A common neural code for similar conscious experiences in different individuals

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The interpretation of human consciousness from brain activity. without recourse to speech or action, is one of the most provoking and challenging frontiers of modern neuroscience. We asked whether there is a common neural code that underpins similar conscious experiences, which could be used to decode these experiences in the absence of behavior. To this end, we used richly evocative stimulation (an engaging movie) portraving real-world events to elicit a similar conscious experience in different people. Common neural correlates of conscious experience were quantified and related to measurable, quantitative and qualitative, executive components of the movie through two additional behavioral investigations. The movie's executive demands drove synchronized brain activity across healthy participants' frontal and parietal cortices in regions known to support executive function. Moreover, the timing of activity in these regions was predicted by participants' highly similar qualitative experience of the movie's moment-to-moment executive demands, suggesting that synchronization of activity across participants underpinned their similar experience. Thus we demonstrate, for the first time to our knowledge, that a neural index based on executive function reliably predicted every healthy individual's similar conscious experience in response to real-world events unfolding over time. This approach provided strong evidence for the conscious experience of a brain-injured patient, who had remained entirely behaviorally nonresponsive for 16 y. The patient's executive engagement and moment-to-moment perception of the movie content were highly similar to that of every healthy participant. These findings shed light on the common basis of human consciousness and enable the interpretation of conscious experience in the absence of behavior.

fMRI | brain injury | disorders of consciousness

A lthough consciousness is a part of all of our lives, we are not privy to the conscious experiences of others. Indeed, our ability to understand and appreciate their experiences depends largely on their self-report, or ability to describe those experiences (1). However, in recent years a population of patients has been identified who are demonstrably conscious, but entirely unable to speak or move willfully in any way, precluding any systematic investigation of their conscious experience of the world (2–8). It remains unknown whether there is a common neural code that can account for how different individuals might form similar conscious experiences and, if so, whether it could be used to interpret those experiences without recourse to self-report.

The "executive" function of the brain refers to those processes that coordinate and schedule a host of other more basic cognitive operations, such as monitoring and analyzing information from the environment and integrating it with internally generated goals, as well as planning and adapting new behavioral schemas to take account of this information (9–11). As such, executive function is integral to our conscious experience of the world as prior knowledge is integrated into the current "state of play" to make predictions about likely future events. Accordingly, executive function may provide an empirical window by which the cognitive aspect of human conscious experience can be quantified. The behavioral and neuronal bases of executive function have been well studied in neuropsychological patients (12–14) and with functional neuroimaging (9, 12, 15–17), which confirm that executive function is supported by a network of brain regions, primarily involving the frontal lobes and the posterior parietal cortex (9, 12, 15–17). However, the open-ended nature of our conscious experiences combined with the narrowly defined scope of most tests of executive function, which rely on responses to specific parameters of a study task, make it challenging to relate executive function to consciousness in real-world situations.

Movie viewing may provide a solution to this problem. By their very nature, engaging movies are designed to give viewers a shared conscious experience driven, in part, by the recruitment of similar executive processes, as each viewer continuously integrates their observations, analyses, and predictions, while filtering out any distractions, leading to an ongoing involvement in the movie's plot. These cognitive, integrative processes are executive in the broad meaning of the word and go beyond processes directly related to planning and execution of motor behavior to encompass "second-order" or "meta" cognitive states that enable viewers to understand a movie. When different individuals watch the same movie, synchronized changes of brain activity across the individuals are observed (18-20). However, it is not known whether any of these synchronized activity fluctuations reflect similar executive function across different individuals in response to the evolving executive demands of the movie plot.

We addressed this question in a series of studies by using a highly engaging short movie by Alfred Hitchcock, the so-called "master of suspense," to drive the conscious experiences of three groups of healthy participants. Initially, the neural correlates of

Significance

Although in our daily lives we engage in many of the same activities as others, we are not privy to their conscious experiences, and can only understand them through their selfreports. Patients who are conscious, but are unable to speak or exhibit willful behavior, are, therefore, unable to report their conscious experiences to others. Indeed, in most cases, it is impossible to know whether they are conscious or not. We introduce a neural index that, in a group of healthy participants, predicted each individual's conscious experience. Moreover, this approach provided strong evidence for intact conscious experiences in a brain-injured patient who had remained behaviorally nonresponsive for 16 y. These findings have implications for understanding the common basis of human consciousness.



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conscious experience common to different individuals were quantified using functional magnetic resonance imaging (fMRI). Subsequently, these correlates were related to measurable (quantitative and qualitative) executive components of the movie plot through two additional behavioral investigations in independent groups of healthy participants to determine the neural basis of executive processes common across individuals. We then applied the same approach in two behaviorally nonresponsive patients with unknown levels of consciousness to examine and quantify their experience of the world in the absence of self-report.

Results

Similar Neural Correlates of Conscious Experience Across Different Individuals. In the first study, we acquired fMRI data from 12 healthy participants while they viewed the short (8 min) movie and also during a "resting state" scan-a scanning period of the same duration in which they were asked to just relax in the absence of any overt visual or auditory stimulation. We also acquired fMRI data from a second healthy group (n = 12) while they viewed a scrambled version of the movie, which was formally identical to the intact one, except for the absence of a detectable plot (Supporting Information). Consistent with previous studies (18–20), we observed widespread and significant (P <0.05; family wise error (FWE) cor) cross-subject synchronization between healthy participants, with sensory-driven (primary and association) visual and auditory cortex, as well as higher-order supramodal regions, showing activity peaks and dips at identical points of the movie in different individuals (Fig. 1A). By contrast, no synchrony was observed in any area of the brain in the resting state data (Fig. 1B). The scrambled movie elicited significant (P < 0.05; FWE cor) synchronization only in sensory-driven visual and auditory cortex (Fig. 1C). Formal comparison between the intact and scrambled movie conditions revealed that the intact movie elicited significantly (P < 0.05; FWE cor) more crosssubject synchronization than the scrambled movie bilaterally in parietal, temporal, motor, and dorsal/ventral frontal/prefrontal cortex (Fig. 1D). Together, these results confirmed that the crosssubject synchronization observed during movie viewing in highorder supramodal regions could not merely reflect modulations in the feed-forward processing load imposed by variations in the audiovisual information, nor any automatic attention effects triggered by the similarity of audiovisual stimuli across participants. Rather, the processing of higher-level properties of the movie itself, including its plot, must be driving the synchronized activity in these regions across participants.

