated scenes depicting socially-relevant and suspenseful content, such as deception or inter-subject conflict. The areas in the posterior temporal lobes also showed sustained activity during continuous actions and were deactivated when actions ended at scene boundaries. Our results suggest that the posterior temporal and dorsomedial prefrontal cortices, as well as the cerebellum and dorsal precuneus, support integration of events into coherent event sequences.

23 **Introduction**

24      Perception of dynamic events in changing environments requires constant

25 accumulation and integration of temporally unfolding information. Interruptions can

26 severely disturb such integration. For example, additional effort is needed to recall what

27 happened in a television series following a commercial break. To integrate temporally

28 unfolding information, the brain builds a predictive model (schema) of the current situation.

29 This facilitates interpretation of future events, detection of event boundaries, and

30 integration of the perceived events with information in memory into a coherent whole (for a

31 review, see Kurby and Zacks 2008).

32      Attention modulates processing of both targets and semantically related objects in

33 wide-spread areas of the cerebral cortex (Çukur et al., 2013; see also Lahnakoski et al.,

34 2014). The temporoparietal junction and parietal cortical areas participate in detection of

35 perceptual event boundaries (Zacks et al. 2001; 2010; 2011), possibly by monitoring the

36 continuity of action sequences from one event (i.e. independent subset of actions) to

37 another. In particular, temporoparietal regions, complemented by the precuneus and

38 superior occipital lobe, are more sensitive to events where the same action continues across

39 a cut-point (i.e., edit) between scenes in a video compared with cut-points where the

40 location or action abruptly changes (Magliano and Zacks 2011). These regions may support

41 the integration of ongoing actions across varying viewpoints into a coherent whole.

42 Moreover, differences in gray matter volume in frontal and temporal cortices are associated

43 with both abnormal perception of event boundaries and difficulties in performing action

44 sequences after seeing them in videos (Bailey et al., 2011). Specifically, reduced gray matter

45 volume in the medial temporal lobe was associated with omitting actions seen in videos

2

46    whereas, against predictions, increased gray matter volume in the dorsolateral prefrontal

47    cortex was correlated with the number of inaccurately performed actions (e.g. packing the

48    correct items but putting them in an inappropriate container) (Bailey et al., 2011).

49        Temporally scrambled versus intact movies (Hasson et al., 2008a) and audio stories

50    (Lerner et al., 2011) result in lower inter-subject correlation (ISC; Hasson et al., 2004) in

51    frontal and posterior temporal regions, while ISC in sensory areas remain unaffected. This

52    may reflect different temporal scales of information accumulation in sensory *vs.* higher-

53    order areas (Hasson et al., 2015). Scrambling a movie reduces prior information that the

54    brain can use about preceding events. This compromises the construction of a coherent

55    predictive model of the movie that, in an unscrambled version, would facilitate

56    understanding of events unfolding over long time windows (Hasson et al., 2015). However,

57    experiments where the chronological order of movie events is simply scrambled cannot

58    distinguish between integration of ongoing, temporally continuous information and

59    integration of information between two parts of the same event sequence when separated

60    in time by intermittent presentation of events from another sequence.

61        Another line of research has shown that when low-level visual continuity (rather

62    than temporal order) of a continuous action sequence is disrupted with camera angle

63    changes, ISC in the frontal cortex remains unaffected while ISCs in the occipital and

64    posterior parietal cortices increase (Herbec et al., 2015). This may be due to the increased

65    visual changes at the cut-points eliciting synchronized onset-responses or higher attentional

66    synchrony introduced by, e.g., particular camera angles (shot sizes) in the videos (Herbec et

67    al., 2015).

Lahnakoski JM                                                                  Event integration

68     Posterior temporal lobes and midline structures such as precuneus and dorsomedial

69     prefrontal cortex process multiple aspects of social information (see e.g. Lahnakoski et al.,

70     2012b). Social perception and particularly speech comprehension relies strongly on

71     contextual prediction of social information and cues (see e.g. Smirnov et al., 2014). Usually,

72     such contextual information accumulates over time. Social perception is thus more likely to

73     be affected by manipulation of the temporal structure of incoming stimuli than processing

74     of simple stimulus features or perception of short and contextually isolated event

75     sequences.

76     **The current study**

77         Here we aimed at resolving how the human brain integrates temporally extended

78     event sequences by showing subjects excerpts from three movies i) consecutively and ii) as

79     interleaved segments with the order of events within each movie retained. We calculated

80     ISCs across subjects in both conditions, and tested whether the strength of the ISC differed

81     across the conditions. We also annotated scene transitions, low-level visual and auditory

82     features, socially relevant content, and suspense in the movies, to reveal those features

83     whose processing is most sensitive to flipping between event sequences. As an additional

84     control analysis, we tested whether continuity disruptions caused deactivations (and

85     continuous cuts activations; Magliano and Zacks 2011) in the brain regions that presumably

86     integrate event-sequence information as suggested by the differences between the

87     conditions in the ISC and general linear model (GLM) analyses. Finally, we used an

88     explorative "reverse correlation" approach (extended from Hasson et al., 2004) for revealing

89     the events in the movies that caused the highest ISC differences across conditions.

Lahnakoski JM                                                  Event integration

90       We hypothesized that viewing the movies as intact *vs.* interleaved segments would

91   trigger stronger ISC in posterior temporal and frontal brain regions (Hasson et al., 2008a;

92   Lerner et al., 2011). We specifically predicted that the processing of social events, rather

93   than low-level physical features, would explain the ISC differences because understanding

94   social events requires longer time periods. By contrast, interleaving is unlikely to affect the

95   processing of low-level features as suggested by findings showing that the inter-subject

96   reliability of early sensory-cortical responses is high even when a movie is played backwards

97   (Hasson et al., 2008a).

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## Materials and methods

### Subjects

Eighteen healthy subjects (21–34 years, mean 28; three female; five left-handed) participated in the study. Subjects reported no history of neurological or psychiatric disorders, and were not taking medications affecting the central nervous system at the time of the study. All subjects provided an informed consent as a part of the protocol approved by the ethics committee of the Hospital District of Helsinki and Uusimaa. The study was carried out in accordance with the guidelines of the declaration of Helsinki.

### Stimuli and procedure

The subjects watched audiovisual excerpts of three feature films: *Star Wars: Episode IV - A New Hope* (SW; length 6 min 38 s), *Indiana Jones: Raiders of the Lost Ark* (IJ; length 6 min 22 s) and the James Bond-movie *Golden Eye* (GE; length 6 min 24 sec). We selected these movies since their storylines are easy to follow and each has a clearly different theme (space opera, classic adventure, and agent adventure, respectively) making it easy for the subjects to know which movie they are currently viewing. The excerpts were taken from the beginning of the films, excluding opening credits and other text. They were subsequently cut into eight short segments (mean length 49 seconds ± 14 seconds, 24 segments in total) following the original cut-points in the movies, so that the abrupt audiovisual changes at the cut-points were similar in the two presentation conditions (see below).

The clips were presented in two ways (**Figure 1**). In the *Consecutive*-condition, the excerpts from each movie were presented one after another without breaks. Thus, the participants viewed the 6-minute excerpts as if they would have been watching the original movies. In the *Interleaved*-condition, the clips were also shown without breaks but their

6

121    order was interleaved in a pseudo-random manner so that the movie (and thus also the

122    plotline) changed after each segment, while the temporal order of segments *within* each

123    original movie was retained. In other words, all the storylines unfolded in their original

124    logical order yet the participants were required to switch between the storylines

125    approximately once every 50 seconds. The presentation order of the conditions was

126    counterbalanced across subjects to remove order effects between the conditions. Subjects

127    were instructed to follow the plot of each of the movies, and to prepare to answer

128    questions about the movie contents after the experiment. However, only ratings of

129    familiarity of the movies and evaluations of the clip transitions were collected after the

130    experiment. To aid the following of the movie events, each movie excerpt depicted only a

131    single sequence of events. Thus, the subjects had to integrate temporally fragmented

132    information only in the interleaved condition.

133        The beginning of the first video was synchronized to the beginning of fMRI sequence

134    using Presentation software (Neurobehavioral Systems Inc., Albany, California, USA). The

135    stimuli were back-projected on a semitransparent screen using a 3-micromirror data

136    projector (Christie X3, Christie Digital Systems Ltd., Mönchengladbach, Germany). The

137    subjects viewed the screen at 34 cm viewing distance via a mirror located above their eyes.

138    Audio was played to the subjects with an UNIDES ADU2a audio system (Unides Design,

139    Helsinki, Finland) via plastic tubes through EAR-tip (Etymotic Research, ER3, IL, USA)

140    earplugs. The intensity of the auditory stimulation was selected to be loud enough to be

141    heard over the scanner noise and was adjusted slightly (±2 dB) if the subject reported the

142    sound to be too loud or too quiet before the experiment.

7

143 In a separate behavioral experiment after the scanning, subjects first saw the *last* 10

144 seconds of a movie segment, which was immediately followed by a one-second-duration

145 arrow indicating the onset of the *first* 10 seconds of the subsequent segment. Then subjects

146 used a 9-point Likert scale to rate i) how easy it was to follow the transition from one

147 segment to another and ii) how natural the transition was. Ratings were given for all

148 possible transitions in the Consecutive and Interleaved movies conditions. In the

149 Consecutive condition these constituted of 20-s excerpts of the natural flow of events in the

150 movies (apart from the two transitions where the last two movies (IJ and GE) started, which

151 were preceded by a different movie in both conditions). Transitions were presented in a

152 random order. Finally, subjects indicated on a 9-point Likert scale how familiar they were

153 with each of the movies (1 - not at all familiar, 9 - extremely familiar). Ratings of one subject

154 were lost due to technical problems.

155 **Functional magnetic resonance imaging**

156 Functional brain imaging was carried out in the Advanced Magnetic Imaging (AMI)

157 Centre of Aalto University with a 3.0 T GE Signa VH/i MRI scanner with HDxt upgrade (GE

158 Healthcare Ltd., Chalfont St Giles, UK) using a 16-channel receiving head coil (MR

159 Instruments Inc., MN, USA). The imaging area consisted of 36 functional gradient-echo

160 planar oblique slices covering the whole brain (thickness 4 mm, no gap, in-plane resolution

161 3.75 mm x 3.75 mm, voxel matrix 64 x 64, TE 30 ms, TR 1800 ms, flip angle 75°, ASSET

162 parallel imaging, R factor 2). ASSET calibration was performed prior to each imaging session.

163 Total of 690 images were acquired continuously during both functional imaging sessions. In

164 addition, a $T_1$-weighted spoiled gradient echo volume was acquired for anatomical

165 alignment (SPGR pulse sequence, TE 1.9 ms, TR 10 ms, flip angle 15°, ASSET parallel imaging,

8

Lahnakoski JM                                                             Event integration

166    R factor 2). The $T_1$ image consisted of 182 axial slices, in-plane resolution was 1 mm x 1 mm,

167    matrix 256 x 256 and slice thickness 1 mm with no gap.

