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Intersubject consistency of cortical MEG signals during movie viewing

K. Lankinen *, J. Saari, R. Hari, M. Koskinen

Brain Research Unit, O.V. Lounasmaa Laboratory and MEG Core, Aalto NeuroImaging, School of Science, Aalto University, P.O. Box 15100, FI-00076 AALTO, Finland

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ABSTRACT

According to recent functional magnetic resonance imaging (fMRI) studies, spectators of a movie may share similar spatiotemporal patterns of brain activity. We aimed to extend these findings of intersubject correlation to temporally accurate single-trial magnetoencephalography (MEG). A silent 15-min black-and-white movie was shown to eight subjects twice. We adopted a spatial filtering model and estimated its parameter values by using multi-set canonical correlation analysis (M-CCA) so that the intersubject correlation was maximized. The procedure resulted in multiple (mutually uncorrelated) time-courses with statistically significant intersubject correlations at frequencies below 10 Hz; the maximum correlation was 0.28 ± 0.075 in the ≤ 1 Hz band. Moreover, the 24-Hz frame rate elicited steady-state responses with statistically significant intersubject correlations up to 0.29 ± 0.12 . To assess the brain origin of the across-subjects correlated signals, the time-courses were correlated with minimum-norm source current estimates (MNEs) projected to the cortex. The time series implied across-subjects synchronous activity in the early visual, posterior and inferior parietal, lateral temporo-occipital, and motor cortices, and in the superior temporal sulcus (STS) bilaterally. These findings demonstrate the capability of the proposed methodology to uncover cortical MEG signatures from single-trial signals that are consistent across spectators of a movie.

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Introduction

Naturalistic stimuli, such as movies, provide a semi-controlled tool to study brain function in experimental conditions mimicking everyday life. Despite the apparent complexity of movies, functional magnetic resonance imaging (fMRI) has revealed notable synchronization of brain activity between different spectators (e.g. Bartels and Zeki, 2004a, 2005; Golland et al., 2007; Hanson et al., 2009; Hasson et al., 2004, 2008a, 2008b, 2010). Differences in synchronous activity likely reflect timelocking of the brain areas to stimulus features, as well as to actual content and events in the movie (Hasson et al., 2010).

Emotional video clips, compared with non-emotional ones, increase intersubject synchronization of voxel-wise fMRI time courses in many brain areas, for example in the dorsal attention network (Nummenmaa et al., 2012). Moreover, movie editing and directing affect the synchronization: a well-directed movie, in contrast to an unstructured video clip showing life on a city square or a simple home video, results in stronger interspectator brain-activity synchrony, possibly reflecting a better control over the viewers' attention (Hasson et al., 2008a; Malinen and Hari, 2011). Synchronized activity in fusiform face area (FFA), collateral sulcus (CoS) and post-central sulcus (PCS) was associated with the presence of

* Corresponding author at: Brain Research Unit, O.V. Lounasmaa Laboratory, School of Science, Aalto University, P.O. Box 15100, FI-00076 AALTO, Finland. Fax: + 358 947022969. *E-mail address:* kaisu.lankinen@aalto.fi (K. Lankinen). faces, buildings, and hand movements, respectively, in the movie (Hasson et al., 2004).

Independent component analysis (ICA) can also uncover consistently behaving voxel groups across spectators (Bartels and Zeki, 2004b, 2005; Jääskeläinen et al., 2008; Lahnakoski et al., 2012; Malinen and Hari, 2011; Malinen et al., 2007; Pamilo et al., 2012). Different independent components react to specific features in the movie, such as motion, contrast, color, or objects (Bartels and Zeki, 2004b; Bartels et al., 2008; Lahnakoski et al., 2012).

Although fMRI is an efficient tool for topographic mapping of brain responses, it suffers from the intrinsic sluggishness of the hemodynamic response. Typically, fMRI tracks fluctuations only below ~1 Hz, while electrophysiological signals, such as MEG and EEG, reflect directly the concerted activity of neuronal populations in the range of milliseconds (for a review, see Hari and Salmelin, 2012). The time resolution of MEG and EEG is clearly superior to that of fMRI, basically enabling tracking of brain responses at the frame rate (e.g. 24 Hz) of a movie, or even faster. However, electromagnetic signals have until now been used only rarely in the study of brain activity during movie viewing, and even then, the study designs have focused on classification of relatively short video clips on the basis of brain activity. For example, the phase patterns of 2-7 Hz MEG signals in auditory and visual cortices discriminated between six 30-s audiovisual video clips (Luo et al., 2010), and just the means and standard deviations of 1-s MEG epochs were enough for classifying videos into five categories with 68% accuracy (Huttunen et al., 2013). Also Spectral Linear Discriminant Analysis (Spectral LDA)