To relate the synchronized activity fluctuations to different and specific aspects of the movie-watching experience, we used Tensor Independent Components Analysis (ICA). Tensor ICA derives spatially orthogonal components, whose spatial and temporal features are common across different individuals (21–23), thus isolating those neural patterns that may be driven from common aspects of



Fig. 1. Brain-wide synchronization of neural activity across subjects. (*A*) Movie viewing elicited significant (P < 0.05; FWE cor) cross-subject correlation across the brain. (*B*) No cross-subject correlation was observed in the resting state. (*C*) The scrambled movie elicited significant (P < 0.05; FWE cor) cross-subject correlation only within primary and association visual and auditory cortex; none was observed in higher-order, supramodal cortex. (*D*) The intact movie elicited significantly (P < 0.05; FWE cor) more cross-subject correlation than the scrambled movie bilaterally in parietal, temporal, motor, and dorsal/ventral frontal/prefrontal cortex. Warmer colors depict higher *t* values of cross-subject correlation.

the movie-watching experience. Group-level Tensor ICA revealed several spatially distinct networks (Fig. 2 *A*–*F* and Fig. S1) in sensory-specific (i.e., visual, auditory, and motor) cortex and regions of the frontal and parietal lobes that are known to support executive processing (9, 12, 15–17). To further confirm that this fronto-parietal network reflected synchronized activity across different participants, we performed single-subject ICAs, which revealed a high correlation between the single-subject time courses for the frontoparietal component [t(11) = 13.2; P < 0.00001; Fig. 2 *G* and *H*]. By contrast, single-subject ICAs demonstrated that brain activity was desynchronized among different participants when they were at rest (Fig. 2*I*).

Neural Basis of Executive Processes Common to Different Individuals.

To test whether the cross-subject synchronization in frontal and parietal regions during movie viewing actually represented commonly experienced executive elements of the movie, two further studies in healthy participants were conducted outside of the scanner. First, the extent to which the movie made demands on executive functioning was quantified with a "dual-task" procedure that has been used previously to investigate executive performance, both in patients with frontal lobe damage (24–26) and in healthy volunteers (27-29). The dual-task framework assumes that, because executive function is a finite resource, in moments when the load on one executively demanding task is greatest, the performance of a second executively demanding task will be impaired, yielding a direct, quantitative measure of the executive demands of the first task across time (Supporting Information). Accordingly, we continually assessed performance on a demanding and widely used test of executive function [the Sustained Attention to Response Task (SART) (30-33), Supporting Information], while 27 healthy participants watched the same Alfred Hitchcock movie. During the SART, participants were required to respond with a key press to a series of randomly presented ("go") digits (one-seven, nine) but withhold responses to one prespecified ("no go") digit (eight) (Fig. 3A). To ensure that participants attended to both the SART and the movie, they were instructed to respond as quickly as they could, while minimizing errors and, in addition, to prepare to answer questions about the movie contents at its conclusion. Performance was assessed as the reaction time to make key-press responses throughout the movie, yielding a continuous measure of the movie's executive load (Supporting Information).

We then used statistical parametric mapping (SPM) to model the relationship between this quantitative measure of the movie's executive load and changes in brain activity over time, assessed in the independent group of healthy participants who had watched the movie without a secondary task in the fMRI scanner. Groupaveraged reaction times from participants who correctly performed both components of the dual task (n = 15) were used as a regressor in the SPM model of movie data. SART reaction times in one (behavioral) group of participants significantly (P <0.05; FWE cor) predicted activity in a brain network involving frontal and parietal regions-which support executive function (9, 12, 15–17)—in the other (fMRI) group of participants (Fig. 3B). This result confirmed that synchronized activity in these regions was driven by the executive load of the movie, as indexed by an entirely independent behavioral measure acquired in a separate group of healthy participants (Fig. S2).

To further confirm that these modulations in frontal and parietal activity reflected a common conscious experience across individuals, we developed a *qualitative* measure of the subjective experience of viewing the movie that reflected, albeit indirectly, its ongoing executive load. A third group of healthy participants (n = 15) watched the movie and were asked to rate how "suspenseful" it was every 2 s from "least" to "most" suspenseful (Fig. 3C). Beyond basic physical properties, such as the amplitude and tone of the musical sound-track, "suspense" in classic Hitchcock movies, such as the one used



in this study, arises through an understanding of the relevance of specific items intrinsic to the plot (e.g., a gun), their potential uses (e.g., to shoot people), the circumstances of the main protagonists (e.g., they are capable of shooting or being shot), and their own "theory of mind" (e.g., they are holding a gun, but they do not know that it is loaded). The ongoing understanding of the plot requires access to executive processing as the current features of the movie are compared with stored knowledge of the world (e.g., guns kill people), what has happened previously in the movie (e.g., the boy has acquired a gun), and what may happen in future (e.g., he may shoot someone). The single-subject suspense ratings throughout the movie showed significant intersubject correlation [t(14) = 25.3; P < 0.0001], once more confirming the common conscious experience of individuals watching it.

Again, we used SPM to model the relationship between this qualitative measure of the movie's executive load and changes in brain activity over time, measured in the independent group of healthy participants who had watched the movie without a secondary task in the fMRI scanner. The group-averaged suspense ratings significantly (P < 0.05; FWE cor) predicted activity in a similar network of brain regions involving the frontal and parietal cortices, with frames rated as "highly suspenseful" predicting stronger activity in this network (Fig. 3D). This result confirmed further that activity in these frontal and parietal regions was driven by the common experience of the movie's executive load, as indexed by a second independent behavioral measure acquired in a separate group of healthy participants (Fig. S2).

