Complex of global functional network as the core of consciousness

Abbreviated title: Complex of global functional network

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Abstract

Finding the neural basis of consciousness is challenging, and the distribution location of the core of consciousness remains inconclusive. Integrated information theory (IIT) argues that the posterior part of the brain is the hot zone of consciousness, especially phenomenal consciousness. The IIT has proposed a “main complex”, a set of elements determined such that the information loss in a hierarchical partition approach is the largest among those of any other supersets and subsets, as the core of consciousness in a dynamic system. This approach may be applicable not only to phenomenal but also to access-consciousness. This study estimated the main complex of brain dynamics using functional magnetic resonance imaging in Human Connectome Project (HCP) and sleep datasets. The complex analyses revealed the common networks across various tasks and rest-state in HCP, composed of executive control, salience, and dorsal/ventral attention networks. The set of networks of the main complex was maintained during sleep. However, compared with the wakefulness stage, the amount of information of these networks and the default mode network, was reduced for the hypnagogic stage. The global interconnected structure composed of major functional networks can comprise the core of consciousness.

Highlights:

- This study estimated the complex of global functional networks.
- The complex consists of multiple task-positive networks.
- These networks showed decreased information during sleep.
- These global networks can comprise the core of consciousness.

Keywords: core of consciousness, integrated information theory, complex, fMRI, sleep

1. Introduction

The mechanisms of consciousness have been studied in various fields; however, it remains unclear where the core of consciousness is distributed in the brain. Several theories of consciousness have been proposed over several decades (Northoff and Lamme, 2020; Seth and Bayne, 2022); among these, the integrated information theory (IIT) (Tononi, 2004) appears to be particularly promising. According to the IIT, for a system to have consciousness, vast amounts of information must be integrated within the internal network, corresponding to the amount of consciousness (Oizumi et al., 2016; Cohen et al., 2020).

Theoretical and empirical controversies exist regarding the core of consciousness (Boly et al., 2017; Odegaard et al., 2017; Melloni et al., 2021). Theoretically, the IIT emphasizes the posterior part of the cortex as the hot zone (Tononi et al., 2016), while the global neuronal workspace theory (GNWT) emphasizes the prefrontal cortex (Mashour et al., 2020). The GNWT suggests that in the conscious state, a network ignition related to recurrent processes amplifies and sustains a neural representation, allowing the corresponding information to be globally accessed by local processors, and that the prefrontal cortex is responsible for this role (Mashour et al., 2020). Empirical evidence is also ambiguous. While well-designed neuropsychological and electrophysiological studies indicate that the prefrontal cortex enables the subjective experience in perception (see Odegaard et al., 2017), lesions and neuroimaging studies demonstrated that regions in the posterior parts of the cortex play a direct role in specifying the contents of consciousness (see Boly et al., 2017). Note that this argument is primarily about content-specific neural correlates of consciousness (NCC).

Although the axiom of integration in the IIT is often exemplified within the framework of visual experience (Tononi, 2004; Oizumi et al., 2014), this concept does not apply only to a particular modality. Furthermore, the information integration must be cross-modal not only in exteroceptive inputs but also between exteroceptive and interoceptive inputs. Several scientists emphasize that affect and emotion are the targets for studying consciousness (Damasio, 1999; Panksepp, 2005; Solms and Friston, 2018); for example, the insula is involved in the representation of interoception in a subjective feeling and may be considered a candidate for NCC (Craig, 2009). In addition to the extrinsic view, as demonstrated by the discovery of DMN (Raichle, 2009), the brain is also an intrinsically driven entity. The intrinsic–extrinsic interaction contributes to the emergence of consciousness (Northoff, 2013). The core of consciousness based on full-NCC must be able to integrate not only exteroceptive information but also other information.

To consider the core of consciousness, the IIT introduced the concept of a “complex”, a subset with a local maximum of integrated information (Tononi, 2008). This quantifies the amount of causally integrated information loss when the system is split and the dependencies between the parts are removed (Oizumi et al., 2014). To reduce computational cost and identify a complex, a hierarchical search approach based on mutual information instead of integrated information has been

proposed (Kitazono et al., 2020). In this approach, the complex is defined as the subsystem with maximum mutual information loss. Applying this approach to macaque electrocorticography data, the complex was inferred to be present in the posterior part of the brain (Kitazono et al., 2020). However, to the best of our knowledge, no study has applied this complex analysis to human brain activity.

The aim of this study is to find a core of consciousness that is independent of whether it is exteroceptive or interoceptive and regardless of sensory modalities. To find such a candidate for the core of consciousness, the complexes of brain activity measured by functional magnetic resonance imaging (fMRI) were estimated based on two approaches. First, this study examined the complexes of different conditions, including multiple tasks and resting states. Tononi (2008) implied that there may be a single complex underlying consciousness at any given time. The complex should be detectable in any state of consciousness, either at rest or when performing a task. Therefore, the core of consciousness can comprise the common complexes estimated from brain activity during various tasks and resting states. Second, this study compared the complexes between wakefulness and sleep using the fMRI data, which contains rich information that allows for distinguishing between wakefulness and light sleep (Tagliazucchi and Laufs, 2014). Understanding how consciousness fades during early sleep can help identify what is necessary and sufficient for the brain to give rise to conscious experience (Tononi and Massimini, 2008). The core of consciousness would be affected by sleep onset.

2. Materials and Methods

2.1. Human Connectome Project (HCP) data

The Human Connectome Project (HCP) is a systematic effort to map the macroscopic circuitry of the human brain and its relationship to behavior in a large population of healthy adults (Markov et al., 2013). The HCP subjects were adults between the ages of 22 and 35 years. MRI measurements were obtained under eight conditions: working memory, gambling, motor, language, social cognition, relational processing, emotional processing, and rest. Subject recruitment methods and informed consent were approved by the Institutional Review Board of the University of Washington.

Datasets were deidentified and publicly shared on the ConnectomeDB database (<https://db.humanconnectome.org>), and the preprocessed imaging and behavioral data were freely accessible. The data (HCP 1200-subject data release, Mar, 2017) used for this study were downloaded as per the HCP minimally preprocessed pipeline with denoising procedures (for details see Glasser et al., 2013). All subjects with complete fMRI sessions were included ($n = 957$). The subjects were divided into two independent groups: 479 subjects in the first half and 478 subjects in

the second half, with no differences in the age and sex ratios between the two groups.

MRI scanning includes four imaging modalities: structural MRI, resting-state fMRI (rfMRI), task fMRI (tfMRI), and diffusion MRI. All subjects were scanned using all four modalities on a customized 3T MRI scanner. HCP established an optimized fMRI protocol (both resting-state and task-evoked) with a multiband factor of 8, spatial resolution of 2 mm isotropic voxels, and repetition time (TR) of 0.7 s (Smith et al., 2013; Uğurbil et al., 2013). Each session included both rfMRI and tfMRI. First, two 15-min resting-state scans (eyes open) were acquired for a total of 1 h of resting-state data over a two-day visit (total of 4 rfMRI runs). Second, approximately 30 min of tfMRI was acquired in each session, including seven tasks split between the two sessions, and each task was run twice (Barch et al., 2013). Structural scans included T1-weighted images acquired at 0.7 mm isotropic resolution. An overview of the imaging protocol can be found on the HCP website (www.humanconnectome.org/hcp-protocols-ya-3t-imaging).