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has been used for classification of MEG responses to auditory, video and tactile stimuli and resting periods (Kauppi et al., 2013). Significant correlations were found between luminance changes of 2-min video clips and the averaged time-courses over 25 single-trial EEG signals (Whittingstall et al., 2010).

In this paper, we demonstrate the feasibility of MEG in revealing cortical responses to an intact feature movie. Building on the pioneering work of Hasson et al. (2004) with fMRI, our aim was to find consistent unaveraged intersubject MEG time-courses in subjects watching a 15-min silent black-and-white film. As the signal characteristics of MEG are very different from those of fMRI, we combined spatial filtering with multi-set canonical correlation analysis (M-CCA). Here, M-CCA can be seen as a data-driven approach that enables estimation of the spatial-filter weights resulting in maximally correlated time series between the subjects throughout the movie. In contrast to ICA, M-CCA enables group-level analysis without transforming subject-wise signals to a common anatomical space. Finally, we assess correlations of the focal source currents with these spatially filtered time-courses, and thus, provide means for topographic mapping of the contributing brain areas.

Material and methods

Subjects

Eight healthy adults (4 females, 4 males; mean age 29 years, range 23–51) participated in the study. All subjects had normal or corrected-to-normal vision. The study had a prior approval by the ethics committee of Helsinki and Uusimaa Hospital district. All participants gave written informed consent for the study.

Recordings

The subjects watched twice a 15-min silent black-and-white film "At Land" by Maya Deren (1944). The film was delivered using the Experiment Builder software (SR Research, http://www.sr-research.com/eb. html) and projected to the screen located 130 cm in front of the subject (viewing angle 22° horizontal, 17° vertical). The frame rate of the film was 23.98 frames/s. For accurate temporal alignment, the software provided trigger signals for the MEG acquisition system at the beginning and end of the movie, with temporal jitter less than ± 1 ms across subjects.

MEG was recorded with a 306-channel neuromagnetometer (Elekta Neuromag, Elekta Oy, Helsinki, Finland). The passband was 0.03–330 Hz and the sampling rate 1000 Hz. Vertical and horizontal electrooculograms (EOGs) were recorded at the same time. Additional 2-min "empty-room data" (with no subject present) were acquired in the same day for noise–covariance computation. For the validation purposes, we also recorded the whole 15-min experiment in empty room without subject (two trials). The anatomical MRIs for the source identification were obtained using a 3.0 T General Electric Signa Scanner (General Electric, Milwaukee, WI, USA) at the Advanced Magnetic Imaging Centre at Aalto University.

Data pre-processing

The external magnetic interference outside the brain was suppressed with signal-space separation (SSS) method (Taulu and Kajola, 2005) implemented in Maxfilter software version 2.2 (Elekta Oy, Helsinki, Finland). Default parameter settings were used. The data were converted into the standard head position with the same software.

Next, the MEG signals were filtered, by MNE Suite software package (http://www.martinos.org/mne/), into 12 frequency bands covering frequencies from 0.03 to 100 Hz, namely 0.03–1, 1–5, 5–10, 10–15, 15–20, 20–25, 25–30, 30–40, 40–50, 50–60, 60–80, and 80–100 Hz, with transition bands of 0.5 Hz. The data were downsampled so that the sampling frequency was 100 Hz for the bands below 10 Hz,

250 Hz for the bands between 10 and 30 Hz, and 500 Hz for the rest of the bands.

Eye movement and eye blink artifacts were suppressed by multiple linear regression applied to the raw MEG data after SSS procedure. Both EOG channels were used in the regression, except for two subjects who had only one successfully functioning EOG channel. The regression was performed separately in consecutive 60-s time windows.

Further analysis was based on the signals of the 204 gradiometers. We applied principal component analysis (PCA) to reduce data dimensionality from the original 204 down to 68, the minimum number of all recordings from the 8 subjects ($N_{signals} = 68$), representing the degrees of freedom (rank) left after the SSS artifact reduction.