Decoding Conscious Experiences in Behaviorally Nonresponsive Patients. The results of the previous three experiments in healthy participants suggested that synchronized activity fluctuations in the frontal and parietal regions tracked the common cognitive experience of different individuals while watching the same movie. In a final study, we asked whether these common patterns of brain activity in healthy individuals could be used to examine and quantify the movie-watching experiences of two entirely behaviorally nonresponsive, severely brain-injured patients with unknown levels of consciousness. In either case, the clinical diagnosis fluctuated at different time points since their injury between vegetative state (34) and minimally conscious state (35). A clinical diagnosis of vegetative state is made after repeated behavioral examinations have yielded no evidence of sustained, reproducible, purposeful or voluntary behavioral response to visual, auditory, tactile, or noxious stimuli (34). A clinical diagnosis of minimally conscious state describes a patient who shows inconsistent, but reproducible evidence of (minimal) awareness (35), ranging from basic (e.g., visual pursuit) to more complex behavioral responses (e.g., command following or communication). Although in isolated occasions since their injury, either patient demonstrated visual pursuit, neither exhibited any higher-order signs of awareness or any form of communication.

Fig. 2. Cross-subject synchronization of neural activity within different functional brain networks. (A) Time courses of group-level ICA components (ICs) clustered into five groups; they were correlated within groups and anticorrelated/less correlated across them (A, 1–5). (*B–F*) Individual ICs clustered into five spatially distinct brain networks (Fig. S1). (G) Individual time courses of independent components (IC) explaining the most variance within the frontoparietal network. (*H*) The single-subject time courses of IC explaining the most variance within each network were significantly synchronized across individuals. (*I*) No synchronization was observed between single-subject ICs of the resting state data, as, for example, shown by the auditory IC explaining the most variance overall in the resting state dataset. S1–12, Subject 1–12.

Previous neuroimaging studies have established that brain function can serve as a proxy for overt behavior in patients who are aware, yet unable to produce any overt physical responses (2-8, 36). To date, these studies have relied on a response according to instruction, albeit a *brain response*, to establish that a significant minority of patients $(\sim 19\%)$ (6, 7) can follow commands and, in some cases, communicate with the outside world (2, 3, 7). However, even for this unique group of patients who are able to follow commands with their brain activity (2–8, 36), it is not yet known how they perceive the world around them and whether their conscious experiences are comparable to those of healthy individuals. By contrast, the present study probed the naturalistic movie-watching experience in the absence of any



Fig. 3. Decoding shared executive engagement in healthy participants. (*A*) Performance on the SART (30) during simultaneous movie viewing. The probability density function, to the *Right*, shows that SART responses followed the canonical pattern (30); i.e., responses preceding the erroneous key press (where responding was automatic; pink) were significantly faster than those preceding the correct withhold (where executive processes were engaged; blue). (*B* and *D*) Overlay of the group-level frontoparietal IC (red) and the frontoparietal activity (P < 0.05; FWE cor.; green) predicted by SART performance (*B*) and frame ratings (*D*); overlap areas are displayed in yellow. (*c*, *Middle*) Group-averaged suspense ratings of movie stills. (*Top*, *a*-*f*) highest-rated and (*Bottom*, *g*-*l*) lowest-rated frames. Higher-rated frames predicted stronger activity within the frontoparietal network (*D*).



Fig. 4. Predicting sensory-driven and higher-order processes in individual participants. (A-C). Single-subject SPM analyses probe individual participants' responses. The processing of the movie's auditory (A), visual (B), and executive (C) information in each healthy participant was significantly (P < 0.05; FWE cor) predicted by the time course of the respective brain network in the leave-one-out group ICA. S1–S12, Subject 1–12.

structured instruction. We reasoned that if one of the patients engaged in executive processing while watching the movie, he would exhibit similar brain activity patterns in frontal and parietal regions to the healthy participants'. Conversely, we could use the healthy participants' frontoparietal activity as a benchmark for assessing the presence of executive function and, therefore, as an index of conscious experience, in the two clinically similar, behaviorally nonresponsive patients. The stereotypicity of brain activity underlying similar executive function across individual healthy participants enabled model-based predictions that could be applied to individual nonresponsive patients.

fMRI data were acquired from the two patients as they freely viewed the Alfred Hitchcock movie. Subsequently, the healthy data served as a model for probing whether each patient showed auditory, visual, and, crucially, executive processing of events in the movie. Probing of brain function in individual brain-injured patients critically depended on the single-subject-level reliability of brain responses in healthy participants. A prior set of leave-one-out analyses in healthy participants had shown that each participant's auditory, visual, and frontoparietal activity could be significantly (P < 0.05; FWE cor) predicted by the time course of the corresponding activity in the rest of the group (Fig. 4 A-C) (Supporting Information). Thus the same method could be used to test the similarity of each patient's functional activity to the healthy participants' by using the time course of the auditory/visual/frontoparietal network in the healthy group as a regressor in the SPM model of each patient's movie data (Supporting Information).

Activity in Patient 1's auditory cortex synchronized to that of the healthy group in this region (P < 0.05; FWE cor; Fig. 5A, Healthy Group vs. Patient 1), suggesting intact processing of the auditory information. No evidence of visual responses or executive function similar to the healthy participants' was observed (Fig. 5 B and C, Healthy Group vs. Patient 1). Previous studies have revealed basic auditory responses in a significant minority (23%) of patients (37) who were diagnosed as vegetative in the absence of any detectible higher-level cognitive function. Moreover, because similar responses have been observed in healthy participants whose cognition was abolished under anesthesia (38), these basic auditory responses are unlikely to indicate conscious processing of the auditory stimuli.

