Functional split brain in a driving/listening paradigm

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We often engage in two concurrent but unrelated activities, such as driving on a quiet road while listening to the radio. When we do so, does our brain split into functionally distinct entities? To address this question, we imaged brain activity with fMRI in experienced drivers engaged in a driving simulator while listening either to global positioning system instructions (integrated task) or to a radio show (split task). We found that, compared with the integrated task, the split task was characterized by reduced multivariate functional connectivity between the driving and listening networks. Furthermore, the integrated information content of the two networks, predicting their joint dynamics above and beyond their independent dynamics, was high in the integrated task and zero in the split task. Finally, individual subjects' ability to switch between high and low information integration predicted their driving performance across integrated and split tasks. This study raises the possibility that under certain conditions of daily life, a single brain may support two independent functional streams, a "functional split brain" similar to what is observed in patients with an anatomical split.

information integration | consciousness | split brain | dual task | fMRI

A remarkable finding in neuroscience is that after the two cerebral hemispheres are disconnected to reduce epileptic seizures through the surgical sectioning of around 200 million connections, patients continue to behave in a largely normal manner (1). Just as remarkably, subsequent experiments have shown that after the split-brain operation, two separate streams of consciousness coexist within a single brain, one per hemisphere (2, 3). For example, in many such studies, each hemisphere can successfully perform various cognitive tasks, including binary decisions (4) or visual attentional search (5), independent of the other, as well as report on what it experiences. Intriguingly, anatomical split brains can even perform better than controls in some dual-task conditions (6, 7). On the other hand, the integration of information between the two hemispheres breaks down (4), such that one hemisphere is not conscious of what the other one is perceiving and thinking (8). Recent studies have provided neurophysiological evidence consistent with the anatomical disconnection, such as a decrease in fMRI functional connectivity between the left and right hemispheres in human patients with a split brain and in animals that underwent surgical callosotomy (9–11).

In the present study, we asked whether it is possible to obtain a functional split, rather than an anatomical one, in the healthy human brain. During most situations of daily life, our brain functions as a unitary system, which is usually a good thing. Consider listening to global positioning system (GPS) instructions when driving in a foreign city: To arrive at the right destination, the auditory instructions should be heard by the same system that sees the visual input and decides on the course of action. Even so, most of us are familiar with some situations in which we seem to undergo a functional split. Consider driving on a quiet road while listening to an engaging radio show: At times, it is as if two separate functional streams were coexisting within the same brain, one doing the driving and one doing the listening. We usually identify with the listener, because we usually attend to the story we hear, reflect on it, and commit it to memory. By contrast, driving seems to proceed as on autopilot, with no need for attention, reflection, or memory as long as the road is smooth and unchallenging. What happens within our brain during these two conditions? Do the interactions between brain networks involved in driving and listening change when we are performing an integrated task, such as following GPS instructions, compared with a split task, such as driving and listening to a radio show? Can we find evidence for functional integration in the case of GPS instructions and for a functional split in the case of the radio show? Finally, can we determine if integrated information between the driving and listening networks is helpful in the GPS task but perhaps harmful when the driving and listening tasks are completely independent, as with the radio show?

To find out, we asked highly trained healthy subjects to perform simulated driving in an fMRI scanner while listening to either GPS instructions or a radio show. We chose driving and listening because of their frequent dissociation during daily life, and because the networks underlying driving and listening performance are known to be partially segregated in the human brain (12). We carefully ensured that task performance and overall levels of brain activation would be comparable in the integrated and split driving tasks. Finally, we developed multivariate measures of functional connectivity and integrated information to evaluate the interactions between driving and listening networks during the integrated and split task conditions.

Results

Behavior. We imaged brain activity in 13 experienced drivers in a driving simulator (Fig. 1). Subjects underwent an fMRI session and were instructed to drive following GPS instructions (integrated task) or while listening to a radio show (split task). The task difficulty, arousal level, and driving performance (measured as the mean deviation from the track centerline subtracted from the theoretical upper bound) did not significantly differ between the integrated and split tasks (Fig. 2 *A–C*; task difficulty: $t = 0.64$, $P = 0.54$; drowsiness: $t = 0.69$, $P = 0.50$; driving performance: $t = 0.80$, $P = 0.44$). Furthermore, there was no significant difference

Significance

When one drives on an easy route and listens to a radio, it is at times as if one's brain splits into two separate entities: one that drives and one that listens. When, instead, one drives while listening to a global positioning system, there is only one functional stream. Here, using measures of information integration, we show that a brain may functionally split into two separate "driving" and "listening" systems when the listening task is unrelated to concurrent driving, but not when the two systems are related. This finding raises the possibility that under certain conditions of daily life, a single brain may support two independent functional streams, a "functional split brain" similar to what is observed in patients with an anatomical split.