Spatial filtering model

To find consistencies in the MEG recordings between the subjects, we combined spatial filtering with multi-set canonical correlation analysis (M-CCA; Kettenring, 1971; Li et al., 2009). Spatial filtering refers to projection $\mathbf{y}_m = \mathbf{W}_m \mathbf{x}_m$, where the output \mathbf{y}_m is a weighted sum of the multidimensional signal \mathbf{x}_m . Here, subscript *m* refers to the dataset of one subject ($m = 1 \dots M$, number of subjects). M-CCA can be used to estimate matrices \mathbf{W}_m in the group so that the projections \mathbf{y}_m , i.e. canonical variates, are mutually uncorrelated but maximally correlated between the subjects. Projections \mathbf{y}_m were computed by optimizing MAXVAR objective function for whitened data in a deflationary procedure repeated *k* times ($k = 1 \dots N_{signals}, N_{signals} = 68$). In brief, the optimization refers to finding the eigenvectors corresponding to the largest eigenvalue of $f(\mathbf{A}) = \mathbf{ARA}$, where

$$\mathbf{A} = \begin{cases} \mathbf{I}, k = 1\\ \mathbf{I} - \mathbf{D}_c (\mathbf{D}_c^T \mathbf{D}_c)^{-1} \mathbf{D}_c, k > 1 \end{cases}.$$

R is the $p \times p$ ($p = k \cdot m$) correlation matrix of whitened data \mathbf{x}_m ,

$$\mathbf{R} = \begin{bmatrix} \mathbf{I} & \mathbf{R}_{12} & \cdots & \mathbf{R}_{1m} \\ \mathbf{R}_{21} & \mathbf{I} & \cdots & \mathbf{R}_{2m} \\ \vdots & \vdots & & \vdots \\ \mathbf{R}_{m1} & \mathbf{R}_{m2} & \cdots & \mathbf{I} \end{bmatrix}$$

and \mathbf{R}_{ij} , i, j = 1...M represents between-sets correlation blocks. Here, $\mathbf{D}_c = diag\{\mathbf{C}_1...\mathbf{C}_m\}$ is a $p \times m$ block diagonal matrix containing the eigenvectors of **ARA**, normalized to unit length, i.e. canonical basis vectors \mathbf{b}_m^k in matrix $\mathbf{C}_m = \{\mathbf{b}_m^1...\mathbf{b}_m^{k-1}\}$ up to stage k - 1. Finally the mixing matrix \mathbf{W}_m is obtained by dewhitening the obtained subjectwise matrices of canonical basis vectors.

To enable utilization of multiple trials in our implementation, the blocks in ${\bf R}$ were computed as

$$\mathbf{R}_{ij} = \frac{\overline{\mathbf{X}}_i \overline{\mathbf{X}}_j^T}{N_t - 1}$$

where N_t is the number of samples in one trial, $\overline{\mathbf{X}}_i$ and $\overline{\mathbf{X}}_j$ are the average over the subject-wise whitened trials (pooled data) for subject *i* and *j* $(i \neq j)$, respectively. In this paper, the number of trials was two.

The first 10 min of both 15-min movie trials were used for model training, i.e. building the model by finding basis vectors that optimize the performance criterion (maximal intersubject correlation of the canonical variates). The obtained basis vectors were applied to the remaining two 5-min single-trial epochs. The statistical significance of the pair-wise correlations of the canonical variates between subjects were evaluated with *t*-test to find out whether the mean of these between-subject single-trial correlations (98 intersubject correlations altogether, pooled from both trials) with the test data would deviate statistically significantly from zero. The significance level with Bonferronic correction was $p < 0.05/N_{signals}$, where $N_{signals} = 68$.

MNE source analysis

To assess the cortical sources of the signals of interest, the canonical variates were correlated with the minimum-norm source current estimates (MNEs) (Hämäläinen and Ilmoniemi, 1994) of the MEG signals by MNE Suite software package (http://www.martinos.org/mne/). The sources were estimated at discrete locations separated by 7 mm on a cortical surface. The default procedure to calculate MNEs was used, with 'loose factor' 0.4 to favor the dipole component normal to the surface, and 'depth weighting' to reduce the bias towards superficial currents. For each subject, the T1-weighted magnetic resonance image of the brain was segmented and the cortical surface was constructed using FreeSurfer software (http://surfer.nmr.mgh.harvard.edu/) with the parameters described in http://surfer.nmr.mgh.harvard.edu/ fswiki/RecommendedReconstruction.