In stark contrast, activity in Patient 2's auditory and visual cortex synchronized to that of the healthy group in these regions (P < 0.05; FWE cor), suggesting intact processing of both auditory and visual information in the movie; most importantly, activity in a network of frontal and parietal regions that are known to support executive processing (9, 12, 15–17) significantly synchronized to that of healthy participants (P < 0.05; FWE cor) (Fig. 5 *A*–*C*, Healthy Group vs. Patient 2). To further test

whether the frontal and parietal activity observed in Patient 2 truly reflected executive processes related to specific events in the movie, we assessed the extent to which it was explained by the quantitative and qualitative measures of the movie's executive load. Both of these measures, derived in healthy participants, significantly (P < 0.05; FWE cor) predicted the patient's activity in the same frontal and parietal regions, revealing analogous networks with bilateral spatial distributions, similar to the frontoparietal distribution of the quantitative and qualitative networks in the healthy participants (Fig. 5 *B* and *C*, Healthy Group vs. Patient 2).

Discussion

In a series of studies, we tested whether a common neural basis can account for how different individuals form similar conscious experiences, in particular those invoking executive processes. We found that when participants attended to naturalistic stimuli evolving meaningfully over time, akin to real-world events-such as those present in a plot-driven movie-they displayed highly synchronized brain activity in supramodal frontal and parietal regions, which support executive function (9, 12, 15-17). The movie's executive demands, assessed quantitatively with a dualtask procedure (30-33), predicted activity in these frontal and parietal regions. Importantly, individual participants had a similar qualitative experience of the movie's executive demands, which also predicted activity in these regions. Together, these results suggested that the movie's executive demands drove brain activity in frontal and parietal regions and, further, that the synchronization of this activity across individuals underpinned their similar experience. By extension, the degree to which each individual's frontoparietal brain activity could be predicted from the rest of the group's represented a reliable neural index of how similar his/her cognitive experience was to the others'. Thus for the first time to our knowledge, these results demonstrate that similar conscious experiences in different individuals are supported by a common neural code, which can be used to interpret these experiences without recourse to self-report. This neural code does not read off the precise details of a person's thoughts. Rather, it can reveal whether two individuals have a highly similar cognitive experience when exposed to the same information (e.g.,



Fig. 5. Decoding executive function in one behaviorally nonresponsive patient. Healthy group: (A) Group-level auditory (purple) and visual (blue) ICs. (*B* and *C*) The healthy group's activity predicted by the quantitative (*B*)/qualitative (C) executive measure (green) is overlaid on the group frontoparietal IC (red); overlap areas are displayed in yellow. Patient 1: (A) The healthy group's auditory IC predicted significant activity in Patient 1's auditory cortex (purple). (*B* and *C*) No evidence of visual responses or executive processing similar to the healthy participants' was observed. Patient 2: (A) The healthy group's auditory and visual ICs predicted significant activity in Patient 2's auditory (purple) and visual (blue) cortex, respectively. (*B* and *C*) The quantitative (*B*) and qualitative (*C*) executive measures predicted activity (green) in the Patient's frontal and parietal regions. Overlap with activity predicted by the healthy group's frontoparietal IC (red) is displayed in yellow.

a movie). Differently to previous methods (39, 40) that use behavioral states to determine how brain activity underlies conscious states in healthy individuals, this approach interprets brain activity and concomitant mental states without recourse to behavior. Thus it is uniquely suited to investigating conscious experience in individuals whose status as conscious agents is uncertain and cannot be tested through behavior or introspective report, as in the case of behaviorally nonresponsive patients.

Critically, this approach can be used to examine whether severely brain-injured patients, who may be conscious but are unable to speak, move, or exhibit any other willful behavior (2-8), maintain conscious experiences similar to those of healthy individuals. We found that one patient who had remained behaviorally nonresponsive for a 16-y period before scanning demonstrated a highly similar brain response to that of the three independent groups of healthy participants. The patient's brain activity in frontal and parietal regions was tightly synchronized with the healthy participants' over time, and, crucially, it reflected the executive demands of specific events in the movie, as measured both qualitatively and quantitatively in healthy individuals. This suggested that the patient had a conscious cognitive experience highly similar to that of each and every healthy participant, while watching the same movie. These neuroimaging results were striking in light of the patient's behavioral profile observed in repeated assessments at his bedside over the 16-y period. During that time the patient showed neither movement to command nor any behavioral signs of functional or nonfunctional communication. He displayed no signs of localization of sound and no visual recognition or interaction with objects or people in his environment, including his family members. In isolated instances since the injury, the patient displayed visual pursuit and, on that basis, was clinically diagnosed as minimally conscious on those occasions. However, the enduring absence of any signs of intermediate or complex auditory, visual, motor, verbal, or communication behavior rendered any "minimal" conscious experiences the patient might have had entirely uninterpretable. By the same token, it was impossible to determine, based on the patient's behavior, whether, or how, he perceived the world around him.

By contrast, this fMRI approach provided strong evidence that the patient could continuously engage in complex thoughts about real-world events unfolding over time and thus that he was consciously aware. Importantly, this was consistent with the patient's positive outcome in an independent, command-following task, the results of which were unknown at the time of the movie experiment. This task was performed on the same scanning visit and reported in a previously published study (2). During the command-following task (41), the patient was asked to pay attention to or ignore specific words, according to study instructions. Indeed, the patient demonstrated that he was able to follow commands by modulating his brain activity to selectively pay attention to some external events (i.e., words) and ignore others over the duration of the task. Furthermore, in the same scanning visit the patient was able to use this method to communicate factually correct answers to two binary (yes/no) questions (see Patient 2, ref. 2).

However, it was impossible to determine, based on the results of the command-following task and the patient's behavioral assessments, whether he maintained conscious experiences comparable to those of healthy individuals in response to real-world events in his environment. By contrast, the patient's brain response to the movie suggested that his conscious experience was highly similar to that of each and every healthy participant, including his moment-to-moment perception of the movie content, as well as his executive engagement with its plot. These processes are likely to include updating the contents of working memory (e.g., to follow the plot), relating events in the movie to past experiences (e.g., to appreciate that a gun is a dangerous weapon), and coding the foreshadowing cues (i.e., events that might have future relevance to the plot) characteristic of movies of this type. Thus, the patient's brain response suggested that he could maintain much more complex mental processes than could ever be inferred based on his behavior or even based on his binary brain response to the fMRI command-following task.