168    **Preprocessing**

169        Data were preprocessed with FSL (Smith et al., 2004; Woolrich et al., 2009). Motion

170    correction was applied using MCFLIRT (Jenkinson et al., 2002), and non-brain matter was

171    removed using BET (Smith 2002). The intensity distortions of the anatomical images were

172    corrected prior to brain extraction, and values for intensity threshold and threshold gradient

173    in BET were searched manually by changing the parameters and visually inspecting each

174    brain-extracted volume. Using FLIRT, the datasets were registered to 2 mm MNI152

175    (Montreal Neurological Institute) standard-space template using the brain extracted $T_1$

176    weighted image of each individual subject as an intermediate step (Jenkinson et al., 2002).

177    Registration both from functional to anatomical images and from anatomical images to

178    standard template volumes was done using 9 degrees of freedom (DOF), allowing for

179    translation, rotation, and scaling. Volume data were smoothed using a Gaussian kernel with

180    full width at half maximum (FWHM) of 8.0 mm. High-pass temporal filtering was applied

181    using Gaussian-weighted least-squares straight line fitting, with sigma 200 s, with the first 4

182    volumes of each dataset discarded to allow the magnetization to stabilize in the tissue (a

183    fixation cross was presented during this time). The last 37 volumes of the data, which were

184    recorded after the end of the stimulus, were removed leaving 649 volumes for the final

185    analyses.

186    **Analysis of behavioral data**

187        Mean ratings for easiness to follow and naturalness of the transitions in the

188    Consecutive *vs.* Interleaved conditions were compared across subjects with paired t-tests.

9

189    The transitions to the first clips of each movie were excluded from the analysis because they

190    required reorienting to a new storyline in both conditions.

191    **fMRI data analysis**

192        All fMRI results are visualized on the "Conte-69" cerebral surface atlas and "Colin"

193    cerebellar surface using Caret software (version 5.616; Van Essen et al., 2001).

194        *Inter-subject correlation analysis*

195        The ISCs for each voxel of the brain over both conditions were calculated using ISC

196    toolbox (https://www.nitrc.org/projects/isc-toolbox/; Kauppi et al., 2014). To test for

197    significance of ISC, we calculated the ISC between conditions (i.e. across pairs where the two

198    participants were watching different (intact *vs.* segmented) versions of the stimuli) to build

199    an empirical null distribution of ISC values. Because the first 50 seconds of stimulation in

200    both conditions was the same, the ISC values in the null distribution were inflated due to the

201    correlated activity during this time window. Thus, we used the $99^{th}$ percentile of the

202    observed values as a conservative threshold of significance without additional corrections[1].

203    Differences in within-condition ISC strength between Consecutive and Interleaved

204    conditions were tested using Pearson-Filon statistics on Z transformed correlation

205    coefficients, as implemented in the ISC toolbox (Kauppi et al., 2014). Specifically, this is

206    accomplished by using a non-parametric permutation test that randomly re-labels the

207    conditions (switching signs of pairwise differences) 25,000 times with the null hypothesis

208    that relabeling does not change the ISC difference across conditions. The test concurrently

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[1] For the sake of comparison, we also calculated the ISCs after removing the first movie clip (which was identical in both conditions) and used the maximum observed ISC value between conditions as a threshold for the within-condition ISC maps. This procedure yielded essentially identical results to the ones calculated with the full timecourses, thus confirming that the chosen threshold effectively controls for multiple comparisons in the current data.

209    controls the family-wise error rate (FWER) at p<0.05 by building the null distribution out of

210    the maximal group differences observed in the whole brain. These differences across

211    conditions were also essentially unchanged when the data was analyzed after excluding the

212    first clip.

213    *General linear model analysis*

214    All GLM analyses were performed in SPM12 (http://www.fil.ion.ucl.ac.uk/spm).

215    Canonical hemodynamic response function was used as the basis function and high-pass

216    filter period was set to 128 seconds. Event-related analysis of the movie transitions was

217    performed by modeling the movie onsets as events in the design matrix, and a contrast was

218    calculated between the transitions in the Consecutive *vs.* Interleaved conditions. The first

219    clips of each movie were excluded from the event related analysis because an abrupt

220    change in the visual stimulus and event context preceded these clips in both conditions.

221    To control for activity related to low-level sensory features, we extracted the visual

222    contrast edges and sound power (root-mean-squared power; RMS) from the stimuli (for

223    details, see Lahnakoski et al., 2012a). Additionally, optic flow was estimated for each frame

224    of the movie using a Matlab toolbox (http://people.csail.mit.edu/celiu/OpticalFlow/, Liu

225    2009) and color intensity was estimated as the product of the mean color saturation and

226    color value (brightness) of each frame (i.e. highly saturated bright colors received a high

227    score and subdued and/or dark colors received a low score). Speech within the sound track

228    of  each  movie  segment  was  annotated  using  Audacity  1.3.12-beta

229    (http://audacity.sourceforge.net/). Additionally, prominence of faces, biological motion and

230    non-biological motion in the movies were annotated manually with 5-Hz sampling frequency

231    by two independent raters using a web-based rating system (based on Nummenmaa et al.,

11

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232    2012). The rating was done by moving a scrollbar beside the video up or down with the

233    mouse while watching the movies. The annotations were loaded to MATLAB, reordered to

234    appropriate order for each condition, rounded to 10-ms resolution, and down-sampled to

235    match the TR of the fMRI data prior to analysis.

236         Stimulus-feature dependent brain responses were analyzed similarly as those related

237    to the movie clip onsets except that each stimulus feature was modeled with an event and a

238    parametric modulator with one value for each functional volume. Correlation matrix and

239    timecourses of the stimulus features after convolution with a canonical hemodynamic

240    response function are shown in **Figure 2**. While most features were independent from each

241    other, presence of faces and speech, non-biological motion and RMS, as well as optic flow

242    and biological motion, were correlated. We performed the analyses both in independent

243    GLMs for each feature and in a combined GLM with all features entered as separate

244    parametric modulators without orthogonalization. Results were similar in both approaches,

245    suggesting that the collinearity does not confound the results.

246         As a validation analysis, we also replicated the analyses from a prior study (Magliano

247    and Zacks 2011) on action-continuity processing in the brain during movie viewing. To this

248    end, we performed a conjunction analysis of areas showing positive responses to all cut-

249    points in the movies and negative responses to action discontinuities at a subset of the cut-

250    points. Each first-level map was thresholded at FDR corrected $q<0.05$ and the binary

251    volumes were multiplied together to produce the conjunction results. For this, all cut-points

252    in all movies were semi-automatically extracted from the videos in Matlab. First, candidate

253    cut-points were extracted based on root-mean-square change of pixel values between

254    subsequent frames. These cut-points were then verified by viewing through the identified

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255    cut-intervals. Incorrectly identified cut points were then removed, and missed cut-points

256    were added frame by frame by annotating each frame either as a cut (first frame after cut-

257    point) or a non-cut. Then, each of the cut-points was inspected to reveal whether the action

258    presented in the movie was continuous over the cut-point. The responses to (i) cut-points

259    depicting discontinuous actions and (ii) all cut-points were then inserted as event onsets in

260    GLM analyses for estimating their conjunction. The analyses were repeated with both

261    models in a single GLM and in two independent GLMs but the results were nearly identical

262    due to low correlation between the models. Thus, we present only the results where the

263    models were estimated independently.

264        Finally, we tested whether segmentation of the movies would break down their

265    suspense, thus possibly leading to decreased ISC in brain regions involved in attention and

266    emotion. To that end, we recruited 10 additional participants who rated continuously their

267    experienced suspense while viewing the videos in either the Consecutive or Interleave

268    condition (five observers per condition). Mean condition-wise suspense ratings were used to

269    predict BOLD responses in a GLM as described earlier, with the exception that we used a

270    lower high-pass filter cutoff frequency (512 s period, corresponding to the length of the full

271    movie excerpts) due to the slowly changing suspense ratings. Given the slow and highly

272    autocorrelated signals, we also performed the GLM analysis 20 times with temporally

273    shifted models (shift >±5 samples; independent shift for each subject) to estimate the true

274    null probability. We used these null analyses to build the null distribution of t-values and

275    find the FDR corrected threshold of statistical significance (q>0.05).

Lahnakoski JM                                                      Event integration

### *Exploratory analysis of timepoints contributing to the ISC differences*

276

277        To localize timepoints that were contributing to ISC differences across conditions, we

278  reordered the timepoints in the Interleaved condition so that volumes recorded during the

279  same moment in the videos were aligned in both conditions. We then standardized the

280  subjects' voxelwise timecourses and computed a matrix of pairwise products of these values

281  over subjects for each timepoint and each voxel:

282        $Z_{x,y,z}(i,j)=(X_{i,x,y,z}-\mu_{i,x,y,z})/\sigma_{i,x,y,z} \circ (X_{j,x,y,z}-\mu_{j,x,y})/\sigma_{j,x,y,z}$

283  where $X_{i,x,y,z}$ is the BOLD timecourse of subject *i* at voxel *[x,y,z]*, $\mu$ and $\sigma$ are the means and

284  standard deviations of the BOLD timecourses, and $\circ$ indicates the Hadamard (element-

285  wise) product. Averaging these products over subject pairs and summing over time and

286  dividing by the number of timepoints minus one directly gives the ISC value for each voxel:

287        $\Sigma_{i,j,t} Z(i,j,t) / (n*(n-1)/2) / (T-1)$,

288        where n is the number of subjects, *n\*(n-1)/2* is the total number of subject pairs and

289  T is the number of timepoints. Thus, the timepoints showing the largest differences are the

290  ones that contribute most to the group difference over the entire dataset. For visualization,

291  we performed paired t-tests over the pairs of subjects for each timepoint and voxel in the

292  brain to find significant differences (p<0.05, Bonferroni corrected). Further, to highlight the

293  instances that showed the most robust differences across groups in the regions showing

294  group differences over the whole movie, we visualized at which time points the voxels in

295  these regions on average showed significant differences (p<0.05, Bonferroni corrected by

296  number of clusters) in the mean Z-score products over subject pairs. For a more stringent

297  hypothesis testing without assumptions regarding the underlying distributions, we also

14

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298    performed a non-parametric permutation test (1000 permutations) of difference

299    normalized by standard error of the mean (corresponding to t-values) across conditions by

300    randomly relabeling the conditions for each subject and by building a null distribution from

301    the observed differences. This test was performed both for individual voxels within the

302    regions of interest (ROIs) and for mean ROI timecourses.

303         To simplify the exploratory visualization of the timecourses, the clusters showing

304    significant ISC differences were first pruned by 2 mm on all sides to detach weakly

305    connected parts from the main clusters. Clusters smaller than 27 voxels (3x3x3 voxels) were

306    removed to reduce the number of ROIs in the exploratory analysis. Edge-voxels that

307    correlated poorly (r<0.5 in the across-subjects mean signal) with the mean timecourse of

308    the clusters were pruned removing in total 71 voxels. This left 2586 voxels for the analysis.