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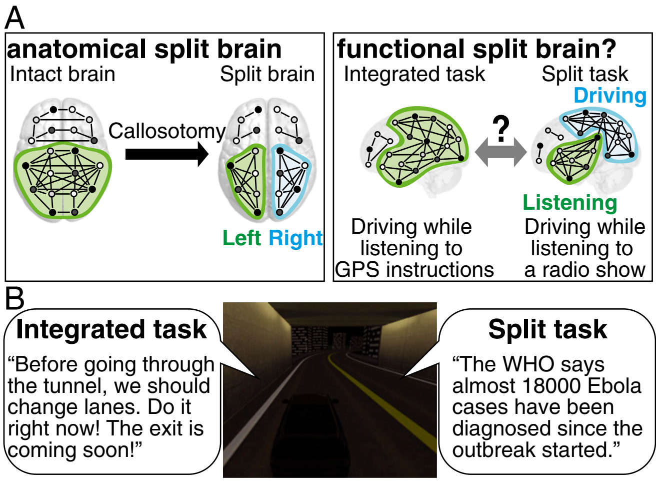

Fig. 1. (*A*) Research question. In patients with an anatomically split brain, callosotomy induces a breakdown of integrated information between the two hemispheres and the creation of two distinct functional entities. During daily life, our brain functions as a unitary system during most tasks, such as when driving while listening to GPS instructions (integrated task). Here, we asked whether it is possible to obtain a functional split, rather than an anatomical one, in the healthy human brain during an incongruent task, such as driving while listening to a radio show (split task). (*B*) Example of a driving simulator scene and of auditory instructions received during the integrated and split tasks.

in listening comprehension scores between sessions where subjects were just listening to the radio or listening while driving (Fig. 2*D*; $t = 0.77$, $P = 0.46$). Nonparametric permutation results are reported in Table S1.

Selection of Networks of Interest. Fig. 3*A* shows the block design paradigms used to identify the driving and listening networks. The “driving network” was defined as the set of areas showing significant activation during at least one block design involving driving. The “listening network” was selected as the set of areas showing significant activation during at least one block design involving listening to either the GPS or the radio show. A small number of voxels overlapping between the two networks were discarded from further analyses (Table S2). The driving and listening networks showed similar activation levels in the integrated and split tasks during block design conditions (Fig. 3*B*; driving network: $t = -1.49$, $P = 0.17$; listening network: $t = -0.25$, $P = 0.81$; combination: $t = -1.06$, $P = 0.31$; also Table S1).

Multivariate Integration. To assess neural interactions during the integrated driving/listening task compared with the split version, we designed a measure of between-network multivariate state shifts. The rationale behind this measure is that when networks cooperate during the integrated task, multivariate changes in activity in one network should be accompanied by corresponding multivariate changes in activity in the other one, irrespective of univariate changes. For example, in the congruent driving task, a new auditory instruction given by the GPS (e.g., turn left now) will likely trigger a new activity pattern in the listening network. In turn, the new instruction will lead to new motor commands and associated visual inputs, which will likely trigger a new activity pattern in the driving network. Over multiple instructions, the multivariate changes in activity patterns over the two networks should be correlated. Univariate correlations between the two networks, triggered, for example, by particular frequencies in the auditory instructions and by particular colors in the visual input, are less likely to be correlated and less sensitive to low-amplitude but spatially coherent changes. Nevertheless, both multivariate and univariate correlations should be lower during the split task.

As a measure of multivariate integration, we measured the similarity of changes in multivariate blood oxygen level-dependent patterns across time within the driving and the listening networks and compared it between the integrated and split tasks (Fig. 4*A*). As predicted, the between-networks state-shift similarity was significantly higher during the integrated task compared with the split task ($t = 3.63$, $P = 0.002$; Fig. 4*B* and also Table S1). Multivariate integration changes between the driving and listening networks were consistent across frontal, parietal, and occipital areas (Fig. S1). Fig. 4*C* shows that the ratio of average between-network versus within-network univariate correlation was also higher in the integrated task compared with the split task ($t = 3.35$, $P = 0.0033$). Increased integration between conditions could not be explained either by changes in physical stimuli correlation (Fig. S2) or by changes in mean signal amplitude or movement (Table S3).