Despite a highly similar clinical and behavioral profile, we found no fMRI evidence of executive processing and, therefore, conscious awareness, in Patient 1. The brain activity differences between the two patients cannot be attributed to differences in arousal, as both maintained the same state of wakefulness throughout the study (Supporting Information). Negative findings in nonresponsive patients must be interpreted with caution and cannot be used as conclusive evidence for lack of awareness, because false negative findings in functional neuroimaging studies may sometime occur even in healthy volunteers. Nevertheless, the aforementioned index of executive processing did reveal significant and similar changes in the frontoparietal network in each and every healthy participant who watched the movie, suggesting that its neural signature is reliably present in all adult and conscious humans. The lack of evidence for any responses in the executive frontoparietal network in Patient 1 was consistent with the lack of evidence for visual processing, a critical function for watching a movie. Moreover, Patient 1's negative outcome in the movie experiment was consistent with his negative outcome in the aforementioned fMRI command-following task, which he performed on the same scanning visit.

To date, neuroimaging studies that have probed consciousness in behaviorally nonresponsive patients have tested whether any given patient could follow commands, and therefore demonstrate conscious awareness, via his/her brain activity (2-8 and 42-44; see 45 for a different approach). However, the requirement that a patient must be able to produce brain responses as prescribed by study instructions to demonstrate that he/she is aware is likely too stringent for many patients who are aware but, due to the effects of brain injury, fail to comply with structured instructions (35, 46, 47). Up to 43% of patients, who on the basis of routine bedside assessment are declared to be in a vegetative state (34), show inconsistent but reproducible behavioral signs of awareness to more careful/intensive bedside assessments (48) and are reclassified as being in a minimally conscious state (35). The discrepancy between the high proportion of nonresponsive patients who are routinely misdiagnosed through bedside assessments (48) and those who are able to demonstrate willful brain-based responses (17-19%) (6, 7) suggests that existing neuroimaging techniques lack the sensitivity to detect conscious awareness in a subset of patients.

We propose a novel approach that is unconstrained by any task commands but, rather, captures attention naturally and therefore might be more effective for detecting conscious awareness. This approach can determine not only whether any given patient is conscious but also infer what the contents of that conscious experience might actually be, thus revealing important practical and ethical implications for the patient's standard of care and quality of life.

Methods

Participants. Ethical approval was obtained from the Health Sciences Research Ethics Board and the Psychology Research Ethics Board of Western University. All healthy volunteers were right-handed and native English speakers and had no history of neurological disorders. They signed informed consent before participating and were remunerated for their time. The respective surrogate decision makers gave informed written consent for each patient's participation. Twenty-four (19–31 y; 12 males), 27 (19–30 y; 13 males), and 15 (19–29 y; 5 males) healthy volunteers participated in experiment 1, 2, and 3, respectively. Two nonresponsive patients (20, 34 y; 1 male) participated in experiment 4.

Procedure and Design. An edited sequence of the black and white TV episode, "Alfred Hitchcock Presents—Bang! You're Dead" and its (visually and auditorily) scrambled version were presented in the intact and scrambled movie conditions, respectively (experiment 1). Participants were asked to simply watch each and follow it as best they could (*Supporting Information*). The SART stimuli consisted of a pseudorandomized sequence of spoken numbers (one-nine), each repeated 45 times (stimulus-onset asynchrony = 1.5 s) superimposed on the movie soundtrack, throughout its duration (experiment 2) (*Supporting Information*). Participants rated 239 consecutive stills created from the movie—one per 2 s of film—on an eight-point scale ranging from least to most suspenseful (experiment 3). Two nonresponsive patients (for clinical histories, see *Supporting Information*) were asked to simply watch the Hitchcock movie and follow it as best they could (experiment 4).

Data Acquisition and Analysis of fMRI Time Series. Functional images were acquired on a Siemens Tim Trio 3 Tesla MRI scanner. Model-based analyses, including standard preprocessing procedures, were performed with SPM8 (*Supporting Information*). Fixed-effect analyses were performed in each subject, corrected for temporal autocorrelation. The regressors were generated by convolving boxcar functions with the canonical hemodynamic response function. Also included in

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the general linear model were nuisance variables, comprising the movement parameters in the three directions of motion and three degrees of rotation, as well as the mean of each session. Linear contrasts were used to obtain subject-specific estimates for each effect of interest. Linear contrast coefficients for each participant were entered into the second-level random-effects analysis. The second-level effects of the intact and scrambled movie conditions were directly compared with a two-sample *t* test. Significant clusters/voxels survived the *P* < 0.05 threshold, corrected for multiple comparisons with the FWE.

Behavioral Analyses. SART performance was analyzed in 19/27 participants who paid adequate attention to the movie (>70% accuracy in the postmovie questionnaire). Only the reaction times of the participants who, in addition to attending to the movie, correctly performed the SART component of the dual task were included in the fMRI data analysis (*Supporting Information*).

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Supporting Information

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SI Methods

Patients' Narrative Clinical Histories. Patient 1 (female; 20 y old) suffered the onset of progressive encephalopathy of unknown etiology in April 2007. Subsequent MRI scans revealed generalized cerebral and cerebellar volume loss with hyperintensities over the frontal lobes and attenuation of the distal arterial branches. Progressive cognitive deterioration that culminated in complete loss of behavioral responsivity ensued. Since July 2009 the patient has received palliative care in the home setting. In five behavioral assessments conducted by the research team in the 3 mo before the functional magnetic resonance imaging (fMRI) testing the patient scored 4-8 (out of a maximum of 23) in the JFK Coma Recovery Scale (CRS-R) (1) and received a diagnosis of either vegetative state (VS) or minimally conscious state (MCS) when visual pursuit could be detected. When admitted for fMRI testing 68 mo postinjury, the patient scored 8/23 and received a diagnosis of MCS. (CRS-R subscores on the day of fMRI testing: auditory, 1-startle; visual, 3-visual pursuit; motor, 1-abnormal posturing; oromotor/verbal, 1-oral reflexive movement; communication, none; arousal:, 2-eye opening w/o stimulation.)