The details of the preprocessing are given in Glasser et al. (2013) and Marcus et al. (2013). In the spatial preprocessing, the functional data were corrected for spatial distortions and head motion and registered to the structural image. The temporal preprocessing included filtering temporal frequencies, regression of global mean time series, and removal of spatiotemporal artifacts (motion artifacts, scanner artifacts, cardiac artifacts, breathing artifacts). MELODIC (Beckmann and Smith, 2004) was applied to the functional data, and artifact components were identified using FIX (FMRIB's ICA-based X-noiseifier; Salimi-Khorshidi et al., 2014). MELODIC was used to decompose the data; while some components represented artifacts, others represented valid neuronally related spontaneous fluctuations. FIX was used to automatically classify components into "bad" and "good." The bad component time series were then regressed from the data, along with head-motion-related confound regressors. Data including the preprocessed time-series data of eight conditions (seven tasks and resting state) were downloaded and analyzed in this study.

2.2 Data of simultaneous electroencephalography and fMRI during wakefulness and sleep

A hypnagogic data provided by Gu et al. (2021) (openneuro.org/datasets/ds003768) were used to compare the complexes of global functional networks between wakefulness and sleep. The data of Gu et al. (2021) were approved by the Ethics Committee of the Faculty of Medicine of the University of Liège, and all participants provided written informed consent. Thirty-three young, healthy, right-handed volunteers were recruited for this database (mean age: 24 ± 3 years, 16 females). The sleep qualities of the participants assessed by the Pittsburgh Sleep Quality Index questionnaire (Buysse et al., 1989) were normal. The sleep schedules were checked using a sleep diary and wrist actigraphy, and it was confirmed that all participants had a constant sleep schedule for three days before the visits.

Imaging data were collected on a 3 tesla Siemens scanner using a 20-channel receive-array

coil. fMRI images were measured with a gradient echo-planar sequence using axial slice orientation (TR: 2130 ms, TE: 40 ms, FA: 90°, 32 slices, slice thickness: 3 mm, 30% interslice gap, field of view: 220 × 220 mm², matrix size: 64 × 64). A structural image was also acquired with T1-weighted 3D MP-RAGE sequence (TR: 1960 ms, TE: 4.43 ms, TI: 1100 ms, FA: 8°, 176 slices, FoV = 230 × 173 mm², matrix size = 256 × 192). The duration of the sleep session with simultaneous electroencephalogram (EEG) and fMRI recordings was 15 min, and multiple recordings were performed for each participant (3–8 sessions). EEG data were recorded using a 32-channel system including an MR compatible amplifier and a synchronization box (Brain Products, Gilching, Germany). The EEG electrodes were placed according to the 10-20 system. Electrooculogram and electrocardiogram were recorded for eye movements and cardiac signals, respectively. EEG data were measured at a sampling rate of 5000 Hz with a band-pass filter of 0–250 Hz.

Denoised EEG data were divided into 30-s intervals, and the sleep stages were evaluated based on the manual of American Academy of Sleep Medicine (Iber et al., 2007). The scored sleep stages of all participants and the EEG and fMRI data were included in the publicly available database. Based on the sleep stages, the 5-min segments to be analyzed during wakefulness and sleep were determined according to the following criteria. (1) The wakefulness or sleep stage must last for at least five consecutive minutes each. (2) The sleep segments were chosen to have a higher proportion of sleep stage 1. (3) The segments of wakefulness and sleep stages must be selected at time intervals as close as possible, such as within an identical session or adjacent sessions. Of all participants, 13 were excluded from the analysis because both wakefulness and sleep stage data could not be secured. MRI data of the remaining 20 participants were preprocessed by C-PAC (The Configurable Pipeline for the Analysis of Connectomes) with default setting. The preprocessing included motion correction, anatomical/functional coregistration, spatial normalization, spatial and temporal filtering, tissue segmentation, slice-timing correction, nuisance signal removal, and motion “scrubbing”.

2.3 Parcellation

The elements of a complex system must have a certain degree of independence. Global fMRI networks obtained by a data-driven approach (independent component analysis) might represent neural mass activity related to the state of consciousness (He and Raichle, 2009). In this study, the preprocessed data were parcellated to the networks defined by Yeo et al. (2011) (https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation_Yeo2011). Yeo et al. (2011) have provided multiple atlases based on a data-driven analysis of resting-state fMRI data collected from the HCP. The atlases consist of seven and seventeen networks (Supplementary Table 1-1, 1-2). The atlas of seven networks comprised a visual network (VN), somatomotor network (SMN), dorsal attention network (DAN), salience/ventral attention network (SN/VAN), limbic network (LN),

executive control network (ECN), and DMN. The atlas of seventeen networks consisted of two VNs, two SMNs, two DANs, VAN, SN, two LNs, three ECNs, a temporal parietal network (TPN), and three DMNs. The average time series of voxels comprising each network were extracted. As the task and rfMRI measurements of HCP were performed in two and four sessions, respectively, the average time series, which was filtered by a trapezoid window (2.5% rise and fall of the session length), were concatenated across runs under each condition. The time series were mainly used for calculating the complex.

As additional analysis to examine the complex in a functional network based on more granular elements, the above-mentioned procedure was conducted using Schaefer's atlas (Schaefer et al., 2018) divided into 100 regions. Furthermore, to examine the effects of task-evoked components, residual time series were calculated from a general linear model including the stimulus onsets and durations (Cole et al., 2013). These residual time series were obtained only in the Yeo's 17 networks atlas.

2.4 Outline of complex estimation

The core networks were estimated using hierarchical partitioning for complex search approach (Kitazono et al., 2018, 2020). The complex is an important concept in IIT and is considered the core of consciousness. Kitazono et al. (2020) mathematically defined a complex as a subsystem in which the amount of information loss based on instantaneous (non-causal) mutual information is locally maximal; this definition differs from other versions using causal information (Barrett and Seth, 2011; Oizumi et al., 2016; Mediano et al., 2019). Information loss based on mutual information satisfies monotonicity; therefore, the hierarchical partitioning for complex search is exact (Kitazono et al., 2020). The computation of the complex was hierarchically performed to narrow down the candidates for the complexes. The main complex is a subsystem in which the maximum amount of information loss occurs for its minimum information partition. The details are given below.

2.5 Information loss

The information loss was defined in the same way as by Kitazono et al. (2020). The information loss function measures the amount of information lost when the interaction between the parts is removed, and mutual information is considered as the information loss function.