The resulting subject-wise inverse operators were used to project the MEG data to source currents for both trials of the 15-min movie. Here, all 306 channels were used. Separately at each dipole location, source currents along three orthogonal coordinate axes (corresponding to two tangential and one normal orientation related to the cortical surface) were correlated with previously computed time series by canonical correlation (i.e. multiple correlation; Rencher, 2002). For group averaging and visualization, the correlation maps of the test data of all eight subjects in both trials were morphed into the 'fsaverage' cortical surface provided by the FreeSurfer software.

Validation of eye-movement effects

As movies can evoke coherent gaze patterns among the viewers (Dorr et al., 2010), the influence of blinks and eye-movements on the canonical variates was further evaluated. Two channels of EOG were filtered into the same frequency bands as the canonical variates, and correlation between these variates and filtered EOG signals was

Validation with empty-room data

To verify that the obtained canonical variates were not artifactrelated, we performed an additional validation with empty-room measurements. The analysis was repeated with the empty-room data (two trials) as the 9th subject. The pair-wise intersubject correlations (16 pairs) between the obtained canonical variates for the empty-room data and other subjects were calculated. In the statistical analysis, *t*-test was used to find out if the mean of the correlation deviated statistically significantly from zero with the Bonferroni-corrected significance level $p < 0.05/N_{signals}$.

Results

Training of the models included data from all subjects (the first 10 min of the two 15-min movie viewing epochs). From the test data, however, the second trial of one subject had to be discarded due to recording artifacts.

In empty-room data, no statistically significant intersubject correlations were found in bands 0.03–1 Hz, 1–5 Hz and 5–10 Hz, or at frequencies of 24 and 36 Hz that were visible in the subjects' data. However, the first canonical variate of 12 Hz survived the significance testing with intersubject correlation of 0.053 \pm 0.055 (mean \pm SD). To be on the safe side, 0.053 was chosen as additional threshold for statistical significance in the analysis of the subjects' data.

The intersubject correlations of the MEG components in the test data were calculated pair-wise between subjects for the two trials. Fig. 1 shows the results for 0.03–1 Hz, 1–5 Hz and 5–10 Hz frequency bands.







Fig. 2. An example of the time-courses of canonical variates for all 8 subjects (2 trials for each). The first canonical variates are shown for the test data in frequency bands 0.03–1, 1–5, and 5–10 Hz. The enlarged segments correspond to each other and the amplitudes of each individual are scaled to have zero mean and standard deviation 1.

The highest statistically significant inter-subject correlations (0.28 \pm 0.075; p < 0.05, correlation > 0.053, Bonferroni corrected), were observed in the lowest 0.03–1 Hz band (with the first canonical variates) where correlations for 5 out of the 68 canonical variates exceeded the statistical threshold (dashed line). In the 1–5-Hz band, statistically significant correlations were obtained for the two first canonical variates, and in the 5–10-Hz band none correlations did not reach statistical significance for any of the canonical variates.

Fig. 2 shows an example of the corresponding time series. Two traces are plotted for each subject and considerable intersubject similarity is evident especially in the lowest frequencies and during large-amplitude transients.

Fig. 3 shows that eye blinks (mainly picked up by EOG ch 1, topmost traces) and saccadic eye movements (mainly picked up by EOG ch 2, second row from top) do not appear to correlate with the changes of the canonical variates.



Fig. 3. An example of the first canonical variates of all subjects in frequency bands of 0.03–1, 1–5, and 5–10 Hz, together with vertical and horizontal EOGs (chs 1 and 2, respectively; topmost two traces). As in Fig. 2, the amplitudes of the canonical variates were scaled to have zero mean and standard deviation 1. The EOG signals are time-locked to the time courses of the canonical variates of MEG signals.



Fig. 4. Spatial maps for the correlations in 0.03–1 Hz (top 5 rows) and 1–5 Hz (bottom 2 rows) bands superimposed on average brain surface. The maps represent the averages of multiple correlation values (between each canonical variate and 3 orthogonal current source estimates) over the subjects.