Patient 2 (male; 34 y old) suffered a cardiac arrest from being kicked in the chest in August 1997. The hypoxic event led to secondary hypoxic ischemic encephalopathy with multiple neurological deficits. After a 3-wk coma the patient received a diagnosis of VS and was discharged to a long-term care facility. In six behavioral assessments conducted by the research team in the 3 mo before the fMRI testing the patient scored 6–10 (out of a maximum of 23) in the CRS-R scale and received a diagnosis of either VS or MCS when visual pursuit could be detected. When admitted for fMRI testing 184 mo postinjury, the patient scored 9/23 and received a diagnosis of MCS. (CRS-R subscores on the day of fMRI testing: auditory, 1—startle; visual, 3—visual pursuit; motor, 2—flexion withdrawal; oromotor/verbal, 1—oral reflexive movement; communication, none; arousal, 2—eye opening w/o stimulation.)

Stimuli and Design. Experiment 1. The edited Hitchcock movie depicted a 5-y-old boy who finds his uncle's revolver, partially loads it with bullets, and plays with it at home and in public, unaware of its power and danger. It was chosen for its age/sex neutrality, wide-ranging appeal, and engaging plot. Moreover, a longer version of this movie has been found to elicit robust brain activity, synchronized across healthy participants. To keep the scanning session brief, the movie was shortened to 8 min by editing scenes while maintaining the primary storyline. The short movie was broken down into smaller (1 s) audiovisual segments in the iMovie software (www.apple.com/ca/support/mac-apps/ imovie/) to create the scrambled movie condition. The segments were arranged in pseudorandom order to avoid any movie narrative within nearby segments. Written feedback at the end of the scanning session confirmed that participants had not been able to uncover a storyline in the scrambled movie or relate it to stored knowledge of previous movies they had seen.

Experiment 2. The dual-task framework has been extensively used to investigate executive performance, as it recruits executive function for the allocation and coordination of attentional resources (2). This framework assumes that because executive function is a finite resource, in moments when the load on one executively demanding task (i.e., the movie) is greatest, the performance of a second executively demanding task will be impaired, yielding a direct, quantitative measure of the executive demands of the first task across time. The dual task in this study

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consisted of simultaneous performance of the Sustained Attention to Response Task (SART)-which measures sustained attention and quantifies executive function (3) - and movie viewing. SART was an optimal choice of an executively demanding task that could be performed while simultaneously watching the movie. SART operates on the principle that insufficient attention to a task can result in slips of action as automatic, unintended action sequences are triggered inappropriately. These automatic actions result in performance errors that can be detected in the SART reaction times. Specifically, in the SART, participants are required to respond with a button press to a series of randomly presented ("go") digits but withhold responses to one prespecified ("no go") digit. A signature of the SART is that a shortening of reaction times indicates a decrement in executive control or, conversely, an increment in response automaticity (3-5). In particular, a shortening of reaction time predicts an increased likelihood of a subsequent incorrect response to a "no go" digit and correlates with electrophysiological measures of waning attention (6).

At the end of the dual task, participants answered 14 multiplechoice questions by selecting one of four answer options. These assessed each participant's encoding of basic facts about the movie and therefore, indirectly, their overall attention to the movie throughout its duration, as they simultaneously performed the SART. These questions and the answer options were (1) What are the boys standing behind when they shoot their toy guns? (Answers: Tree/Bush/House/Fence); (2) What kind of hat is the boy wearing throughout the movie? (Answers: Baseball Cap/Private Hat/Cowboy Hat/Newsboy Hat); (3) What does the boy find in the uncle's luggage when he's unpacking? (Answers: Knife/Baseball/New hat/Real gun); (4) Which toy animal does the boy ride in front of the supermarket? (Answers: Cow/Elephant/Unicorn/Horse); (5) What does the supermarket clerk tell the boy to do? (Answers: Feed the meter/Get off/Find your parents/Be careful); (6) When the boy is on the ride, what does he drop on the ground? (Answers: Dimes/Bullet/Gun/Hat); (7) What does the girl's father give the boy to get him to get off the ride? (Answers: Lollipop/Money/Chocolate/Nothing); (8) What reason does the boy give for not getting off the ride? (Answers: He paid for it/It was his/He got there first/He wanted to play); (9) What is the maid's name? (Answers: Mary/Jackie/Cleo/Susan); (10) What breaks when the boy shoots the gun at the end? (Answers: Statue/Mirror/Mask/Picture Frame); (11) The father is holding the gun at the end of the movie; what is the uncle holding? (Answers: Mask/Glass of wine/His hat/The bullet); (12) What is the boy standing behind when he shoots the gun at the end? (Answers: Door frame/Kitchen table/Dinning room chair/ Couch); (13) What is the supermarket clerk pushing when the boy is on the ride? (Answers: Milk crates/Shopping carts/A floor display/Cart full of apples); (14) Who does the boy run toward at the end, after shooting the gun? (The maid/The father/The mother/The uncle).