This analysis considers a probabilistic system consisting of N elements with a distribution $p(x_V) = p(x_1, \dots, x_N)$, where V denotes the set of elements ($V = \{1, \dots, N\}$), and x_V denotes the $(x_1, \dots, x_N) = (x_i)_{i \in V}$. In subset S of V , x_S denotes $(x_i)_{i \in S}$. In this study, each variable x_i was time-series data from a brain network, and N was the number of brain networks ($N = 7, 17$).

Next, it considers a bipartition (S_1, S_2) of a subset S , which is partitioned into two disjoint

parts, S_1 and S_2 ($= S \setminus S_1$). Then, it considers a disconnected distribution $q(x_S) = q(x_{S_1}, x_{S_2})$, where the interactions between S_1 and S_2 are removed. The amount of information lost by partitioning $f(S_1; S_2)$ is defined as the Kullback–Leibler divergence between the original distribution p and the disconnected distribution q :

$$f(S_1; S_2) = D_{KL}(p(x_S) || q(x_S)) = \int p(x_S) \log \frac{p(x_S)}{q(x_S)} dx. \quad (1)$$

The Kullback–Leibler divergence is interpreted as information loss when q is used to approximate p (Burnham and Anderson, 2003), and f is interpreted as the information loss caused by removing the interactions between the two parts.

The amount of information lost by partitioning was also estimated by mutual information, which quantifies the statistical dependence between the two parts. It considers the disconnected probability distribution q :

$$q(x_S) = p(x_{S_1})p(x_{S_2}), \quad (2)$$

where S_1 and S_2 are independent because any dependence between S_1 and S_2 is removed. By substituting Eq. (2) into Eq. (1), the following formula can be derived:

$$I(S_1; S_2) = \int p(x_S) \log \frac{p(x_S)}{p(x_{S_1})p(x_{S_2})} dx_S. \quad (3)$$

Mutual information measures how strongly the two subsystems are statistically dependent on each other; it is larger when the two parts are strongly dependent and smaller when the two parts are independent. Here, as the entropy H of subset S is $-\int p(x_S) \log p(x_S) dx_S$, Eq. (3) can be rewritten as follows:

$$I(S_1; S_2) = H(S_1) + H(S_2) - H(S). \quad (4)$$

At the analytical level, the entropy of an N -dimensional Gaussian distribution with a covariance matrix Σ is given by $\frac{1}{2} \log |2\pi\Sigma| + \frac{N}{2}$. Σ_1 and Σ_2 are covariance matrices of S_1 and S_2 . Because the mean of the Gaussian distribution does not affect the mutual information, it can be assumed to be zero. By substituting this into Eq. (4), the following can be derived:

$$I(S_1; S_2) = \frac{1}{2} \log \frac{|\Sigma_1||\Sigma_2|}{|\Sigma|}. \quad (5)$$

2.6 Minimum information partition

The approach proposed by Kitazono et al. (2020), called “hierarchical partitioning for complex search”, is exact when the measure of the information loss satisfies monotonicity. Instantaneous mutual information used in this study satisfies this property. Minimum information partition (MIP) is the bipartition with the smallest amount of information loss among all bipartitions (Figure 1), and the amount of information loss of MIP in a system is denoted as I_{MIP} . For example, in Figure 1A, element 6 is separated from the whole. In this case, I_{MIP} of element 6 assigned

$I(S_{(1,2,3,4,5)}; S_{(6)})$ because $I(S_{(1,2,3,4,5)}; S_{(6)})$ is smaller than I of other partition patterns. Thus, all elements have I greater than 0 even if they are not included in the main complex. The number of possible bipartitions is $2^{N-1} - 1$, and each element is assigned to one of two subsets. When searching for the MIP of a system by comparing all partitions, the computation time increases exponentially with the number of elements in the system. The Queyranne algorithm was used to reduce the computation time (Queyranne, 1998; Hidaka and Oizumi, 2018; Kitazono et al., 2018).

Minimum Information Partition (MIP)
Figure 1. (A) Minimum information partition. Edges represent a connection between two elements, and their width indicates the connection strength. Information loss is computed for all partition patterns. The lowest value of information loss among all patterns is defined as the amount of information in the system. (B) In the subset of the system with the least information loss, the procedure of minimum information partition is repeated. Colored circles represent the system or subsystem of the analysis target for minimum information partition. In hierarchical partitioning, a subsystem becomes the main complex when the information loss in its minimum information partition is higher than that of all supersets and subsets.

2.7 Complex

The main complex of the system was estimated using an algorithm of hierarchical partitioning for complex searches (Kitazono et al., 2020). In a system, a subsystem is called a complex if the I_{MIP} is non-zero and greater than the I_{MIP} in all supersets. Furthermore, a complex is called a main complex if the I_{MIP} is greater than or equal to that of all its subsets (Figure 1B). Thus, the greater the I_{MIP} , the more information is integrated by that complex. The set of elements consisting of the main complex corresponds to the core of consciousness. Note that the definition of complex used in our study differs from the canonical one in the IIT, which grants the status of complex to the subset with a local maximum of integrated information (Oizumi et al., 2014).

2.8 Complex search for HCP and hypnagogic data

In this study, the main complex was searched for under each condition of the individual subjects. The probability distributions of the signal were calculated by multivariate Gaussian distributions using the extracted time series of 7 and 17 brain networks. Under the Gaussian assumption, the I_{MIP} and main complex using Eq. (5) with hierarchical partitioning for the complex search algorithm were computed. Figure 2 shows a sample of I_{MIP} and a complex estimation at the individual level. In this sample, multiple complexes were detected, and the complex with the highest I_{MIP} was regarded as the main complex of this individual. The I_{MIP} of each network was defined as the maximum I_{MIP} in the hierarchical complex containing the region (see Figure 2).

Figure 2. Complex estimation using data of 17 networks in a sample subject. The elements are arranged on a circle in a virtual space with the x and y axes. The z axis and color indicate the information loss in the minimum information partition (I_{MIP}). Complexes are superimposed and the uppermost complex is the main complex.

2.9 Statistical analysis

This study aimed to identify the main complex as the core of consciousness using time-series data of functional brain networks. The participation rate was defined as the percentage of subjects that included a specific network in the individual main complex and was calculated for each network. Networks included in the main complex should have a greater I_{MIP} and a higher participation rate to the main complex than other networks that are not part of the main complex. This study used permutation tests for I_{MIP} and participation rate of HCP data, respectively (Figure 3). In the permutation tests, data were shuffled across networks at each individual level. After shuffling, the mean of the data was computed for each network. This process was repeated 10,000 times, and the distribution of the participation rate was obtained. The p -value was then computed by estimating

how many permuted mean I_{MIP} and participation rates were larger than the mean value in the actual data. Statistical criteria were set at $p < 0.05$ and a step-up procedure (Benjamini and Hochberg, 1995) was applied to control the false discovery rate (FDR). The permutation test was performed for each condition. The analysis reveals which networks contribute more to the main complex. Networks that were significantly related to the main complex under all conditions were considered as common networks related to the core of consciousness. These statistical analyses were independently conducted for the two groups of HCP.