Fig. 4 shows spatial maps for correlations between the canonical variates and the source current estimates in bands 0.03-1 Hz and 1-5 Hz superimposed on brain surface. In both bands, prominent correlation is seen bilaterally in the early visual cortices and in the posterior parietal cortex. Moreover, distinct activity is seen in the 0.03-1 Hz band in the superior temporal sulci (STS) (the first canonical variate in the right and the second canonical variate in the left hemisphere) and in the frontal lobe (the third and fourth canonical variates). The fifth canonical variate likely reflects activity of the right-hemisphere motion-sensitive visual area (V5) or extrastriate body area. Band 1–5 Hz shows correlation, in addition to PPC and early visual areas, in left inferior parietal cortex (the first canonical variate). Additional correlations were found in the left motor cortex (the first canonical variate). Please note that these correlation maps do not spatially coincide with the topographical maps of source current amplitudes (shown in Supplementary Fig. 1), implying that they do not reflect just signal power.

Some canonical variates that did not survive our correlation threshold still pinpointed distinct brain areas, typically in the early visual cortices. For example, Fig. 5 shows a functionally feasible correlation map involving visual cortices for the first canonical variate in the 5–10 Hz band; the correlation values had not exceeded our significance level (see Fig. 1, right).

Above 10 Hz, the most prominent intersubject correlations occurred around 12, 24, and 36 Hz (Fig. 6), likely triggered by the frame rate of the movie. To inspect these frequencies in more detail, we filtered the MEG signal into narrow \pm 0.2-Hz passbands centered around the



Fig. 5. Spatial map for the first canonical variate in the 5–10 Hz band superimposed on average brain.

peaks (0.2 Hz transition bands; MNE Suite software package). In these bands, the maximum intersubject correlations were 0.19 \pm 0.1, 0.25 \pm 0.08 and 0.29 \pm 0.12, respectively. At each band, 2–3 statistically significant canonical variates were found (Fig. 7).

Fig. 8 shows the spatial maps for significant correlations between the canonical variates and the source current estimates at 12, 24, and 36 Hz. As within the lower bands, intersubject correlation is most prominent in early visual areas. However, the locations of the first and second canonical variates at each band differ to some extent. For instance, the maps for the first and the second canonical variates at 12 Hz seem largely complementary to each other.



Fig. 6. An example of power spectral density (in normalized units) of selected gradiometer signals from one subject showing peaks at 12, 24, and 36 Hz.



Fig. 7. Pair-wise intersubject correlations of statistically significant canonical variates around 12, 24, and 36 Hz. Boxes represent the mean \pm 1 SD for the distribution of the pair-wise correlations (gray dots).

Discussion

We have demonstrated coherent intersubject MEG time courses (canonical variates) reflecting similarly fluctuating brain activity patterns in spectators of a silent black-and-white movie. These mutually uncorrelated time-courses showed association with the source currents of the MEG signals in both hemispheres and distinct cortical areas, likely reflecting sensitivity of these brain areas to visual features or content of the 15-min movie.

Most prominently, the source currents in the early visual areas correlated with canonical variates in frequencies below 5 Hz and at 12, 24, and 36 Hz. Notably, source currents in the early visual areas were associated with several canonical variates, which in combination of slightly different anatomical correlation maps may reflect activity of more than one sources. Some time-courses were referred to extrastriate activity in the region of the motion-sensitive visual area MT/V5 (Tootell et al., 1995) and/or the extrastriate body area (Downing et al., 2001), as demonstrated by the 5th component in the 0.03–1-Hz band. Previous fMRI studies have commonly reported activity in visual areas during movie watching (e.g. Bartels and Zeki, 2004a; Bartels and Zeki, 2005; Bartels et al., 2008; Hasson et al., 2004; Lahnakoski et al., 2012; Pamilo et al., 2012). Relatively high correlations in posterior brain regions agree with the conjecture that these areas belong to extrinsic brain networks (Golland et al., 2007) that are most directly driven by visual stimuli.

Moreover, canonical variates were associated with source currents in the posterior parietal cortex (PPC), the superior temporal sulci (STS), and the prefrontal cortex (PFC). PPC activity occurred in frequency bands of 0.03–1 and 1–5 Hz. This finding goes along with previously reported consistent fMRI activity in the posterior parietal cortex during movie viewing (e.g. Bartels and Zeki, 2004a; Bartels et al., 2008; Golland et al., 2007; Hasson et al., 2008b; Lahnakoski et al., 2012; Malinen and Hari, 2011; Nummenmaa et al., 2012; Pamilo et al., 2012), likely related to activation of the dorsal attention network (Corbetta et al., 2008).