309    Finally, the voxels within the ROIs were grouped with hierarchical clustering (correlation

310    distance, average distance linkage) to find temporally consistent regions that showed

311    distinct synchrony patterns compared with each other. Clustering was repeated with 2–10

312    clusters to find the optimal number of clusters where within-cluster correlation distribution

313    was maximally separable from across-clusters distribution (i.e. there was minimal overlap of

314    correlation values between these two distributions). The optimal number of clusters was 4

315    with this measure. For visualization, the remaining clusters were inflated by 3 mm on all

316    sides to make them better visible when plotted on the inflated brain surface.

317         To compare temporal distributions of peaks in the Z-score products, we calculated

318    the kurtosis of the mean timecourse values of each cluster over both conditions, which

319    describes the heaviness of the tails of the distribution. We also calculated the kurtosis of the

320    across-conditions difference of the mean timecourses. To characterize how uniformly

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321    synchrony peaks were distributed over time we further calculated the burstiness (B) of the

322    timecourses (Goh and Barabási 2008) that is defined as

323        $B \equiv (\sigma_\tau - m_\tau)/(\sigma_\tau + m_\tau)$,

324        where $m_\tau$ and $\sigma_\tau$ are the mean and standard deviation of the number of events in

325    time windows of a given size. A completely regular signal would thus have a burstiness value

326    of -1 and a maximally bursty signal a value 1.  For defining the threshold of an event (peak)

327    we binarized the mean timecourses at Bonferroni corrected (over 4 clusters and 649

328    timepoints) $p<0.05$ from a surrogate distribution of a million values calculated assuming that

329    the underlying signal values for each subject were independently drawn from a standard

330    normal distribution. We repeated the calculation for windows of 20 to 200 samples in 20-

331    sample intervals (20,40,...,200).

332        To find the most consistent peaks of synchrony across voxels for reverse correlation

333    exploration, we performed a t-test over the voxels in the clusters at each timepoint to find

334    occasions where differences across conditions were maximal, thus maximally contributing

335    to the ISC difference. To pinpoint the most robust differences, we also performed a

336    permutation test with 1000 permutations similar to the one described above for difference

337    in voxel and ROI timecourses over subjects.

Lahnakoski JM                                          Event integration

## Results

338

339     Following the movies after clip transitions was significantly more difficult in the

340     Interleaved (M=8.56) *vs.* Consecutive (M=6.36) condition ($t$(16)≈4.1, $p$≈0.001; **Figure 3a**).

341     Transitions within a movie (M=8.29) were also perceived as significantly more natural than

342     those between movies *(*M=1.67; $t$(16)≈25.6, $p$≈2*10$^{-14}$; **Figure 3b**).

343     **Figure 4** depicts brain areas with significant (p<0.01 in across-conditions ISC

344     distribution; uncorrected) ISC during both conditions. These areas were very similar

345     including wide bilateral areas in occipital, temporal and parietal cortex, frontal eye fields

346     (Paus 1996) extending to ventral premotor cortex, and cerebellum.

347     As shown in **Figure 5,** Consecutive *vs.* Interleaved movies resulted in stronger ISC in

348     temporal regions (left posterior STS, temporoparietal junction and middle temporal gyrus

349     and right posterior STS), in bilateral superior and medial occipital cortices, and in the

350     precuneus and cerebellum. The areas that showed different sensitivity to speech across

351     conditions (white outlines in **Figure 5**; see also **Figure 7**) overlap extensively with the

352     posterior temporal lobe areas showing significantly stronger ISC. Cluster centroid

353     coordinates are listed in **Table I**. Interleaved *vs.* Consecutive movies caused higher ISCs in

354     small clusters in bilateral extrastriate visual cortex and right superior temporal gyrus.

355     Due to the differences in difficulty of following movie *vs.* scene transitions, we also

356     tested whether responses to the transitions were driving the ISC differences across

357     conditions in our analyses. **Figure 6** shows brain regions responding significantly (in a GLM)

358     to scene and movie transitions in the Consecutive and Interleaved conditions. Transitions

359     significantly activated the precuneus, posterior cingulate cortex, lateral parietal cortex, and

360     Crus II of the cerebellum. These areas did not overlap with the clusters showing ISC

17

361  differences indicated with white outlines. We found no statistically significant differences

362  between the two conditions (q>0.05 FDR corrected) although, in the thresholded results,

363  movie transitions in the Interleaved condition additionally correlated significantly with

364  activity in anterior middle frontal gyrus (MFG) / frontal pole (FP) and small clusters in the

365  anterior cingulate.

366     Next we tested whether continuous *vs.* Interleaved presentation of the stimuli

367  selectively influences the processing of a set of physical stimulus features (**Figure 7**). Hot

368  colors indicate brain regions responding to different physical stimulus features over both

369  conditions. Auditory and visual areas responded to low-level sensory features (RMS energy

370  of soundtrack, high-frequency contrast edges, color intensity, and optic flow in the video).

371  The loudness of the sound track also correlated with the activity of lateral and ventral visual

372  regions, presumably due to relatively high correlations with visual features and sound RMS

373  (see **Figure 2**). Optic flow and biological motion activated similar areas in or near the

374  V5/MT+ and superior occipital cortex. Speech and faces activated relatively similar areas in

375  the temporal lobe, however, speech also activated wide spread areas of the superior

376  temporal lobes around the primary auditory cortices whereas faces did not. Conversely,

377  faces but not speech activated occipital regions. The brain responses to low-level visual and

378  acoustic features were very similar in the Interleaved *vs.* Consecutive conditions. Significant

379  differences were observed only for speech (filled green outline), for which especially

380  posterior temporal responses were stronger in the Consecutive condition. These areas are

381  highly similar to regions showing significant differences in ISC strength across conditions

382  (see **Figure 5**).

383    The areas showing ISC differences were visually very similar to those reported to

384    participate in action continuity processing in a prior study by Magliano and Zacks (2011).

385    Therefore, we next examined whether the areas showing significant differences in ISC and

386    speech-related responses would also be selectively active during continuous actions *vs.*

387    action discontinuities in our data. To this end, we replicated a conjunction analysis of

388    Magliano and Zacks (2011) to reveal regions that were selectively activated by cut-points

389    depicting continuous actions and deactivated by cut-points with action discontinuities. As

390    shown in **Figure 8**, areas that were active during action continuity processing (hot colors)

391    are partly overlapping with the areas of the pSTS and MTG that showed differences in ISC

392    (white outlines) and speech responses (turquoise outlines) across conditions. This was,

393    however, observed only in the Consecutive condition. In the Interleaved condition, only

394    small bilateral clusters in the inferior bank of the STS was significantly activated by action

395    continuity processing, yet the difference between Consecutive *vs.* Interleaved conditions

396    was not statistically significant. Other areas showing ISC differences (Pcu, mPFC and Crus II)

397    also showed negative, yet non-significant, correlations with action discontinuities. The mOC

398    was an exception, as it was activated in all cut-points, including those where action was

399    discontinuous (see Supplementary Figure S1).

400    To reveal the specific moments that triggered across-conditions differences in ISC

401    strength, we explored the time-courses of the clusters showing significantly higher ISC in

402    Consecutive *vs.* Interleaved condition. **Figure 9** shows the time-courses of products of Z-

403    scores (instantaneous similarity) of subject pairs. The timecourses have been reorganized so

404    that responses to the same timepoints in the stimuli are aligned in both conditions. Panel A

405    shows the hierarchical clusters of voxels, displayed with color-coding in the correlation

Lahnakoski JM                                              Event integration

406    matrix of the timecourses. Different clusters are indicated by the same colors on the right

407    and bottom of the matrix, and the same color-coding indicates the location of the clusters

408    on the brain surface.

409         Generally, the voxels form two main groups: medial occipital cortex (yellow), and the

410    other brain areas. The latter are further subdivided into ventral temporal cluster (green),

411    PCu-mPFC cluster (purple) and a cluster consisting of areas of bilateral pSTS/MTG, right

412    mPFC and left Crus II (orange). Panel B shows mean plots of Z-score products for both

413    conditions and timepoints of significant group difference for the clusters. Overall, the yellow

414    mOC cluster shows several short synchrony peaks and across-condition differences that are

415    relatively uniformly distributed over time. By contrast, time courses of other clusters show

416    longer-duration peaks that are specific to isolated parts of the movies. This is corroborated

417    by lower kurtosis and consistently lower burstiness of timecourses in the mOC compared

418    with the other clusters (kurtosis of timecourses in mOC was 9.6 *vs.* 13.0 to 21.8 in other

419    areas, mean burstiness over time window sizes -0.6 *vs.* -0.3 to -0.1; kurtosis for difference

420    across conditions 6.7 *vs.* 7.4 to 22.0, burstiness −0.6  *vs.* −0.4 to −0.2). Thus, the relatively

421    long periods of significant group differences in the pSTS/MTG, Crus II, PCu, mPFC and vTC

422    presumably corresponded to events that are particularly differently processed when task

423    switching is required. Panel C shows the consistent between-condition differences (in t-

424    tests) in the orange, purple and green clusters that assumedly show moments of content-

425    specific synchrony. These moments are described in **Table II** and depicted in **Video 1**. They

426    contain mainly instances of conflict, deception and escape, and also include the opening

427    scenes of the second and third movies when subjects start following a new long narrative.

428    Timepoints that survived a more conservative permutation test are marked with an asterisk.

429    Instances of higher ISC in Consecutive *vs.* Interleaved conditions that were caused by

430    increased deactivations in Consecutive condition are marked with minus signs in panel C and

431    **Table II** (see red and blue dashed lines in **Figure 9** C).

432         Finally, because the participants might have experienced higher suspense during the

433    continuous movies we investigated the role of suspense in modulating ISC. **Figure 10 A**

434    shows the areas where brain activity correlated with the suspense ratings across both

435    conditions (positive: parametric in green, non-parametric in hot colors; negative: parametric

436    in purple, non-parametric in cold colors). Statistically significant differences across

437    conditions inside the areas showing significant suspense-related activity are indicated by red

438    (Consecutive>Interleaved) and blue (Interleaved>Consecutive) outlines. The areas showing

439    ISC differences are outlined in white. Suspense ratings correlated positively with nearly all

440    regions showing significant ISCs in the standard parametric t-test. However, only regions in

441    the vicinity of V5/MT+, FEF, posterior parietal cortex and opercular parietal cortical regions

442    survived the non-parametric test. Negative responses were seen in lateral parietal and

443    anterior cingulate cortices (ACC), but only a small cluster in the right ACC was significant in

444    the non-parametric test. Figure 10 B shows the timecourses of the suspense ratings in

445    Consecutive (red) and Interleaved (blue) conditions. The scenes showing highest ISC

446    differences in **Figure 9** C are indicated by gray bars at the bottom of the plot.