Inter-class correlation (ICC) (McGraw and Wong, 1996) was applied to determine which atlas (7 or 17 networks) was more appropriate for detecting the core of consciousness. In this study, the conditions comprised the analysis class. As consciousness is present under all conditions, a stable set of networks must be detected as the main complex over long time scales, regardless of which condition is working. The regional distribution of I_{MIP} and participation rates must be similar across the conditions. In other words, a higher ICC is expected with a more appropriate atlas.

In the hypnagogic data, I_{MIP} and participation rates were compared between the wakefulness and sleep stages. I_{MIP} was examined with paired t -tests for each network, and the participation for main complex was examined with Wilcoxon's rank-sum test. Statistical criteria were set at $p < 0.05$, adjusted by step-up procedure (Benjamini and Hochberg, 1995) to control the FDR.

The toolbox for the complex estimation is available at <https://github.com/oizumi-lab/PhiToolbox>, and the MATLAB codes and data of the complex for the statistical analyses and presentation are available at <https://github.com/onodak1/Complex>.

Figure 3. Permutation test. (A) Data were repeatedly shuffled across networks in each individual (rep 10,000 times), and the mean value of each network was computed in each shuffle. (B) The p -value was computed as the rate of the mean value of shuffled data above the actual mean to the total. This procedure was applied not only to participation in main complex but also to I_{MIP} .

3. Results

3.1. HCP: Main complex of 7 networks

The I_{MIP} was computed for each condition and individual level, and the second level analysis was independently conducted in each of the two groups. Figure 4 shows the mean I_{MIP} and participation rate for the main complex in each network (element). An observation of the spider plots of the I_{MIP} shows all conditions demonstrated similar patterns, with values ranging from 0.5 to 0.8 for all conditions and networks (Figure 4A). The main complex was computed using the I_{MIP} , and the participation rate of the main complex showed different patterns between the networks (Figure 4B). Some networks, including DAN and SN/VAN, showed relatively high participation rates on average across the conditions, while others (especially LN) did not.

To test the statistical difference among the seven networks, permutation tests were conducted for each condition, which should indicate which networks have a greater I_{MIP} or participation rate for the main complex compared to the other networks. The networks with significantly higher I_{MIP} values or participation rates under each condition are presented as brain mapping in Supplementary Figure 1. For each network, the number of conditions that showed a significantly higher participation rate is shown in Figure 4C. If the number of networks is eight, it implies that the network participates in the main complex under all conditions. However, none of the networks showed significantly higher participation rates under all conditions. In Group 1, the DAN met the statistical criteria under seven conditions ($ps < 0.0003$), while the social task condition of the DAN did not show a significant participation rate for the main complex (Figure 4C, detailed in Supplementary Figure 1 and Supplementary Table 2-1). Similarly, the SN/VAN met the criteria under seven conditions ($ps < 0.0102$), except the relational processing condition. The SMN showed a significant participation rate for the main complex under five conditions ($ps < 0.0011$), while the other networks showed almost no significant participation rates. Importantly, these results were comparable between Groups 1 and 2 (Supplementary Figure 1 and Supplementary Table 2-2).

Figure 4. Results of main complex estimation using seven networks. (A) Spider plots of information loss of minimum information partition (I_{MIP}) under each condition. Each colored line is assigned the I_{MIP} of each condition. WM: working memory. (B) Spider plots of participation rate for main complex under each condition. The color matching with the condition is the same as in (A). The detailed statistics are presented in Supplementary Figure 4-1. (C) Brain mapping of the number of significant conditions.

3.2. HCP: Main complex of 17 networks

The statistical procedures for the main complex of 7 networks were also applied to the data of 17 networks. Figure 5A shows the distribution of the I_{MIP} in each network. In these spider plots, the I_{MIP} is distributed around 0.6–1.2, and there does not appear to be a large difference between the

networks; however, the I_{MIP} in LN and DMN-b showed a slight decrease. Unlike I_{MIP} , the participation rate of the main complex varied substantially (Figure 5B). The DANs, VAN, SN, and ECNs demonstrated high participation rates, while LNs, TPN, and DMN-c had low participation rates. The permutation tests revealed that the participation rates of the two DANs, VAN, SN, and ECN-a were significantly higher than those of the other networks in all conditions of Group 1 ($p < 0.0067$) (Figure 5C, detailed in Supplementary Figure 2 and Supplementary Table 3-1). The ECN-b showed a significant participation rate under seven conditions (all task conditions, $p < 0.0001$) but not in the rest condition ($p = 0.0421$). These results were similar, with close concordance between groups (Supplementary Figure 2 and Supplementary Table 3-2).

Figure 5. Results of main complex estimation using 17 networks. (A) Spider plots of information loss of minimum information partition (I_{MIP}) in each condition. Each colored line is assigned the I_{MIP}

of each condition. (B) Spider plots of participation rate under each condition. The color matching with the condition is the same as in (A). Detailed statistics are in Supplementary Figure 5-1. (C) Brain mapping of the number of significant conditions. The yellow area (significant in all conditions) consists of the executive control network (ECN), dorsal attention network (DAN), ventral attention network (VAN), and salience network (SN).

3.3. HCP: Comparison of atlases with 7 and 17 networks

The ICCs of the mean I_{MIP} or the participation rate between the conditions are shown in Figure 6. This index shows the degree to which the spatial distribution of the mean I_{MIP} or participation rate is consistent across the conditions. In both I_{MIP} and participation rate, the ICC in 17 networks was higher than that in 7 networks in both groups. This implies that more common features across the conditions can be detected when using the atlas with 17 networks compared to the one with 7 networks.

Figure 6. Inter-class (condition) correlation of regional distribution of mean information loss of minimum information partition (I_{MIP}) and participation rate for the main complex across networks. The error bar denotes the 95% confidence interval.

3.4. Additional analyses

First, we examined whether the complex is composed of similar networks when using a more granular atlas. For this purpose, we used Schaefer's atlas (Schaefer et al., 2018) with 100 regions and computed the I_{MIP} and participation rate for each condition (except the emotional processing task with the shorter duration). In this analysis, we confirmed that the I_{MIP} and participation rates of the prefrontal and parietal cortex were significantly higher than those of the other regions under all

analyzable conditions (Supplementary Figure 3). Next, we conducted the complex analysis using the residual time series removing the effects of stimulus presentation or task structure for each condition (except the rest condition). In this analysis, Yeo's 17 network atlas was applied. Independent of the stimulus or task, the DANs, VAN, SN, and ECN had commonly higher participation rates for the main complex than the other networks, which means that the main results were replicated (Supplementary Figure 4).

3.5. Hypnagogic data

As described above, the atlas with 17 networks showed more stable complexes than that with 7 networks. Therefore, the results of hypnagogic data are shown only for the atlas with 17 networks (Figure 7).

The I_{MIP} values of the wakefulness and sleep periods in each network are shown in Figure 7A. In general, the values of I_{MIP} in the wakefulness period were higher than those in the sleep periods. Especially, the I_{MIP} values of DANs, VAN, SN, ECNs, and DMNs decreased significantly with falling asleep ($t(19) > 3.14$, Cohen's $ds > 0.70$, $ps < 0.006$). The networks with significant I_{MIP} decreases are depicted in Figure 7B.