Data Acquisition and Model-Driven Analysis of fMRI Time Series. *Healthy participants.* Participants lay supine in the scanner looking upward into a mirror box that allowed them to see a projection screen behind their head. Noise cancellation headphones (Sensimetrics, S14; www.sens.com) were used for sound delivery. Functional echo-planar images were acquired [33 slices, voxel size: $3 \times 3 \times 3$, interslice gap of 25%, repetition time = 2,000 ms, echo time (TE) = 30 ms, matrix size = 64×64 , flip angle (FA) = 75 degrees]. The movie, resting state, and scrambled movie scans had 246, 256, and 238 scans, respectively. An anatomical volume was

obtained using a T1-weighted 3D magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence (32 channel coil, voxel size: $1 \times 1 \times 1$ mm, TA = 5 min and 38 s, TE = 4.25 ms, matrix size = $240 \times 256 \times 192$, FA = 9 degrees). The imaging data were preprocessed and analyzed using statistical parametric mapping 8 (SPM8) (Wellcome Institute of Cognitive Neurology, www. fil.ion.ucl.ac.uk/spm/software/spm8/) and the automatic analysis pipeline software (www.cusacklab.org). The processing steps were correction for timing of slice acquisition, motion correction, normalization to a template brain, and smoothing. The data were smoothed with a Gaussian smoothing kernel of 10 mm FWHM (7). Spatial normalization was performed using SPM8's segmentand-normalize procedure, whereby the T1 structural was segmented into gray and white matter and normalized to a segmented Montreal Neurological Institute-152 template. These normalization parameters were then applied to all echo plannar images. The time series in each voxel was high-pass-filtered with a cutoff of 1/128 Hz to remove low-frequency noise and scaled to a grand mean of 100 across voxels and scans in each session. The preprocessed data were analyzed in SPM8 using the general linear model. Before analyses, the first five scans of each session were discarded to achieve T1 equilibrium and to allow participants to adjust to the noise of the scanner. Group-level correlational analyses explored, for each voxel, the cross-subject synchronization in brain activity by measuring the correlation of each subject's time course with the mean time course of all other subjects.

Brain-injured patients. Patient scanning was performed using the same 3 Tesla Siemens Tim Trio system, 32-channel head coil, and data acquisition parameters as for the healthy participants. Both patients maintained continuous spontaneous eye opening during the movie conditions, as monitored with an infrared camera placed inside the scanner. The same data preprocessing procedures as for healthy participants were applied to patient data.

Data-Driven Analyses of fMRI Time Series. Independent component analysis (ICA) is especially suited for exploring the neural dynamics from naturalistic stimulation, such as during movie viewing, where complex interactions between several stimulus factors modulate the brain activity (8), and it is not possible, without making a large number of assumptions, to create a model of the variables that drive the brain signal. As a datadriven method, ICA can reveal complex neural dynamics in the absence of a temporal model by dividing the fMRI signal into statistically independent components. Each component has a time course that describes its activity peaks and dips over the stimulus duration and a spatial distribution, which describes the brain regions that generate this activity time course. Thus, ICA can be used to reveal spatially or temporally independent parts of the fMRI signal that represent different sensory and cognitive processes within functional subsystems of the brain.

We performed Tensor ICA, a method that derives spatially orthogonal components, whose spatial and temporal features are similar across subjects. The Melodic software (http://fsl.fmrib.ox. ac.uk/fsl/fslwiki/MELODIC) was used to perform ICA with a 20-component cutoff (9). Initially, group-level analysis was performed to test whether the widespread cross-subject synchronization pattern observed during movie viewing could be separated into functionally specific spatiotemporal elements. The nonneuronal components-driven by artifacts such as movement, breathing, vascular pulsation, etc.-were identified based on their distribution in frequency (e.g., signal dominated by high frequencies) and space (e.g., signal originating outside the head) and removed. We observed 12 spatially independent neuronal components, whose time courses clustered into five groups; they were correlated within groups and anticorrelated/or less correlated between them, suggesting different functional roles. The spatial distribution revealed that the individual components clustered into five spatially distinct brain networks (Fig. S1).

Subsequently, single-subject ICAs were also performed to calculate the cross-subject correlation within each of these networks. The five networks were identified in each participant's individual ICA. The time course of the component explaining the most variance from each network was correlated with the time course of the homologous ICA component in corresponding leave-one-out ICA (i.e., of the group minus that individual). A highly significant cross-subject correlation was observed for each network: *auditory*, t(11) = 43.1; P < 0.00001; *visual*, t(11) = 11.9; P < 0.00001; *frontoparietal*, t(11) = 13.2; P < 0.00001; *motor*, t(11) = 4.5; P < 0.001; and *precuneus*, t(11) = 8; P < 0.00001.

Model-Based and Data-Driven Analyses of fMRI Time Series. Based on the stereotypical brain activity observed in healthy participants during movie viewing, a model of healthy brain function could be generated against which preserved brain function in individual patients could be tested. As robustness at the single-subject level is a determining criterion for any work with individual braininjured patients, initially, we tested whether activity in the rest of the group could predict that in each healthy participant. Singlesubject analyses were focused on the three main networks, the auditory, visual, and frontoparietal, which were functionally critical for higher-order cognition during movie viewing. For each of these networks, 12 leave-one-out Tensor ICA analyses were performed, where each participant was, in turn, left out of the ICA analysis. Thus, the time course of each network in the participant subgroups was identified. Each network's time course (derived from the ICA of the group minus one participant) was then used as a regressor in the SPM data model of the participant not included in the ICA analysis. Twelve such SPM analyses were performed for each network.

Similarity of Executive Networks Revealed by the Movie Analysis, Behavioral Testing, and Large-Scale Metaanalysis. Initially, we calculated the pairwise similarity of the frontoparietal network elicited by movie viewing and the frontoparietal networks reflecting performance of the executive tasks. Their patterns were found to be highly similar to one another [Fig. S2; r(48) = 0.31-0.44; both pairs P < 0.05]. Subsequently, to demonstrate that the frontoparietal network revealed by each of the three tasks (i.e., movie viewing, dual task, and suspense rating) mapped directly onto the "canonical" frontoparietal network that has been repeatedly implicated in executive function, we obtained an independent localization of the executive network by using Neurosynth, a platform for large-scale metaanalysis of fMRI data from published studies (http://neurosynth.org/). Pairwise comparison between this executive network and the frontoparietal activation patterns in each of the three tasks in our study revealed that all three were statistically similar to the canonical executive network [Fig. S2; r(48) = 0.49-0.59; all P < 0.49-0.590.001]. Together, these results supported the primary results reported in the manuscript and, similarly, suggested that the moviedriven frontoparietal activation and the frontoparietal networks revealed by the behavioral tasks did indeed reflect the executive processes engaged during movie viewing. Finally, the spatial variability of the frontoparietal network across individuals was quantified with a leave-one-out analysis, where each individual's activation pattern was compared with that of the rest of the group. Individual frontoparietal networks were found to be highly similar to one another [r(48) = 0.78-0.91; all P < 0.0001].