Lahnakoski JM                                                    Event integration

## Discussion

Our main finding was that when the natural flow of action sequences was interrupted and frequent switching between parallel event-sequences was required, the inter-subject reliability of brain responses was decreased in the bilateral posterior STS region and left MTG, mOC and smaller clusters in the mPFC and cerebellum (**Figure 5**). Particularly, responses associated with speech in the posterior temporal lobe were significantly weaker during interleaved movies (**Figure 7**). By contrast, low-level sensory responses were similar in both conditions. Explorative timepoint-by-timepoint reverse correlation comparison revealed that events depicting social conflict and deception contributed strongly to the ISC group difference in temporal lobes, medial prefrontal cortex and Crus II. By contrast, differences in the occipital visual areas were diffusely distributed in time throughout the movie stimuli (**Figure 9**). Our results suggest that i) temporal interleaving specifically modulates processing of social aspects of stimuli, particularly speech, in the STS/MTG, Crus II, vTC and mPFC, and that ii) early sensory processes are either not affected or, in the case of early visual cortex, show general reduction of ISC that is not specific to particular events.

### Temporal integration of events

The ISC maps in both Consecutive and Interleaved conditions were visually very similar (**Figure 4**) and accord with those reported in prior studies (see e.g. Hasson et al., 2004; Hasson et al., 2008a; Lerner et al., 2011). However, statistically testing revealed that shifting back and forth between the different movies markedly reduced ISC in occipitotemporal cortices (pSTS/TPJ) occipital cortex and precuneus (**Figure 5**). Prior research has established that these regions maintain a temporally consistent model of

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470   action sequences depicted in movies across "continuity edits" that depict the same

471   continuous action from different camera angles; such edits are continuous over time, space

472   and action. This is in contrast with edits with a discontinuity, such as between two

473   consecutive shots that show different locations or people. Discontinuous edits where place,

474   time or action changed during the transition showed little consistent activity (Magliano and

475   Zacks 2011). In line with this, shuffling a movie using discontinuity edits markedly lowers ISC

476   in higher-order associative and frontal cortices across observers (Hasson et al., 2008a;

477   Lerner et al., 2011). In contrast, adding continuity edits to depiction of continuous action

478   actually increases ISC in the occipital, ventral temporal and parietal cortices (Herbec et al.,

479   2015) leaving ISCs in the posterior temporal regions unaffected. Indeed, we did not observe

480   significant differences in the event-related responses to scene onsets when the clips were

481   preceded by the previous clip of the same movie (Consecutive condition) *vs.* a clip from a

482   different movie (Interleaved condition; **Figure 6**) despite the reported decrease of

483   naturalness and ease of following the movie *vs.* scene transitions (**Figure 3**). Moreover, most

484   subjects found following the events in the Interleaved condition relatively easy and the

485   event related activity due to movie/scene transitions was markedly different from the foci

486   showing differences across conditions in ISC and speech-related GLM analysis. This suggests

487   that the circuitry activated by scene transitions between movies is also activated similarly at

488   scene transitions during the natural flow of a movie, which also requires reorientation and

489   updating the contents of working memory (Kurby and Zacks 2008). Together with the

490   present results (see **Figure 5**), these findings suggests that the pSTS region, precuneus,

491   ventral temporal and medial prefrontal cortices and part of Crus II are involved in building

492   and maintaining a temporally extended model of observed events.

Lahnakoski JM                                              Event integration

493    However, simply following continuity of actions between movie cut-points cannot

494    explain the observed differences in brain responses between conditions, although areas

495    revealed by the conjunction analysis partially overlapped those showing ISC differences in

496    the pSTS/MTG (no differences across conditions; **Figure 8**). Moreover, the regions of the

497    temporal lobe showing the greatest deactivations to action discontinuities extend anteriorly

498    from the regions showing ISC/speech-sensitivity differences and those reported previously

499    (Magliano and Zacks 2011). Furthermore, no significant effects were observed in the

500    precuneus and posterior parietal cortex, which have previously been associated with

501    continuity processing (Magliano and Zacks 2011). This may depend on the definition of

502    discontinuity or the complexity of the stimuli. For example, the Magliano and Zacks (2011)

503    study used a children's movie with relatively simple actions and practically no speech, while

504    we found that speech consistently activated the anterior parts of STS/MTG that also showed

505    continuity effects in our data. Altogether these data suggest that not all aspects of action

506    continuity processing are similarly affected by action sequence interleaving in the timescales

507    studied here.

508    The capacity for prediction and temporal integration may be one of the key

509    properties that allow the pSTS region to serve as a 'hub' for social processing (Lahnakoski et

510    al., 2012b). The pSTS/TPJ region has been proposed to participate in several functions such

511    as integration of "what" and "where" information (Allison et al., 2000), inference of

512    intentionality (Nummenmaa and Calder 2009) and perception of social awkwardness in

513    naturalistic scenes (Pantelis et al., 2015). These functions could be subserved by a more

514    general function of updating a model of the concurrent situational context used to predict

515    the upcoming events and detect prediction violations. Similar predictive schemes have been

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516 proposed to underlie comparison of "efference copies" from the motor/premotor system to

517 current percepts in perception-action cycles, for example, during speech production (for a

518 review, see e.g. Rauschecker and Scott 2009). Updating predictions of the current situation

519 is a continuous process, which may be interrupted by a sudden change in stimulus events.

520 This, in turn, may lead to reduction in the response reliability across observers.

521 **Social and sensory feature driven brain responses**

522 We found that speech-sensitive areas in the pSTS/TPJ showed greatest interleaving

523 effects, and presence of human speech correlated more with the activity in these areas in

524 the Consecutive *vs.* Interleaved condition (**Figure 7**). By contrast, the low-level stimulus

525 features (visual motion, contrast, color, and sound loudness) were associated with

526 activation of the corresponding sensory regions in both conditions, with no differences

527 across conditions in the GLM analysis. This suggests that the observed differences in brain

528 activity may relate specifically to processing of language and possibly other socially relevant

529 movie content. However, our stimulus model is not exhaustive and we cannot rule out that

530 processing of non-modeled low-level features could also be affected due to top-down

531 influences, such as attention (see e.g. Çukur et al., 2013), although the stimulus material

532 itself was the same in both conditions.

533 Presence of speech also predicted activity in the Crus II of the cerebellum whose

534 synchrony timecourse was similar to that in pSTS. This is in accordance with the emerging

535 view of cerebellar contribution to social processing (Van Overwalle et al., 2014). In speech

536 perception, cerebellum appears to participate in temporal, or sequential, prediction (for a

537 review, see Moberget and Ivry 2016). This finding supports its role in prediction and

538 following of ongoing social events, suggested here.

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Lahnakoski JM                                                    Event integration

539  **Reverse correlation analysis**

540     In the pSTS/MTG, mPFC, vTC and Crus II, reduced ISC in Interleaved *vs.* Consecutive

541  condition was mainly explained by a few scenes and not by either constantly higher ISC or

542  differences at the transition moments between movie clips. Reverse correlation analysis

543  revealed that the scenes showing most consistent between-conditions differences in the

544  temporal and frontal regions contained most often deception or conflict (e.g. a man

545  sneaking up and pulling a gun behind Indiana Jones before being disarmed by him;

546  discussion about princess Leia hiding plans in an escape pod after she was questioned).

547     Half of the scenes showing significantly higher ISCs in Consecutive *vs.* Interleaved

548  condition were driven by stronger deactivations rather than activations in the Consecutive

549  *vs.* Interleaved condition. ISC differences in all of the scenes containing speech were driven

550  by high activation peaks, as suggested by the stronger speech related responses. In contrast,

551  none of the scenes where ISC difference was driven by deactivation contained speech.

552  While some of the peaks of synchrony in the precuneus coincide with those in the speech-

553  sensitive areas, we did not see speech-related responses in those parts of precuneus that

554  show ISC differences. The synchrony peaks in precuneus were infrequent compared with

555  those in the speech sensitive regions and thus difficult to interpret alone (see **Figure 9** C for

556  timepoints, **Table II** for scene descriptions and **Video 1** for excerpts from the marked

557  timepoints and the associated synchrony of brain activity). Importantly, since the scenes

558  with the greatest ISC differences do not consistently coincide with movie transitions in the

559  Interleaved condition, there is no obvious need for integrating information differently

560  during these scenes in the two conditions. This suggests that there is a more general

561 difference in the mode of information processing of these brain regions in the two

562 conditions that warrants further study in the future.

563 In contrast to the areas discussed above, the mOC showed ISC differences

564 throughout the experiment in activity peaks that were relatively uniformly distributed in

565 time. While most of these peaks were of short duration, some peaks lasted for several

566 seconds. Most prominent peaks correspond to scenes with significant change in lighting (lit

567 torch, golden glow of an idol and ending the shooting of lasers). However, these are not the

568 only scenes with prominent lighting changes. Additionally, in contrast to the temporal lobes,

569 suspense modulated the activity in the visual cortex more strongly in the Interleaved *vs.*

570 Consecutive condition. This result was in a direction opposite to the ISC results, and the

571 difference in suspense-related brain activity was slightly more posterior than the areas

572 showing differences in ISC.

573 **Brain responses to suspense during movie viewing**

574 Scenes showing highest differences in ISC timecourses also contained moments of

575 high suspense. In the GLM analysis, suspense was associated with activity in corticolimbic

576 areas whose ISC and BOLD-GLM responses is modulated by affective arousal (Nummenmaa

577 et al., 2012; Nummenmaa et al., 2014), which is an important component of suspense

578 experience (Lehne and Koelsch 2015). However, due to the slowness of the signals, the

579 parametric test was very liberal. With a stricter FDR corrected non-parametric threshold,

580 the significant effects were restricted to the dorsal attention network (posterior parietal

581 cortex and areas surrounding the bilateral middle temporal visual areas and frontal eye

582 fields, respectively), according with the well-established influence of affective significance

583 on attention (Vuilleumier 2005).

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Lahnakoski JM                                                              Event integration

584        Suspense ratings also differed across the conditions, but of the areas showing ISC

585   differences, only small parts of the left posterior temporal lobe showed higher suspense-

586   related responses in the Consecutive *vs.* Interleaved condition. Moreover, the differences in

587   ISC did not seem to coincide exclusively with moments of high suspense or with moments

588   where the ratings of suspense differed across conditions. Therefore, we conclude that

589   suspense may have contributed to the differences seen in the ISCs and speech responses

590   between conditions in the temporal lobes, but it is not sufficient to explain all of the

591   differences seen in other analyses.

592   **Time scales of integration and memory**

593        The time windows studied here were relatively long in comparison to time-scales

594   studied for lower-level integration effects such as change detection in the auditory cortex at

595   a millisecond scale (Mustovic et al., 2003) or behavioral accounts of event integration in

596   videos in the order of 2–3 seconds (Fairhall et al., 2014). Prior fMRI studies employing

597   scrambling the temporal order of video clips or audio stories (Hasson et al., 2008a; Lerner et

598   al., 2011) have found that the correlation of activity in areas of the posterior temporal lobes,

599   parts of mPFC and precuneus is decreased – either across or within subjects – when the

600   stimuli are scrambled in short *vs.* long time windows. Temporal integration windows in fMRI

601   data seems to increase up to timescales of 30–40 seconds, where the areas of significant ISC

602   appear indistinguishable from those elicited by intact videos. However, by testing the

603   magnitude of ISC statistically, we demonstrated that even at scales of 50 seconds, brain

604   processing of stimuli is affected even if the regions in the thresholded ISC maps are visually

605   very similar. Moreover, in contrast to the studies employing temporal scrambling, the

606   subjects of the current study could still follow the storylines in their entirety, as the order of

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Lahnakoski JM                                              Event integration

607     movie parts remained unchanged for each stimulus. Additionally, earlier studies did not test

608     which aspects of the stimuli were integrated over long time periods in these brain areas.