The participation rates for main complex in the wakefulness and sleep periods are shown in Figure 7C. The distribution of the participation rates in the two periods were approximately the same. No significant difference of the participation rates between the two conditions was observed in any network. Figure 7D shows the brain map of the mean participation rates of the two periods. The distribution pattern of participation rates for main complex was substantially similar to that of HCP. Furthermore, the networks with higher participation rate for the main complex were almost identical to the regions with significant decreases of I_{MIP} .

Figure 7. Comparisons of the main complex during wakefulness and light sleep. (A) Information loss of minimum information partition (I_{MIP}) in the two periods. (B) Distribution of regions where the I_{MIP} decreased significantly due to falling asleep. (C) The participation rate under the two periods. (D) Brain mapping of mean participation rate between the two periods.

4. Discussion

This study aimed to find a candidate for the core of consciousness using the concept of a complex, which can be identified by information theory. The main complex was estimated from the dynamic system of fMRI data during tasks and rest, and common networks across the various conditions were identified; specifically, DAN, VAN, SN, and ECN were found to constitute the main complex. The structure of this main complex was maintained during early sleep, and the multiple networks with the addition of DMNs showed a decreased amount of information with sleep onset.

The IIT claims that consciousness contains various qualities at once (e.g., a mix of colors,

sounds, emotions, and thoughts) and that the qualities within consciousness are unified under a single point of view (Tononi, 2004; Oizumi et al., 2014). One aspect of this notion was conceptualized as a complex by the IIT (Tononi, 2004, 2008) and mathematically formulated for a dynamic system with Gaussian processes (Hidaka and Oizumi, 2018; Kitazono et al., 2018, 2020). A physical system such as the brain is likely to contain a main complex, and at any given time, there may be a single main complex containing comparatively much more information that underlies the dominant experience (Tononi, 2008). This study applies the complex to global functional networks measured by fMRI. Multiple networks were commonly detected as elements of the complex during multiple tasks, rest, and sleep. This means that the brain network is highly organized and has a stable complex within it.

Because it does not depend on the conditions, the complex detected in this study might correspond to the full-NNC. The main complex is embedded into larger complexes with less information and can be causally connected to unrelated elements (Tononi, 2008). The IIT suggests such elements can indirectly influence the state of the main complex without contributing directly to the conscious experience it generates (Tononi and Sporns, 2003). This suggestion might correspond to the fact that this study excluded the primary sensory and motor networks from the complex. Notwithstanding, when considering a content-specific NCC, the primary sensory cortex can also be included in the complex (Tononi et al., 2016).

The empirical evidences on the NCC supporting the importance of the prefrontal cortex or the posterior cortex are *unclear* (Boly et al., 2017; Odegaard et al., 2017). Because the within-state comparison paradigm detected a posterior cortical area (Siclari et al., 2017), which was consistent with the findings of content-specific NCC during arousal (Frässle et al., 2014; Noy et al., 2015), researchers of the IIT refer to the posterior cortex as the hot zone (Koch et al., 2016). However, according to Koch et al. (2016), they did not neglect the prefrontal cortex, as the posterior regions of the cortex are not the only areas that comprise the full-NCC (Lumer et al., 1998; Dehaene et al., 2001; Bellet et al., 2022), and admitted the importance of examining NCC in the prefrontal cortex.

The result of the analysis of the HCP in this study may be the rediscovery of the task-positive networks (Fox et al., 2005; Cole and Schneider, 2007; Cole et al., 2013); however, the concept of two large task-positive or task-negative networks may be over-simplified. Certain components of the task-positive network, referred to as the ECN in this study, contribute to executive control, which is the ability to deliberately guide action based on goals, and switch between activations of the DAN and DMN (Vincent et al., 2008; Gao and Lin, 2012). The ECN comprises separate subsystems: ECN-a is connected to the DAN and is involved in the regulation of perceptual attention, whereas ECN-b is connected to the DMN and is involved in the regulation of internal processes (Dixon et al., 2018). Furthermore, a part of the ECN, along with the SN, forms a multiple demand pattern associated with diverse cognitive demands (Duncan, 2010). This study may

extend these concepts both anatomically and functionally. That is, the brain has a stable core of functional networks (ECN, DAN, and SN) independent of the task in which it engages.

The extended network core may correspond to the GNWT (Dehaene et al., 1998; Mashour et al., 2020). The GNWT restricts its focus to conscious access, which is global information availability. What is subjectively experienced as conscious access is considered the selection, amplification, and global broadcasting to many distant areas of a single piece of information selected for its salience or relevance to current goals (Baars, 1989). The GNW is a neural instantiation of the global workspace in which the perceptual content acted upon by a local processor becomes conscious only after the information has been widely transmitted to other processors (Baars, 2005). It is postulated that the GNW is activated through a phenomenon called ignition in which a subset of workspace neurons encoding the current conscious content is suddenly, coherently, and exclusively activated, while the remaining workspace neurons are suppressed (Dehaene et al., 2003). Ignition can be triggered by external stimuli or may occur spontaneously at rest (Karahanoğlu et al., 2013) and just before waking up (Alcaide et al., 2021). The GNW allows consciousness based on long-distance cortical connections, particularly of the pyramidal cells of the prefrontal, cingulate, and parietal regions (Dehaene and Changeux, 2011). The central core sets, which consist of the frontal and parietal cortices, form a structural bottleneck, which enables the routing of information among other cortical processors (Markov et al., 2013). Considering these various findings, the complex obtained in this study may reflect conscious access, while previous studies that have emphasized the posterior part of the brain (Vanhaudenhuyse et al., 2010; Frässle et al., 2014; Wu et al., 2015; Sasai et al., 2016; Siclari et al., 2017; Kitazono et al., 2020) reflect phenomenal consciousness.

Furthermore, our results may also correspond to the information generation hypothesis (Kanai et al., 2019), which proposes that the function of consciousness is to internally generate counterfactual representations detached from current sensory events. In this hypothesis, consciousness has an internally generated model of the environment and self. The internal model of the environment and the motion of the self are located in the DAN, especially the parietal cortex (Land, 2014), and the internal model of the self that reflects the interception is represented in a network that includes SN and VAN (Barrett, 2017). A small-world system such as the brain has higher causal density, which is a measure of the overall causal interactivity (Barrett and Seth, 2011); these networks, including the ECN, have significant effective connectivity and strongly affect each other (Liao et al., 2010).