Intersubject correlations occurred in the STS region bilaterally and they were most prominently related to the first three canonical variates in the lowest, 0.03–1-Hz band. STS involvement was to be expected because of the multitude of social stimuli and biological motion in the movie (for a review, see Allison et al., 2000).

The canonical variates in 0.03–1 Hz band included activity in PFC that could reflect emotional engagement to the movie (Jääskeläinen et al., 2008; Kauppi et al., 2010; Nummenmaa et al., 2012; Pamilo et al., 2012).



Fig. 8. Spatial maps for correlations at 12, 24, and 36 Hz for the SSRs. Other details are the same as in Fig. 4.

Interestingly, the first component in the 1–5 Hz band correlated with activity in the motor cortex in the precentral gyrus. This finding could reflect the involvement of the motor cortex in processing of seen actions (Hari et al., 1998; for a review, see Rizzolatti and Craighero, 2004). Accordingly, motor cortex activation in previous brain-imaging studies with movie stimuli has been suggested to reflect perceived actions, such as crawling and climbing (Pamilo et al., 2012) or hand movements (Hasson et al., 2004).

The MEG signals also showed clear spectral peaks at 12 Hz, 24 Hz, and 36 Hz, i.e. at frequencies corresponding to the movie frame rate (23.98 frames/s) and its sub-harmonic component (with its multiple) that elicited steady-state responses (SSRs). Notably, also SSRs involved multiple mutually uncorrelated canonical variates and slightly different spatial correlation maps, potentially referring to distinct source areas. SSRs were most prominently seen in early visual cortices, but also in PPC and lateral occipital areas. In general, visual SSRs are elicited by any periodic visual stimuli, e.g. by changes in the illumination, pattern, color, or motion (for a recent review, see Vialatte et al., 2010). In our stimuli, the movies comprised a sequence of still pictures, that is frames, shown at 24 Hz.

Prior work indicates that visual perception may also be associated with gamma-frequency range (>25 Hz) activity (e.g. Muthukumaraswamy and Singh, 2008; Swettenham et al., 2009; Tallon-Baudry et al., 1996; Tallon-Baudry et al., 1997). Our analyses did not display consistent gamma-range activity, except in SSRs, likely because we analyzed single-trial data that are much more noisier than the typically examined averaged evoked or induced responses.

In the following, we make four methodological remarks. First (i), it is useful to note that CCA-based analysis finds latent signal components on the basis of the signals' consistent temporal structure in the group of subjects, irrespective of amplitude scales (Rencher, 2002) or (average) signal power in general. This structure is influenced by temporal variations in amplitude and phase, and possibly also by fluctuations in signal-to-noise ratio (see e.g. Muthukumaraswamy and Singh, 2011). Second (ii), similarly as with the prior work with inter-subject synchronization, an additional encoding model between the movie features and brain signals would be needed for reasoning the functions of the involved brain areas. Thus, further studies are needed to provide explicit interpretations for our findings. Third (iii), we note that the presented methodology efficiently uncovers consistent intersubject MEG time-courses and brain locations of the contributing source currents. Fourth (iv), our analysis based on unaveraged single-trial MEG traces suffered from "brain noise". In further studies, signal-to-noise ratio could be improved by collecting more data for M-CCA training by using longer movies or by adding more subjects.

In conclusion, M-CCA-based spatial filters were able to uncover coherent time-courses (canonical variates) from single-trial recordings across subjects viewing a movie. The obtained mutually uncorrelated time-courses originate from distinct cortical areas, possibly reflecting functional segregation of processing. It is also useful to note that the same brain areas may contribute to several uncorrelated time-courses, likely reflecting the involvement of these regions in different functional processes. Most prominently, the time courses reflected activity in the early visual, posterior and inferior parietal, lateral temporo-occipital, and motor cortices, and in the STS region. The findings are concordant with previous fMRI studies but extend their findings by temporal information. For example, we found significant intersubject synchrony up to 10 Hz, as well as SSRs related to the frame rate of 24 Hz. MEG, providing far better temporal resolution than fMRI, thus seems feasible for extracting relevant brain events elicited by a movie, a naturalistic complex stimulus.

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.neuroimage.2014.02.004.

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