Comparison of Brain Activity in Patients and Healthy Participants. In the previous three experiments with healthy participants we generated a model of healthy brain function during movie viewing against which preserved brain function in individual patients could be tested. This novel approach for directly predicting any given patient's brain activity from the time course of brain activity in healthy participants initially relies on the temporal similarity of the activity patterns to identify homologous processes in the two groups. Subsequently, the spatial extent of regional activity in the two groups is compared to interpret their functional correspondence. Slight differences in localization are expected not only due to differences in any given patient's morphological organization (e.g., widespread atrophy, enlarged ventricles, etc.) compared with controls, but also due to the normal anatomical variation observed even among individual healthy participants.

SI Results

The SART operates on the principle that insufficient attention to a task can result in slips of action as automatic, unintended action sequences are triggered inappropriately. These automatic actions result in performance errors that are detectable in the SART reaction times. In particular, a shortening of SART reaction times indicates a decrement in executive control or, conversely, an increment in response automaticity. Moreover, a shortening reaction

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time predicts an increased likelihood of a subsequent incorrect response to a "no go" digit and correlates with electrophysiological measures of waning attention. Group-level analyses. Group-averaged (n = 19) SART performance followed the canonical pattern. Specifically, reaction times in trials immediately preceding an incorrect button-press response (i.e., to a "no go" trial) were significantly shorter than those immediately preceding correctly withheld responses [t(18) = 4.37; P < 0.0005], suggesting that errors were due to lapses of attention (failure to inhibit a response to a "no go" trial), which may be driven by the simultaneous movie viewing. Single-subject analyses. Four out of nineteen of the participants did not show a SART effect in reaction times, whereas 15/19 showed both a SART effect (P < 0.05) and over 70% accuracy (1/15 had >71% accuracy; 14/15 had >78% accuracy) in the postmovie questionnaire. The reaction times of those participants (15/27) who were deemed to have correctly performed both components of the dual task were included in the fMRI analysis.

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Fig. S1. Spatial clustering of independent components (IC) in healthy participants. The spatial distribution of the individual ICs revealed clustering into five spatially distinct functional brain networks, color-coded according to the respective grouping in the correlation matrix (Fig. 2): (1) auditory, (2) frontoparietal, (3) visual, (4) motor, and (5) precuneus. From left to right: each network is displayed on the lateral cortical surface bilaterally and on nine horizontal (ventral to dorsal) slices.



Region Fig. S2. Executive networks revealed by the movie analysis, behavioral testing, and large-scale metaanalysis. From Top to Bottom, the frontoparietal activation patterns are shown for the independent component of the movie fMRI data, the correlation with the dual-task performance, the correlation with the suspense ratings, and the executive network defined by the Neurosynth metaanalysis. Each bar represents the normalized regional activation in one of 48 regions, providing complete cover of the frontal (red) and parietal (blue) lobes (Harvard–Oxford atlas, http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Atlases). A similar subset of regions within the frontal and parietal lobes are activated by each different task: movie viewing, dual task, and suspense rating. Pairwise similarity comparisons between frontoparietal networks activated by the different tasks were calculated as the correlation between each pair of activation patterns. The frontoparietal activation patterns revealed by the dual task and the suspense ratings were significantly similar to that observed in the ICA of the movie data. Moreover, the frontoparietal activation patterns from the three tasks were statistically similar to the canonical executive network (Neurosynth). Significance values are shown to the Right: *, P < 0.05; **, P < 0.01. The numbers from left to right on the x axis label the 48 regions: 1. Left Frontal Pole; 2. Right Frontal Pole: 3. Left Insular Cortex: 4. Right Insular Cortex: 5. Left Superior Frontal Gyrus: 6. Right Superior Frontal Gyrus: 7. Left Middle Frontal Gyrus: 8. Middle Frontal Gyrus; 9. Left Inferior Frontal Gyrus, pars triangularis; 10. Right Inferior Frontal Gyrus, pars triangularis; 11. Left Inferior Frontal Gyrus, pars opercularis; 12. Right Inferior Frontal Gyrus, pars opercularis; 13. Left Precentral Gyrus; 14. Right Precentral Gyrus; 15. Left Frontal Medial Cortex; 16. Right Frontal Medial Cortex; 17. Left Juxtapositional Lobule Cortex (formerly Supplementary Motor Cortex); 18. Right Juxtapositional Lobule Cortex (formerly Supplementary Motor Cortex); 19. Left Subcallosal Cortex; 20. Right Subcallosal Cortex; 21. Left Paracingulate Gyrus; 22. Paracingulate Gyrus; 23. Left Cingulate Gyrus, anterior division; 24. Right Cingulate Gyrus, anterior division; 25. Left Cingulate Gyrus, posterior division; 26. Right Cingulate Gyrus, posterior division; 27. Left Frontal Orbital Cortex; 28. Frontal Orbital Cortex; 29. Left Frontal Operculum Cortex; 30. Right Frontal Operculum Cortex; 31. Left Central Opercular Cortex; 32. Right Central Opercular Cortex; 33. Left Postcentral Gyrus; 34. Right Postcentral Gyrus; 35. Left Superior Parietal Lobule; 36. Right Superior Parietal Lobule; 37. Supramarginal Gyrus, anterior division; 38. Right Supramarginal Gyrus, anterior division; 39. Left Supramarginal Gyrus, posterior division; 40. Right Supramarginal Gyrus, posterior division; 41. Left Angular Gyrus; 42. Right Angular Gyrus; 43. Left Precuneous Cortex; 44. Right Precuneous Cortex; 45. Left Cuneal

Cortex; 46. Right Cuneal Cortex; 47. Left Parietal Operculum Cortex; 48. Right Parietal Operculum Cortex.