This study revealed that the configuration of the complex was sustained during hypnagogic periods; however, the amount of information (I_{MIP}) within the complex was lower for the light sleep stage than the wakefulness stage. Consciousness fades during non-REM sleep, yet cortical neurons remain active (Steriade et al., 2001; Steriade and Timofeev, 2003), continue receiving sensory inputs (Kakigi et al., 2003), and show patterns of synchronous activity (Bullock et al., 1995), as well as

maintain global functional networks detected by BOLD activity (Fukunaga et al., 2006; Horovitz et al., 2008, 2009; Larson-Prior et al., 2009; Tagliazucchi et al., 2013). According to the IIT, the firing rate, sensory input, and synchronization are not critical for consciousness, but the ability of the system to integrate information is. A combinational study of transcranial magnetic stimulation (TMS) and EEG (Massimini et al., 2005) reported that as soon as the participants transitioned into sleep stage 1, the evoked response to the TMS changed markedly. The authors have interpreted the result as a disruption of the differentiation and integration of cortical activity, that is, information integration (Casali et al., 2013).

Several fMRI studies have reported changes in brain activity associated with fading of consciousness during light sleep: larger fluctuation in some parts of the DMN and VN (Horovitz et al., 2008), breakdown of thalamocortical connectivity (Kaufmann et al., 2006; Spoormaker et al., 2010), increased corticocortical connectivity (Spoormaker et al., 2010), decreased nodal efficiency in some regions of the DMN and ECN (Uehara et al., 2014), increased scaling parameters of the cluster size power-law distributions (Bocaccio et al., 2019), and decreased stability within and between functional networks (Kung et al., 2019). Furthermore, despite the subjective ambiguity of retrospective discrimination between wakefulness and sleep states (Hsiao et al., 2018), machine learning using support vectors for the functional connectivity matrix can classify between wakefulness and sleep state 1 (Tagliazucchi and Laufs, 2014; Altmann et al., 2016), which means that the fMRI data during sleep contain abundant information to distinguish the states. The IIT approach, including the complex used in this study, may be a salient methodology for detecting loss of consciousness, and it is necessary to apply this analysis to dynamic networks from wakefulness to sleep, not only to static networks.

Even in NREM sleep, retrospective reports show a high rate of dreaming phenomena immediately after awakening (Stickgold et al., 2001). In the within-state comparison approach, brain activity is compared between the presence or absence and content of dreaming phenomena (Siclari et al., 2017, 2018; Sterpenich et al., 2020). For example, in both NREM and REM sleep, the full-NCC is localized in the temporal-parietal-occipital regions associated with perceptual experiences and in frontal regions associated with thoughtful experiences (Siclari et al., 2017). Further, the subjective experience of fear during sleep is related to the anterior cingulate cortex and insula (Sterpenich et al., 2020). The results of previous studies agree with our findings that the complex, including the ECN and SN, was maintained during light sleep.

One of the key structures in consciousness is the DMN (Leech and Sharp, 2014), which is an essential cluster of hubs in the global functional network, as well as the ECN and DAN (Gordon et al., 2018). However, in our analysis using HCP, the task-positive networks (ECN, DAN, VAN, and SN) were included in the main complex, whereas the DMN was excluded. In unconscious states, such as coma, anesthesia, and deep sleep, the DMN is affected but not eliminated (Boly et al., 2008).

Therefore, the DMN plays an essential role in an aspect of consciousness, however, it may not be a part of the core. The other possibility is that this study failed to detect the DMN as the main complex owing to brain parcellation. Although the DMN is a task-negative network that deactivates during task engagement, the hubs of the DMN contribute to task-positive activation in support of executive control (Christoff et al., 2009; Wade et al., 2018). Considering this evidence, a part of the DMN may be detected as the main complex when using fine-scale brain parcellation.

Studies exploring the core of brain networks have primarily used the indices of graph theory (Meunier et al., 2009; van den Heuvel and Sporns, 2011; Harriger et al., 2012; van den Heuvel et al., 2012; Crossley et al., 2013; Collin et al., 2014; Grayson et al., 2014; Sporns and Betzel, 2016; Deco et al., 2017; Gordon et al., 2018). Recently, Deco et al. (2017) introduced a new dynamic measure of the binding of information in which regions within the network are more integrative across both space and time. The dynamic workspace of the binding elements is defined by a measure of entropy linked to the binding problem, i.e., the problem of how distributed information can be bound and can become available for consciousness and awareness (Crick and Koch, 1990). When removing the dynamic workspace of binding elements from the system, the integration and information capabilities of the brain critically decrease (Deco et al., 2017). The core of the networks detected in their study is consistent with our findings in that it included association areas in the frontal, parietal, and temporal lobes, but it differs in that it includes primary visual areas.

There are some limitations of this study. One is that the complex was originally a concept based on causal information integration (Tononi, 2008; Oizumi et al., 2014), but this study calculated the surrogate measure based on instantaneous mutual information. That is, unidirectional connectivity should be used in calculating the complex. Directed connectivity of fMRI has the restriction that the network can only be identified with a time delay of approximately 1 s. However, much of neural causality acts at delays shorter than this and, therefore, would appear as instantaneous correlations. Furthermore, a new complex calculation based on causal connectivity was recently proposed (Kitazono et al., 2022). Future research must examine whether the complexes computed by causal and functional connections are compatible. Another limitation is that the number of elements comprising the functional network is small. Our main result was replicated in the analysis using the brain atlas with 100 regions (see Supplementary Figure 3). If departing from the scales of the other functional units such as neurons and columns, 100 parcels may be regarded as too large given the average level of granularity for brain atlases based on functional neuroimaging. Therefore, a more granular brain atlas analysis is needed to confirm that the complex is independent of the number of elements in the network.

5. Conclusion

In summary, multiple main functional networks (ECN, DAN, VAN, and SN) were

identified as the main complex. The decreased information within these networks and the DMN corresponded with the loss of consciousness due to sleep. These results imply that these functional networks can comprise the core of consciousness. Importantly, this evidence using IIT-inspired measures is consistent with the prediction of the GNW theory. In terms of where the core of consciousness is distributed in the brain, the two theories are not in conflict, but may be complementary (Northoff and Lamme, 2020).

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Figure 1. (A) Minimum information partition. Edge shows a connection between two elements, and the width implies the connection strength. Information loss is computed for all participation patterns. The lowest value of information loss among all patterns is defined as the amount of information in the system. (B) In the subset of the system with the least information loss, the procedure of minimum information partition is repeated. Colored circles represent the system or subsystem of the analysis target for minimum information partition. In hierarchical partitioning, a subsystem becomes the main complex when the information loss in its minimum information partition is higher than that of all supersets and subsets.

Figure 2. Complex estimation using data of 17 networks in a sample subject. The elements are arranged on a circle in a virtual space with the x and y axes. The z-axis and color indicate the information loss in the minimum information partition (I_{MIP}). Complexes are superimposed, and the uppermost complex is the main complex.

Figure 3. Permutation test. (A) Data were repeatedly shuffled across networks in each individual (repeated 10,000 times), and the mean value of each network was computed in each shuffle. (B) The p -value was computed as the rate of the mean value of shuffled data above the actual mean to the total.

Figure 4. Results of main complex estimation using seven networks. (A) Spider plots of information loss of minimum information partition (I_{MIP}) under each condition. Each colored line is assigned the I_{MIP} of each condition. WM: working memory. (B) Spider plots of participation rate for main complex under each condition. The color matching with the condition is the same as in (A). The detailed statistics are presented in Supplementary Figure 1. (C) Brain mapping of the number of significant conditions.