609     Our results demonstrate that even though similar levels of ISC differences may be seen in

610     multiple brain regions, different areas may have different profiles that account for the

611     increased ISC. Thus, in future studies, it is important to consider what particular aspects of

612     stimuli are integrated in each area.

613     Finally, it is possible that differences in ISC may be related to subsequent memory of

614     the events. Earlier results suggest that improved memory encoding during movie viewing is

615     linked with increased ISC (Hasson et al., 2008b) in STS and TPJ that partly overlap with the

616     areas showing ISC differences in the current study. It is thus possible that some of the

617     differences reported here are related to the encoding to or retrieval from long-term

618     memory.

## Conclusions

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620     Following multiple interleaved events forces the brain to constantly reorient to a

621     new scene, thus reducing the predictability of the events. We conclude that posterior

622     temporal, medial parietal and lateral frontal cortical areas are the key regions participating

623     in the integration of ongoing events. We propose that these regions build and maintain a

624     temporally extended predictive model of ongoing sequence of events.

Lahnakoski JM                                                    Event integration

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Lahnakoski JM                                            Event integration

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## Figure legends

734    **Figure 1: Illustrations of the stimuli used in the current study (top) and**

735    **experimental design with Consecutive (bottom left) and Interleaved (bottom right) event**

736    **sequence conditions.** The background color of each condition indicates the movie and

737    numbers indicate the index of the clip within the movie. In the Consecutive condition the

738    movie clips were shown in the correct temporal order and movies were shown one after

739    another. In the Interleaved condition the movie changed after each short clip, but the order

740    of the clips within each movie was retained. The presentation order of the conditions was

741    counterbalanced across subjects.

742    **Figure 2: Correlation matrix and timecourses of the stimulus models.** The pairwise

743    correlation coefficients (r) of the stimulus features are presented in the upper triangle

744    entries. Color coding indicates the correlation coefficient. The diagonal entries with black

745    borders indicate how much of each stimulus feature model is explained by all other stimulus

746    features together (r) after linear fitting. Normalized timecourses of the stimulus models

747    convolved with a canonical HRF are shown next to the correlation matrix. Color coding

748    indicates the amplitude of the stimulus features at each time point. The arrow heads

749    indicate the starting points of the movie clips.

750    **Figure 3: Distributions of self-reported ease of following events from one clip to**

751    **another (A) and naturalness of movie scene transitions (B) in the Consecutive and**

752    **Interleaved conditions.** Distributions are depicted as symmetrical binned histogram violin

753    plots to show the full distribution of ratings where zero is at the middle of the bars parallel

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754    to the y-axis. Empty bins are indicated by the line in the middle of the histogram (zero). P-

755    values are from paired t-tests.

756    **Figure 4: Brain areas showing significant inter-subject correlation during movie**

757    **viewing in the Consecutive and Interleaved conditions.** The data are thresholded at p<0.01

758    (uncorrected p-value in the ISC distribution calculated across conditions).

759    **Figure 5: Brain regions showing different ISC between Consecutive and Interleaved**

760    **conditions.** The data are thresholded at p<0.05, FWER corrected. Warm colors correspond

761    to areas showing increased ISC in Consecutive and cold colors increased ISC in Interleaved

762    condition. White line indicates areas showing different sensitivity to speech in Consecutive

763    *vs.* Interleaved condition in **Figure 7**. Abbreviations: mOC – medial occipital cortex, mPFC –

764    medial prefrontal cortex, MTG – middle temporal gyrus, PCu – precuneus, pSTS – posterior

765    superior temporal sulcus, TPJ – temporoparietal junction.

766    **Figure 6: Brain regions responding to scene transitions in the Consecutive (red) and**

767    **Interleaved (blue) conditions (q<0.05, FDR).** Statistically significant effects in both

768    conditions is shown in yellow. ISC differences from Figure 5 are indicated by white outlines.

769    Abbreviations: FP – frontal pole, MFG – middle frontal gyrus, LPC – lateral parietal cortex,

770    PCC – posterior cingulate cortex.

771    **Figure 7: Brain regions responding to physical stimulus features across both**

772    **conditions.** Filled green outline indicates regions showing stronger stimulus-dependent

773    responses to speech in the Consecutive *vs.* Interleaved condition (no differences were

774    observed to other features). White outlines indicate the areas showing significant

775    differences in ISC across conditions. Abbreviations as in Figure 5, additionally: AC – auditory

776 cortex, EBA – extrastriate body area, LO – lateral occipital cortex, M1 – primary motor

777 cortex, OP – occipital pole, PMC – premotor cortex, PPC – posterior parietal cortex, SOC –

778 superior occipital cortex, STG – superior temporal gyrus, STS –superior temporal sulcus,

779 V5/MT+ – middle temporal visual area, VC – visual cortex. The data are thresholded at

780 q<0.05, FDR).

781 **Figure 8: Areas activated during following of continuous action in Consecutive (red)**

782 **and Interleaved (blue) conditions**. Colored areas indicate the conjunction of the responses

783 to (positive) cut-points and (negative) action discontinuities. Overlapping areas in both

784 conditions are indicated by yellow. Both cut-points and action discontinuities have been

785 thresholded at q<0.05 (FDR corrected). The area of conjunction corresponds to the areas

786 where both effects overlap. Outlines indicate areas showing differences ISC (white) in

787 speech sensitivity (turquoise) across conditions (see **Figure 5** and **Figure 7**, respectively).

788 **Figure 9: Timecourses of products of Z-scores over subject pairs (instantaneous**

789 **similarity) contributing to the mean ISCs and ISC group differences. A:** (Left) Correlation

790 matrix and clustering of the voxels showing significantly higher ISC in Consecutive *vs.*

791 Interleaved condition. The different clusters are separated by black lines and indicated by

792 the colors on the right and bottom of the matrix. (Right) Locations of the clusters are

793 indicated by colors on the brain visualizations on the right. Abbreviations as in **Figure 5**, in

794 addition: vTC – ventral temporal cortex, dmPFC a/p – dorsomedial prefrontal cortex,

795 anterior/posterior. **B:** Mean timecourses of Z-score products across subject pairs for the

796 clusters. Consecutive condition is show in red and Interleaved condition in blue. Timepoints

797 where the mean timecourse of each cluster showed significant (p<0.05, Bonferroni

798 corrected; t-test light gray, permutation test dark gray) between-condition difference are

Lahnakoski JM Event integration

799 indicated with gray vertical bars. Arrow heads indicate the onset times of each short movie

800 segment and the full duration of each movie excerpt is indicated by the braces on top of the

801 plots. The clusters are indicated by the colored bars on the right side of the plots. **C:** Mean

802 difference of Z-score products between conditions across all voxels in the orange, purple

803 and green clusters. Significant differences (p<0.05, Bonferroni corrected) are indicated by

804 gray bars (t-test result with lighter and permutation test results in darker gray). Red and

805 blue dashed lines indicate the mean standardized activity over subjects and voxels in the

806 orange, purple and green clusters. Time windows marked with a–p indicate instances where

807 the mean timecourses showed most consistent differences across all voxels in the three

808 clusters. Windows shorter than 3 TRs have been omitted and windows that are separated by

809 less than 3 TRs have been collapsed into one longer window. The error bars on all plots

810 indicate 95% confidence intervals. Time windows containing timepoints that were

811 significant in the permutation test are indicated by the astrerisks (*). Timepoints of

812 significant difference across conditions caused by deactivations in the Consecutive condition

813 are marked by minus (⁻) signs.

814 **Figure 10: Brain regions responding to experienced suspense.** A: Main effects of

815 suspense in a GLM analysis across both conditions. Due to the autocorrelation structure of

816 the slow signals in the model, the results are thresholded (p<0.05, FDR corrected) based on

817 both standard parametric t-test and null GLMs where the models were circularly shifted.

818 Parametric effects are shown in green (positive) and purple (negative) tones. Differences

819 across conditions in the GLM results are shown in red (Consecutive>Interleaved) and blue

820 (Interleaved>Consecutive) outlines. White outlines indicate areas showing ISC differences in

821 **Figure 5**. B: Mean ratings (±95% CI) of suspense in the Consecutive (red) and reordered

Lahnakoski JM                                                    Event integration

822    Interleaved (blue) condition. Movie clip onsets are indicated by arrows and gray dashed

823    lines. Gray bars at the bottom of the plot show the differences across conditions in **Figure 9**

824    C. Abbreviations as in Figures 5–7.


825          **Video 1: Timepoints showing most consistent differences across conditions in the**

826    **pSTS/TPJ, PCu, dmPFC and Crus II clusters.** The clips are preceded by the annotated labels

827    in **Figure 8 C** and the movie abbreviation and clip number that was playing at the onset of

828    each time window (some time windows span the ending of one clip and beginning of the

829    next one)**.** The timecourses of stimulus features are depicted by the bar graphs on the

830    bottom of the video. The brain images on the left of the video show the difference of Z-

831    score products at each voxel similar to cluster timecourses in **Figure 9**. The maps are

832    thresholded based on the 95th percentile of non-significant Z-score product differences in

833    the voxels contained in the clusters in **Figure 9**.


834          **Figure S1: Unthresholded results showing negative (warm colors) and positive (cold**

835    **colors) responses to action discontinuities.** Color scale is inversed because the

836    corresponding contrast vector entry was negative in the conjunction analysis. White

837    outlines indicate areas showing differences in ISC and turquoise outline differences in

838    speech sensitivity across conditions like in **Figure 8**.