Figure 5. Results of main complex estimation using 17 networks. (A) Spider plots of information loss of minimum information partition (I_{MIP}) in each condition. Each colored line is assigned the I_{MIP} of each condition. (B) Spider plots of participation rate under each condition. The color matching with the condition is the same as in (A). Detailed statistics are in Supplementary Figure 2. (C) Brain mapping of the number of significant conditions. The yellow area (significant in all conditions) consists of the executive control network (ECN), dorsal attention network (DAN), ventral attention network (VAN), and salience network (SN).

Figure 6. Inter-class (condition) correlation of regional distribution of mean information loss of minimum information partition (I_{MIP}) and participation rate for the main complex across networks. The error bar denotes the 95% confidence interval.

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914 Figure 7. Comparison of main complex during wakefulness and light sleep. (A) Information loss of
915 minimum information partition (I_{MIP}) in the two periods. (B) Distribution of regions where the I_{MIP}
916 decreased significantly due to falling asleep. (C) The participation rate under the two periods. (D)
917 Brain mapping of mean participation rate between the two periods.

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Supplementary Table 1-1. Names of 7 networks considered by Yeo et al. (2011)

No	Name by Yeo et al. (2011)	Abbreviation in this study
1	Visual	VN
2	Somatomotor	SMN
3	Dorsal Attention	DAN
4	Salience / Ventral Attention	SN/VAN
5	Limbic	LN
6	Control	ECN
7	Default	DMN

https://github.com/ThomasYeoLab/CBIG/blob/master/stable_projects/brain_parcellation/Yeo2011_fcMRI_clustering/1000subjects_reference/7NetworksOrderedNames.csv

Supplementary Table 1-2. Names of 17 networks considered by Yeo et al. (2011)

No	Name by Yeo et al. (2011)	Abbreviation in this study
1	Visual Central (Visual A)	VN-c
2	Visual Peripheral (Visual B)	VN-p
3	Somatomotor A	SMN-a
4	Somatomotor B	SMN-b
5	Dorsal Attention A	DAN-a
6	Dorsal Attention B	DAN-b
7	Salience / Ventral Attention A	VAN
8	Salience / Ventral Attention B	SN
9	Limbic A	LN-a
10	Limbic B	LN-b
11	Control C	ECN-c
12	Control A	ECN-a
13	Control B	ECN-b
14	Temporal Parietal	TPN
15	Default C	DMN-c
16	Default A	DMN-a
17	Default B	DMN-b

https://github.com/ThomasYeoLab/CBIG/blob/master/stable_projects/brain_parcellation/Yeo2011_fcMRI_clustering/1000subjects_reference/17NetworksOrderedNames.csv

Supplementary Figure 1-1. Results of the main complex estimation using seven elements. (A) Spider plots of information loss of minimum information partition (I_{MIP}) and participation rate for the main complex in each condition. Each colored line was assigned the I_{MIP} and participation rate under each condition. WM: working memory, VN: visual network, SMN: somatomotor network, DAN: dorsal attention network, SN/VAN: salience network/ventral attention network; LN: limbic network; ECN: executive control network; DMN: default mode network. (B) Brain mapping of I_{MIP} and participation rate for each condition. Colored networks had significantly high values than those of other networks. (C) Brain mapping of the number of significant conditions.

Supplementary Table 2-1. Participation rates for main complex of 7 networks and p values of permutation test in group 1.

	WM	Gambling	Motor	Language	Social	Relational	Emotion	Rest
VN	0.27	0.40	0.05	0.10	0.33	0.67	0.32	0.48
	1.0000	0.9842	1.0000	1.0000	1.0000	0.0000	1.0000	1.0000
SMN	0.53	0.33	0.60	0.28	0.63	0.35	0.59	0.73
	0.0011	1.0000	0.0000	1.0000	0.0000	1.0000	0.0000	0.0000
DAN	0.73	0.75	0.57	0.68	0.30	0.85	0.66	0.63
	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0003
SN/VAN	0.59	0.49	0.90	0.71	0.72	0.39	0.67	0.70
	0.0000	0.0102	0.0000	0.0000	0.0000	0.9860	0.0000	0.0000
LN	0.18	0.29	0.06	0.29	0.37	0.13	0.33	0.44
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
ECN	0.58	0.41	0.20	0.42	0.40	0.36	0.46	0.43
	0.0000	0.9640	1.0000	0.3013	0.9997	1.0000	0.9728	1.0000
DMN	0.40	0.43	0.15	0.36	0.51	0.31	0.46	0.57
	1.0000	0.6940	1.0000	0.9912	0.0099	1.0000	0.9861	0.4506

Supplementary Table 2-2. Participation rates for main complex and of 7 networks and p values of permutation test in group 2.

	WM	Gambling	Motor	Language	Social	Relational	Emotion	Rest
VN	0.22	0.45	0.06	0.08	0.33	0.65	0.28	0.46
	1.0000	0.7743	1.0000	1.0000	1.0000	0.0000	1.0000	0.9926
SMN	0.55	0.35	0.69	0.24	0.65	0.37	0.56	0.67
	0.0000	1.0000	0.0000	1.0000	0.0000	0.9998	0.0000	0.0000
DAN	0.69	0.77	0.57	0.69	0.30	0.85	0.65	0.58
	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000
SN/VAN	0.61	0.50	0.92	0.72	0.73	0.39	0.67	0.62
	0.0000	0.0559	0.0000	0.0000	0.0000	0.9927	0.0000	0.0000
LN	0.17	0.30	0.05	0.28	0.36	0.13	0.35	0.38
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
ECN	0.54	0.43	0.22	0.41	0.38	0.39	0.41	0.33
	0.0000	0.9676	1.0000	0.2479	1.0000	0.9901	0.9997	1.0000
DMN	0.39	0.47	0.15	0.33	0.49	0.29	0.45	0.49
	0.9994	0.4610	1.0000	0.9979	0.1102	1.0000	0.9053	0.7036

Supplementary Figure 1-2. (A) Information loss of minimum information partition (I_{MIP}) based on the combinations of 7 networks. (B) Matrix of the number of significant conditions. VN: visual network, SMN: somatomotor network, DAN: dorsal attention network, SN/VAN: salience network/ventral attention network; LN: limbic network; ECN: executive control network; DMN: default mode network. (C) Brain mapping of the number of significant conditions.

Supplementary Figure 2-1. Results of main complex estimation using 17 elements. (A) Spider plots of information loss of minimum information partition (I_{MIP}) and participation rate for the main complex in each condition. Each colored line was assigned the I_{MIP} and participation rate under each condition. WM: working memory, VN: visual network, SMN: somatomotor network, DAN: dorsal attention network, SN/VAN: salience network/ventral attention network; LN: limbic network; ECN: executive control network; DMN: default mode network. (B) Brain mapping of I_{MIP} and participation rate for each condition. Colored networks had significantly high values than those of other networks. (C) Brain mapping of the number of significant conditions.