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### Table I: Locations of clusters showing significant ISC differences.

| | MNI coordinates | | |
| --- | --- | --- | --- |
| | X | Y | Z |
| Crus II | 34.7 | 21.9 | 19.9 |
| MTG L | 18.5 | 46.7 | 28.3 |
| MTG/STS R | 75.1 | 43.6 | 37.2 |
| mOCC | 45.5 | 21.1 | 39 |
| TPJ/pSTS L | 16.6 | 39.4 | 42.1 |
| PCu | 43.6 | 32.3 | 62.8 |
| dmPFC a | 50.6 | 76.2 | 65.2 |
| dmPFC p | 55.2 | 63.8 | 69.4 |

**Table II: Description of movie scenes showing most consistent differences across conditions in ISC**. Time windows containing timepoints that were significant in the permutation test in Figure 9 are indicated by the astrerisks (*). Timepoints of significant difference across conditions caused by deactivations in the Consecutive condition are marked by minus (⁻) signs.

| Label | Movie clip at onset | Description |
|---|---|---|
| a* | GoldenEye 4 | Sneaking in an enemy base, agent 007 is surprised by agent 006 speaking in Russian impersonating an enemy guard; 007 recognizes 006 and the two agents exchange pleasantries and continue the infiltration of the base. |
| b | GoldenEye 8 | Agent 006 is held as a hostage at gunpoint to lure out 007; 006 encourages 007 to blow up the chemical containers with explosives they planted rather than surrender. |
| c | GoldenEye 8 | Enemy leader counts down from ten to force 007 out and then shoots 006 despite 007 was apparently surrendering. |
| d | GoldenEye 8 | Enemy leader orders the enemy soldiers to stop shooting as 007 has dived behind gas tanks that might explode; |

|  |  |  |
|---|---|---|
|  |  | 007 continues to escape using the tanks as cover. |
| e*⁻ | Indiana Jones 1 | Indiana studies a map with his companion looking on as a man sneaks behind them and cocks a gun. |
| f*⁻ | Indiana Jones 1 | Man escapes holding his hand after Indiana disarms him with his whip. Indiana and his companion continue to climb up to a cave. |
| g*⁻ | Indiana Jones 2 | After a short conversation, Indiana and his companion enter the cave sneaking carefully. |
| h⁻ | Indiana Jones 2 | Indiana and his companion continue sneaking inside the cave. |
| I | Indiana Jones 3 | Indiana orders his companion to stop as he finds a beam of light he suspects is a trap and continues to disarm it. |
| j* | Indiana Jones 5 | Indiana disarms another trap and orders his companion to stay behind as he sneaks forward. |
| k* | Indiana Jones 7 | Indiana and his companion escape the collapsing cave; Indiana exchanges the idol they found for his whip to get over a chasm but his companion escapes without giving the whip after he receives the idol. |

| l*[-] | Star Wars 1 | Star destroyer chases and fires at a rebel ship. |
| m[-] | Star Wars 2 | Rebel ship is caught by the Star destroyer as rebel soldiers prepare for an invasion of the imperial soldiers. |
| n[-] | Star Wars 4 | Darth Vader enters the ship and looks around at the bodies of dead soldiers. |
| o | Star Wars 4 | Surrendered rebel soldiers are being led away by armed storm troopers as a pair of storm troopers finds princess Leia. |
| p | Star Wars 4 | After interrogation of princess Leia, a report comes of a jettisoned escape pod; princess Leia is suspected to have lied, and hidden rebel plans in the escape pod. |
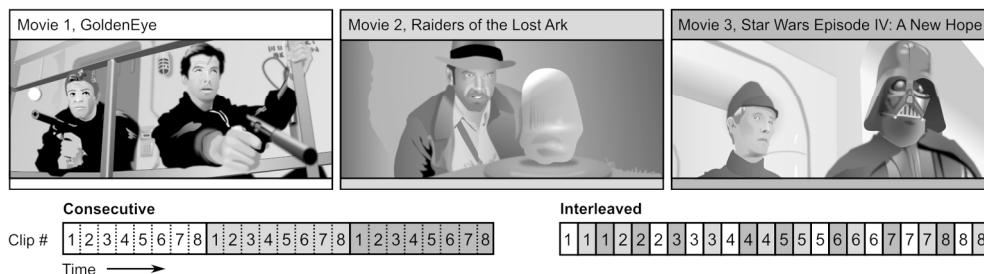
Figure 1: Illustrations of the stimuli used in the current study (top) and experimental design with Consecutive (bottom left) and Interleaved (bottom right) event sequence conditions. The background color of each condition indicates the movie and numbers indicate the index of the clip within the movie. In the Consecutive condition the movie clips were shown in the correct temporal order and movies were shown one after another. In the Interleaved condition the movie changed after each short clip, but the order of the clips within each movie was retained. The presentation order of the conditions was counterbalanced across subjects.
Experimental design
164x46mm (300 x 300 DPI)
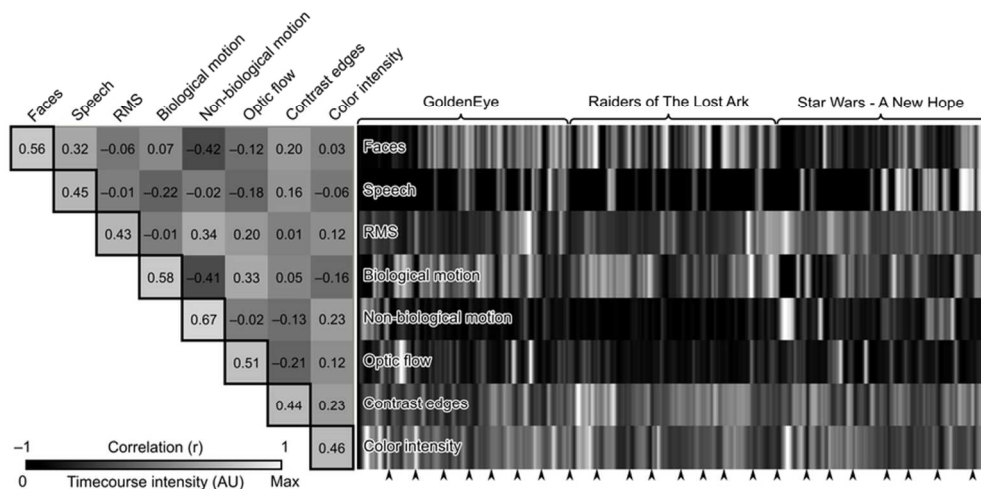
Figure 2: Correlation matrix and timecourses of the stimulus models. The pairwise correlation coefficients (r) of the stimulus features are presented in the upper triangle entries. Color coding indicates the correlation coefficient. The diagonal entries with black borders indicate how much of each stimulus feature model is explained by all other stimulus features together (r) after linear fitting. Normalized timecourses of the stimulus models convolved with a canonical HRF are shown next to the correlation matrix. Color coding indicates the amplitude of the stimulus features at each time point. The arrow heads indicate the starting points of the movie clips.
Stimulus model correlations
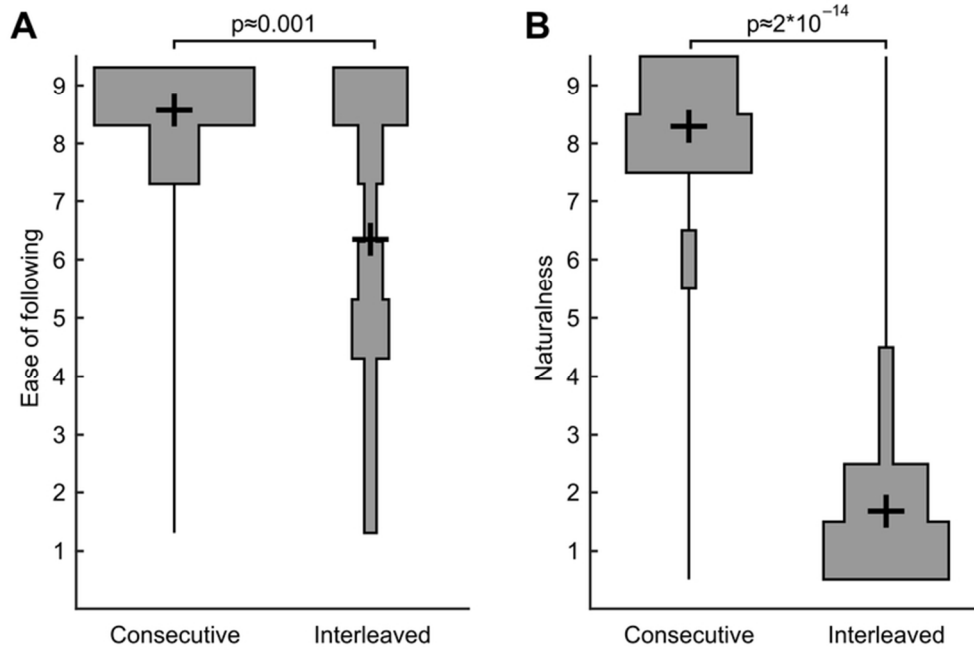81x40mm (300 x 300 DPI)

Figure 3: Distributions of self-reported ease of following events from one clip to another (A) and naturalness of movie scene transitions (B) in the Consecutive and Interleaved conditions. Distributions are depicted as symmetrical binned histogram violin plots to show the full distribution of ratings where zero is at the middle of the bars parallel to the y-axis. Empty bins are indicated by the line in the middle of the histogram (zero). P-values are from paired t-tests.
Scene transition ratings
70x46mm (300 x 300 DPI)
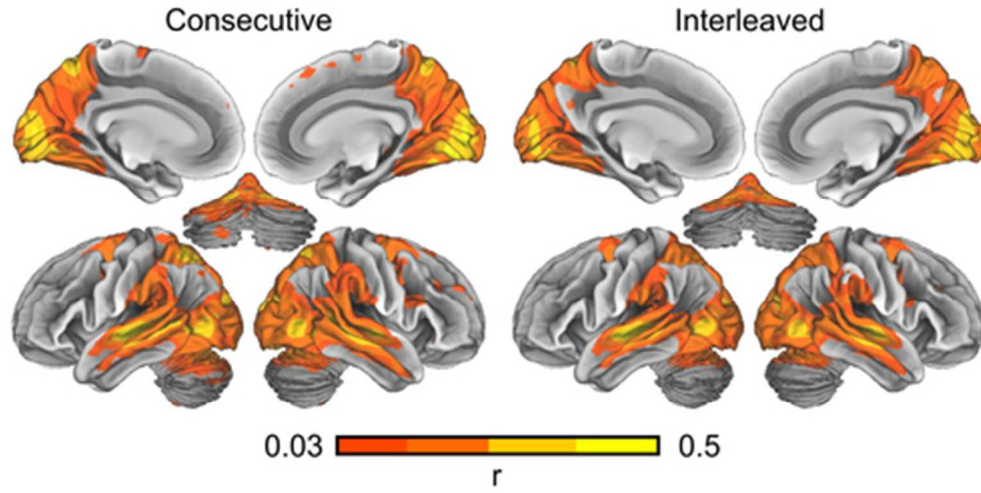
Figure 4: Brain areas showing significant inter-subject correlation during movie viewing in the Consecutive and Interleaved conditions. The data are thresholded at p<0.01 (uncorrected p-value in the ISC distribution calculated across conditions).
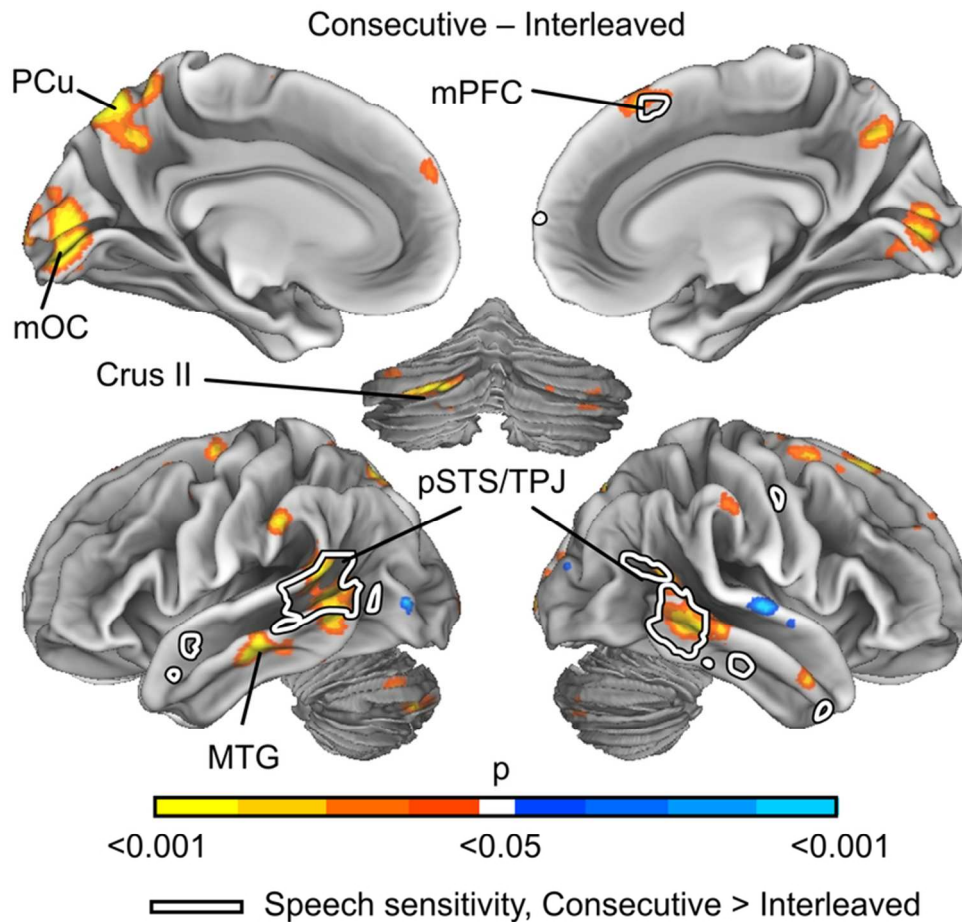Mean inter-subject correlation
42x21mm (300 x 300 DPI)

Figure 5: Brain regions showing different ISC between Consecutive and Interleaved conditions. The data are thresholded at p<0.05, FWER corrected. Warm colors correspond to areas showing increased ISC in Consecutive and cold colors increased ISC in Interleaved condition. White line indicates areas showing different sensitivity to speech in Consecutive vs. Interleaved condition in Figure 7. Abbreviations: mOC – medial occipital cortex, mPFC – medial prefrontal cortex, MTG – middle temporal gyrus, PCu – precuneus, pSTS – posterior superior temporal sulcus, TPJ – temporoparietal junction.
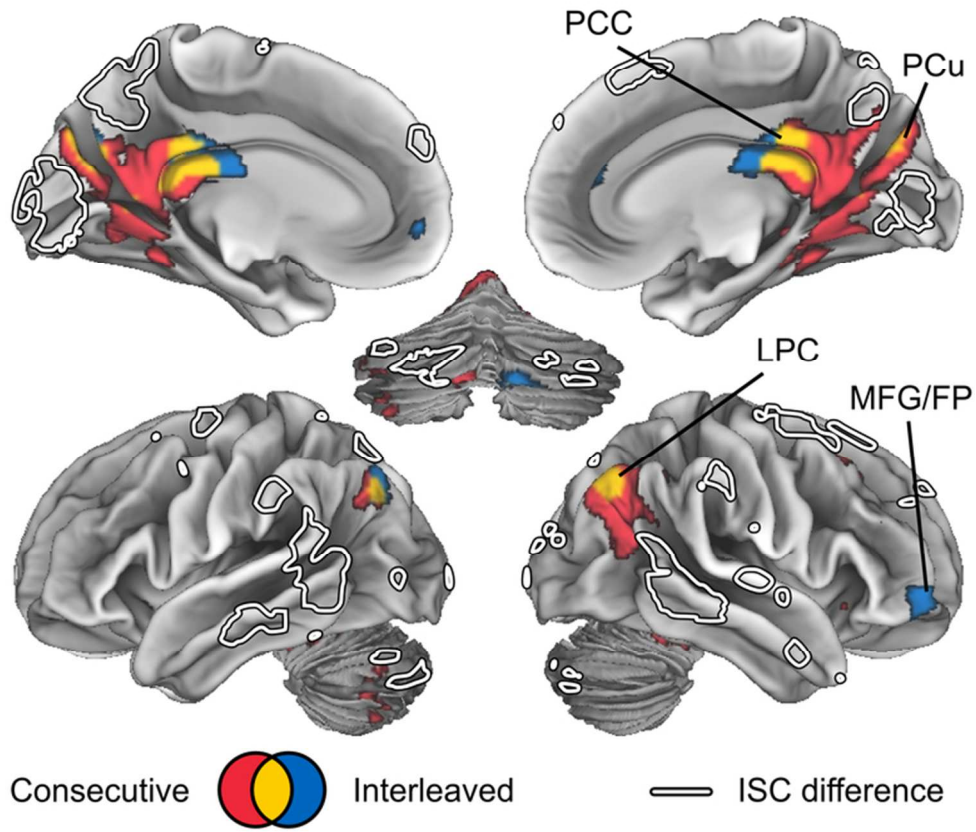ISC differences
72x68mm (300 x 300 DPI)

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Figure 6: Brain regions responding to scene transitions in the Consecutive (red) and Interleaved (blue) conditions (q<0.05, FDR). Statistically significant effects in both conditions is shown in yellow. ISC differences from Figure 5 are indicated by white outlines. Abbreviations: FP – frontal pole, MFG – middle frontal gyrus, LPC – lateral parietal cortex, PCC – posterior cingulate cortex.
Responses to scene transitions
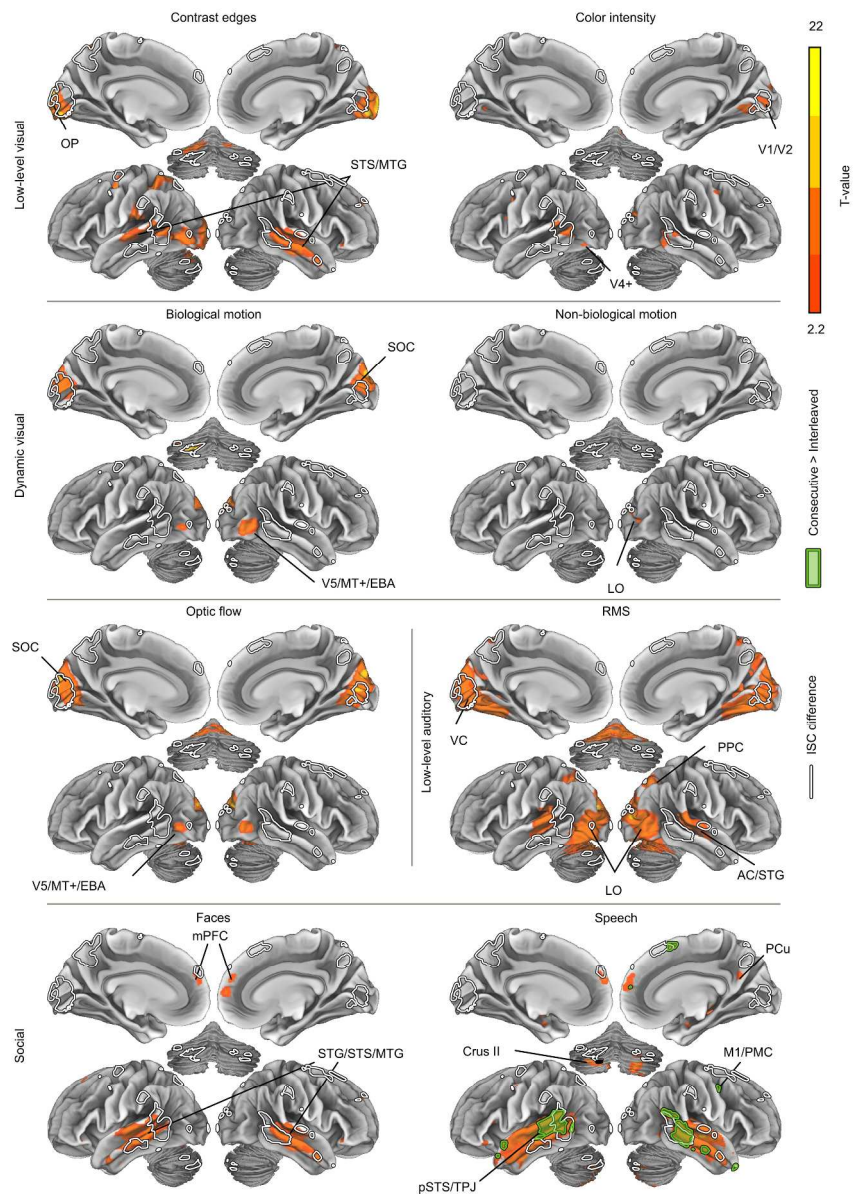67x59mm (300 x 300 DPI)

Figure 7: Brain regions responding to physical stimulus features across both conditions. Filled green outline indicates regions showing stronger stimulus-dependent responses to speech in the Consecutive vs. Interleaved condition (no differences were observed to other features). White outlines indicate the areas showing significant differences in ISC across conditions. Abbreviations as in Figure 5, additionally: AC – auditory cortex, EBA – extrastriate body area, LO – lateral occipital cortex, M1 – primary motor cortex, OP – occipital pole, PMC – premotor cortex, PPC – posterior parietal cortex, SOC – superior occipital cortex, STG – superior temporal gyrus, STS –superior temporal sulcus, V5/MT+ – middle temporal visual area, VC – visual cortex. The data are thresholded at q<0.05, FDR).
Stimulus-related brain activit
240x337mm (300 x 300 DPI)