Supplementary Table 3-1. Participation rates for main complex of 17 networks and p values of permutation test in group 1.

	WM	Gambling	Motor	Language	Social	Relational	Emotion	Rest
VN-c	0.38	0.65	0.24	0.26	0.40	0.73	0.63	0.40
	0.9999	0.0000	1.0000	1.0000	0.0078	0.0000	0.0002	0.1452
VN-p	0.13	0.36	0.28	0.19	0.12	0.53	0.66	0.25
	1.0000	1.0000	1.0000	1.0000	1.0000	0.0000	0.0000	1.0000
SMN-a	0.58	0.55	0.49	0.44	0.32	0.36	0.72	0.70
	0.0000	0.0046	0.0030	0.7233	0.9897	0.9775	0.0000	0.0000
SMN-b	0.49	0.51	0.12	0.25	0.30	0.31	0.60	0.76
	0.0847	0.3398	1.0000	1.0000	0.9994	1.0000	0.0489	0.0000
DAN-a	0.71	0.80	0.57	0.57	0.94	0.80	0.81	0.60
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
DAN-b	0.71	0.74	0.80	0.71	0.89	0.57	0.82	0.65
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VAN	0.74	0.74	0.93	0.72	0.47	0.55	0.85	0.56
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
SN	0.77	0.70	0.78	0.90	0.46	0.57	0.74	0.47
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
LN-a	0.05	0.09	0.05	0.15	0.10	0.06	0.25	0.05
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
LN-b	0.02	0.05	0.05	0.03	0.03	0.03	0.14	0.02
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
ECN-c	0.33	0.29	0.29	0.54	0.16	0.17	0.30	0.18
	1.0000	1.0000	1.0000	0.0000	1.0000	1.0000	1.0000	1.0000
ECN-a	0.83	0.74	0.69	0.83	0.46	0.66	0.77	0.42
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0067
ECN-b	0.79	0.67	0.60	0.75	0.45	0.54	0.69	0.41
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0421
TPN	0.32	0.39	0.40	0.28	0.35	0.12	0.38	0.26
	1.0000	1.0000	0.9595	1.0000	0.6326	1.0000	1.0000	1.0000
DMN-c	0.01	0.18	0.14	0.06	0.06	0.08	0.22	0.09
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
DMN-a	0.48	0.53	0.46	0.50	0.26	0.39	0.56	0.31
	0.1241	0.0704	0.1048	0.0076	1.0000	0.7963	0.7628	0.9997
DMN-b	0.50	0.53	0.46	0.52	0.35	0.38	0.57	0.30
	0.0194	0.0840	0.0471	0.0006	0.7152	0.8519	0.4499	1.0000

Supplementary Table 3-2. Participation rates for main complex of 17 networks and p values of permutation test in group 2.

	WM	Gambling	Motor	Language	Social	Relational	Emotion	Rest
VN-c	0.38	0.70	0.21	0.20	0.42	0.69	0.56	0.43
	1.0000	0.0000	1.0000	1.0000	0.0000	0.0000	0.2388	0.0052
VN-p	0.10	0.37	0.23	0.16	0.12	0.50	0.59	0.29
	1.0000	1.0000	1.0000	1.0000	1.0000	0.0000	0.0356	1.0000
SMN-a	0.55	0.51	0.46	0.41	0.29	0.40	0.66	0.75
	0.0000	0.1676	0.0255	0.9356	0.9996	0.5328	0.0000	0.0000
SMN-b	0.51	0.49	0.09	0.24	0.34	0.34	0.59	0.75
	0.0126	0.4951	1.0000	1.0000	0.7396	0.9998	0.0214	0.0000
DAN-a	0.71	0.81	0.58	0.55	0.95	0.81	0.77	0.61
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
DAN-b	0.69	0.69	0.81	0.70	0.89	0.60	0.79	0.67
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VAN	0.74	0.73	0.92	0.71	0.46	0.57	0.83	0.59
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
SN	0.77	0.70	0.79	0.89	0.44	0.58	0.72	0.46
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
LN-a	0.05	0.10	0.07	0.17	0.12	0.04	0.22	0.06
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
LN-b	0.01	0.04	0.04	0.03	0.04	0.01	0.13	0.01
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
ECN-c	0.37	0.28	0.26	0.56	0.13	0.15	0.32	0.14
	1.0000	1.0000	1.0000	0.0000	1.0000	1.0000	1.0000	1.0000
ECN-a	0.83	0.70	0.68	0.82	0.43	0.68	0.74	0.42
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0206
ECN-b	0.76	0.65	0.60	0.73	0.40	0.55	0.71	0.39
	0.0000	0.0000	0.0000	0.0000	0.0021	0.0000	0.0000	0.2757
TPN	0.28	0.41	0.37	0.25	0.35	0.14	0.33	0.26
	1.0000	1.0000	0.9957	1.0000	0.4294	1.0000	1.0000	1.0000
DMN-c	0.01	0.17	0.16	0.06	0.04	0.07	0.24	0.09
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
DMN-a	0.53	0.48	0.44	0.50	0.22	0.38	0.59	0.29
	0.0002	0.5925	0.2088	0.0023	1.0000	0.9106	0.0194	1.0000
DMN-b	0.56	0.49	0.45	0.50	0.35	0.39	0.59	0.30
	0.0000	0.4123	0.0951	0.0004	0.6136	0.7234	0.0341	1.0000

Supplementary Figure 2-2. (A) Information loss of minimum information partition (I_{MIP}) based on the combinations of 17 networks. (B) Matrix of the number of significant conditions. VN: visual network, SMN: somatomotor network, DAN: dorsal attention network, SN/VAN: salience network/ventral attention network; LN: limbic network; ECN: executive control network; DMN: default mode network. (C) Brain mapping of the number of significant conditions.

Supplementary Figure 3. Results of main complex estimation using 100 elements (Schaefer's atlas). (A) Brain mapping of I_{MIP} and participation rate for each condition. Colored networks had significantly high values than those of other networks. The results of the emotional task were not available due to the shorter duration. The large differences in I_{MIP} value across the conditions can be ascribed to the disparate number of scans (data length) recorded under each condition. (B) Brain mapping of the number of significant conditions.

Supplementary Table 4. Inter-class coefficient analysis for Schaefer's atlas.

ICC	
I_{MIP}	0.846 (0.794-0.889)
Participation rate	0.817 (0.755-0.867)

Supplementary Figure 4. Results of main complex estimation using residuals of 17 elements. (A) Spider plots of information loss of minimum information partition (I_{MIP}) and participation rate for the main complex in each condition. Each colored line was assigned the I_{MIP} and participation rate under each condition. WM: working memory, VN: visual network, SMN: somatomotor network, DAN: dorsal attention network, SN/VAN: salience network/ventral attention network; LN: limbic network; ECN: executive control network; DMN: default mode network. (B) Brain mapping of I_{MIP} and participation rate for each condition. Colored networks had significantly high values than those of other networks. (C) Brain mapping of the number of significant conditions.