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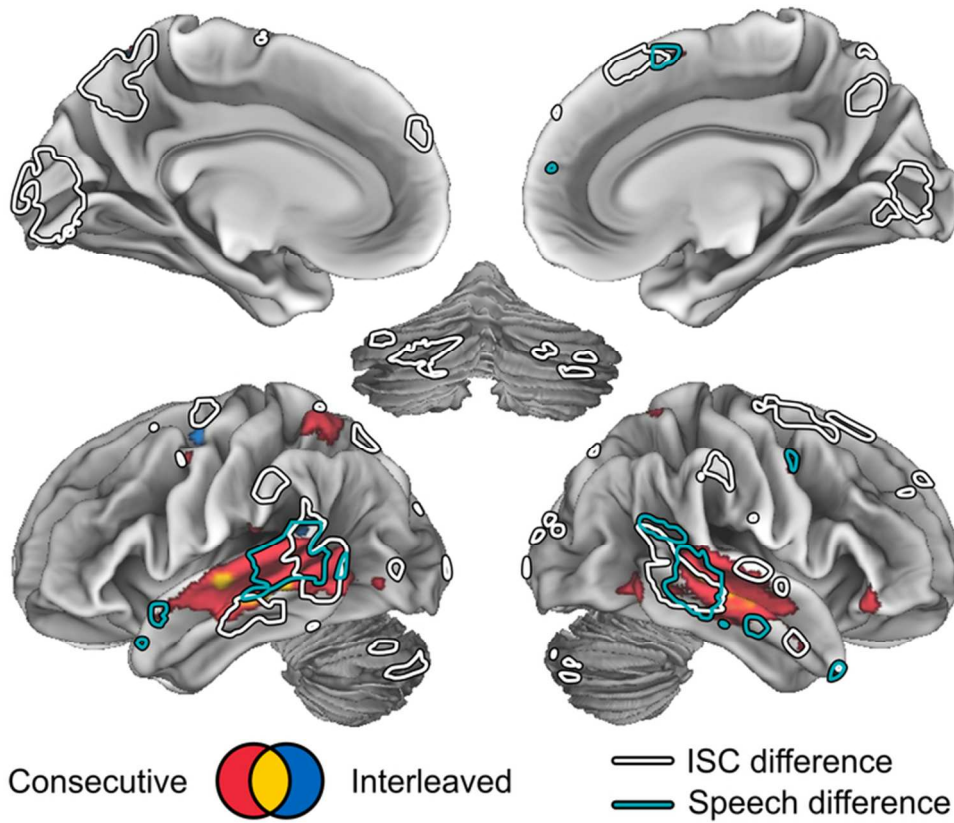46
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Figure 8: Areas activated during following of continuous action in Consecutive (red) and Interleaved (blue) conditions. Colored areas indicate the conjunction of the responses to (positive) cut-points and (negative) action discontinuities. Overlapping areas in both conditions are indicated by yellow. Both cut-points and action discontinuities have been thresholded at q<0.05 (FDR corrected). The area of conjunction corresponds to the areas where both effects overlap. Outlines indicate areas showing differences ISC (white) in speech sensitivity (turquoise) across conditions (see Figure 5 and Figure 7, respectively).
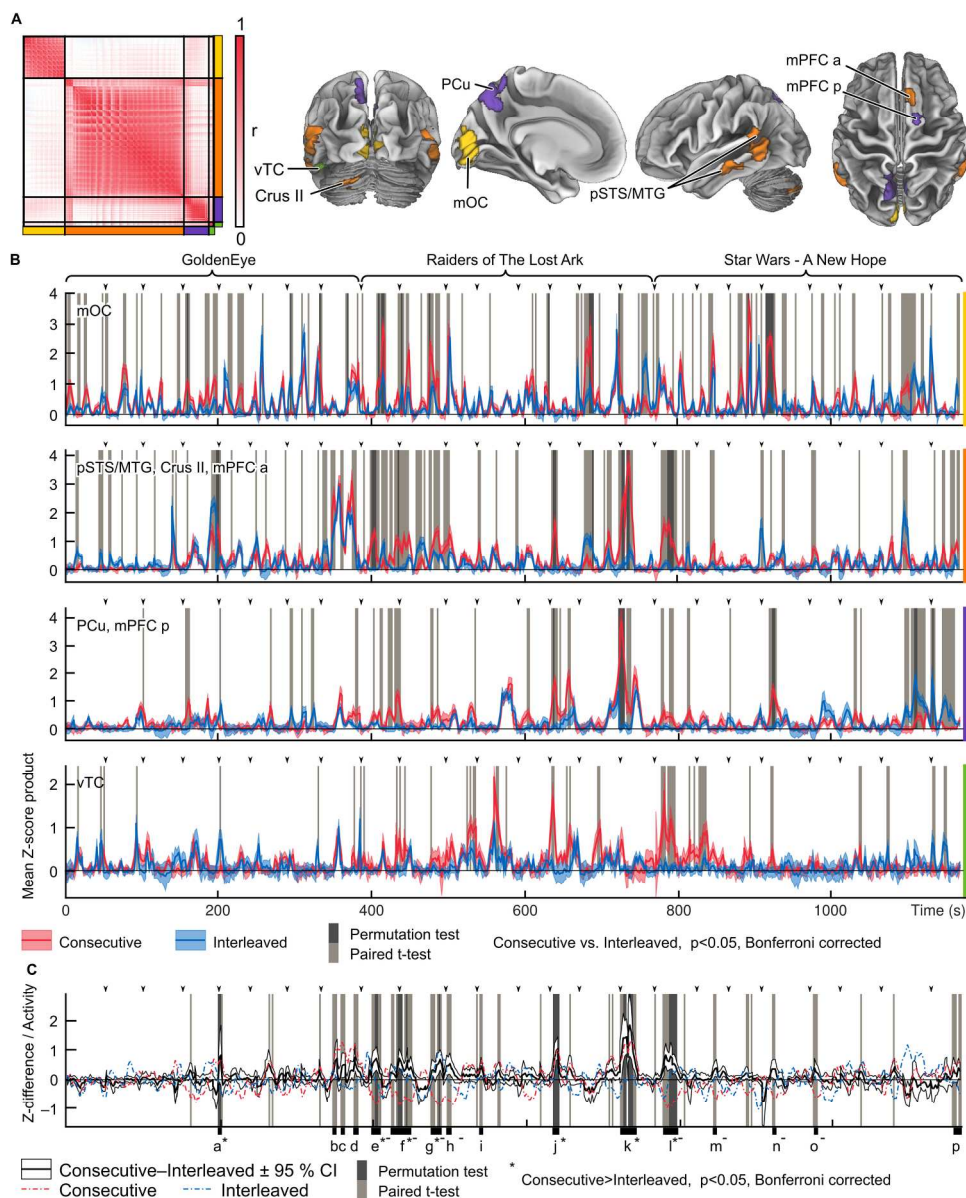Continuity-selective responses
67x59mm (300 x 300 DPI)

Figure 9: Timecourses of products of Z-scores over subject pairs (instantaneous similarity) contributing to the mean ISCs and ISC group differences. A: (Left) Correlation matrix and clustering of the voxels showing significantly higher ISC in Consecutive vs. Interleaved condition. The different clusters are separated by black lines and indicated by the colors on the right and bottom of the matrix. (Right) Locations of the clusters are indicated by colors on the brain visualizations on the right. Abbreviations as in Figure 5, in addition: vTC – ventral temporal cortex, dmPFC a/p – dorsomedial prefrontal cortex, anterior/posterior. B: Mean timecourses of Z-score products across subject pairs for the clusters. Consecutive condition is show in red and Interleaved condition in blue. Timepoints where the mean timecourse of each cluster showed significant (p<0.05, Bonferroni corrected; t-test light gray, permutation test dark gray) between-condition difference are indicated with gray vertical bars. Arrow heads indicate the onset times of each short movie segment and the full duration of each movie excerpt is indicated by the braces on top of the plots. The clusters are indicated by the colored bars on the right side of the plots. C: Mean difference of Z-score products between conditions across all voxels in the orange, purple and green clusters. Significant

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differences (p<0.05, Bonferroni corrected) are indicated by gray bars (t-test result with lighter and permutation test results in darker gray). Red and blue dashed lines indicate the mean standardized activity over subjects and voxels in the orange, purple and green clusters. Time windows marked with a–p indicate instances where the mean timecourses showed most consistent differences across all voxels in the three clusters. Windows shorter than 3 TRs have been omitted and windows that are separated by less than 3 TRs have been collapsed into one longer window. The error bars on all plots indicate 95% confidence intervals. Time windows containing timepoints that were significant in the permutation test are indicated by the astrerisks (*). Timepoints of significant difference across conditions caused by deactivations in the Consecutive condition are marked by minus (-) signs.

Synchrony timecourses
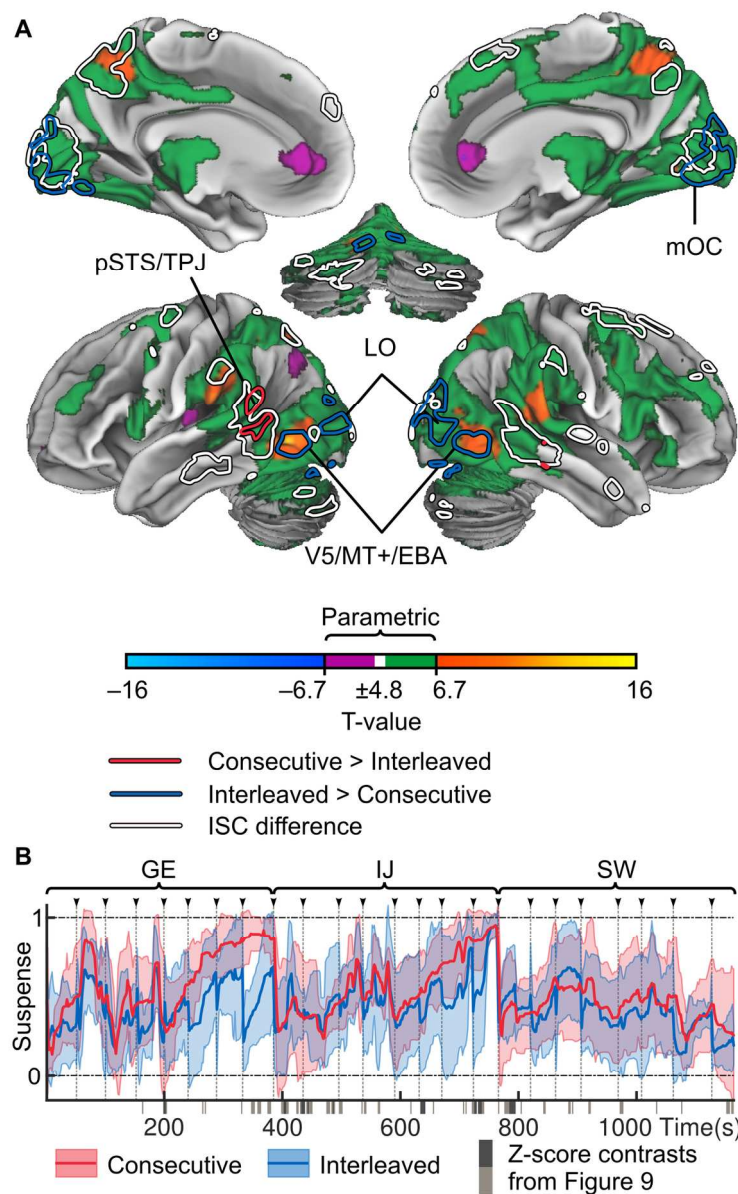202x249mm (300 x 300 DPI)

Figure 10: Brain regions responding to experienced suspense. A: Main effects of suspense in a GLM analysis across both conditions. Due to the autocorrelation structure of the slow signals in the model, the results are thresholded (p<0.05, FDR corrected) based on both standard parametric t-test and null GLMs where the models were circularly shifted. Parametric effects are shown in green (positive) and purple (negative) tones. Differences across conditions in the GLM results are shown in red (Consecutive>Interleaved) and blue (Interleaved>Consecutive) outlines. White outlines indicate areas showing ISC differences in Figure 5. B: Mean ratings (±95% CI) of suspense in the Consecutive (red) and reordered Interleaved (blue) condition. Movie clip onsets are indicated by arrows and gray dashed lines. Gray bars at the bottom of the plot show the differences across conditions in Figure 9 C. Abbreviations as in Figures 5–7.
Suspense-related activity
124x200mm (300 x 300 DPI)