Integrated Information. Although high functional connectivity between two networks is consistent with the occurrence of cooperative interactions, it could also be the result of common input from shared sources. To evaluate the cooperative interactions between the two networks explicitly, we developed a measure of integrated information based on the improvement of multivariate prediction by the whole network over its parts. Specifically, we used a multivariate least absolute shrinkage and selection operator (LASSO) algorithm (13) to predict the future states (after one to 10 scan time lags) of the driving and listening networks when taken together and when taken separately (Fig. 5*A*). Integrated information was defined as the improvement in multivariate prediction when using the whole-system activity patterns to predict itself, compared with the prediction accuracy obtained using driving and listening networks separately predicting themselves. In contrast to correlation-based measures, high values of integrated information require both high integration and high differentiation of neural activity patterns. For example, if the information shared between the networks were to reflect common input, it would be redundant; hence, it would not add to prediction accuracy. Following this rationale, we hypothesized that integrated information would be higher in the integrated task compared with the split task. As shown in Fig. 5*B*, the mean integrated information over time lags was significantly greater than zero in the integrated task ($t = 3.44$, $P = 0.0028$), but not in the split task ($t = -0.027$, $P = 0.51$). Integrated information was also significantly higher in the integrated task compared with the split task ($t = 2.75$, $P = 0.0094$). Table 1 shows that this result remained true when considering each individual time lag. Average functional connectivity values were 0.391 ($t = 9.13$, $P < 0.001$) in the integrated task and 0.294 ($t = 7.43$, $P < 0.001$) in the split task (Fig. 5*C*). Mean functional connectivity was

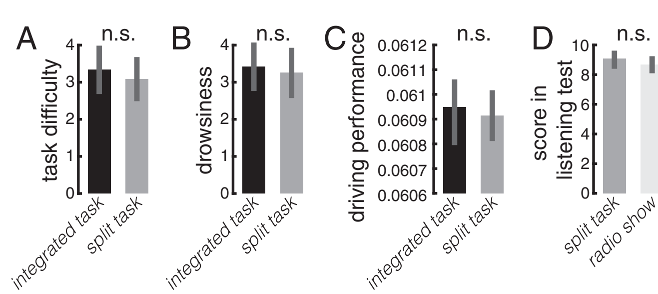

Fig. 2. Behavioral results. Group average of subjective ratings of task difficulty (*A*) and drowsiness (*B*) during the integrated and split tasks. Ratings ranged from 1 (minimum) to 10 (maximum). (*C*) Group average of the driving performance in the integrated and split task conditions. The driving performance was defined as the deviation from the centerline of the track. (*D*) Group average of scores in listening comprehension tests (out of 10 items). No significant difference (n.s.) was found in any of the behavioral measures between the integrated and split task conditions.

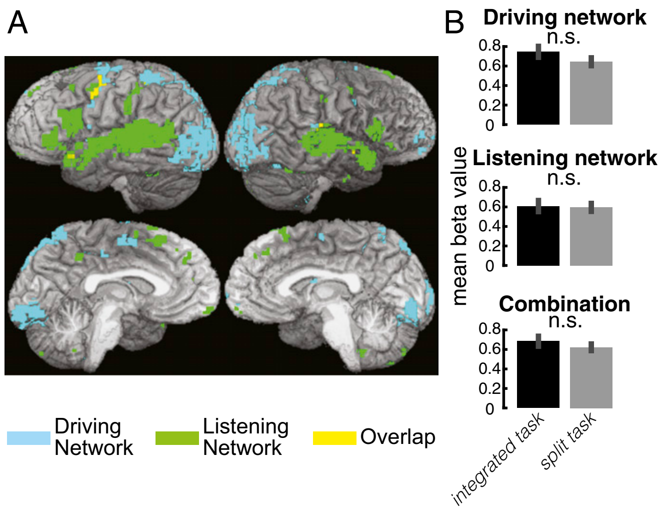

Fig. 3. Networks of interest. (*A*) Voxels included in the driving network (blue) and listening network (green) in a representative subject. Overlapping voxels (in yellow) were discarded from further analysis. (*B*) Mean task-related activity (beta values) of voxels within each network and their combination in the integrated and split task conditions. There was no significant difference between the integrated and split tasks.

significantly higher in the integrated task compared with the split task (t = 2.50, P = 0.015; also Table S1). Interestingly, integrated information was greater than zero during resting state scans and in all single task scans; only in the split condition did it decrease to a zero mean (Fig. S3 and *SI Discussion*). Fig. S3 reports increased multivariate integration, integrated information, and average functional connectivity values during resting state tasks and single tasks compared with the split task condition.

Multivariate integration and integrated information measures remained virtually unchanged after removing time periods containing spatial attention instructions unrelated to driving (Fig. S4 and *SI Discussion*). Moreover, excluding occipital time series from the analysis did not modify the results (Fig. S5).

Integrated Information and Behavior. We further hypothesized that integrated information would be predictive of driving performance. As shown in Fig. 6*A*, integrated information was positively correlated with performance in the integrated task (r = 0.65, P = 0.032). This result suggests that in the integrated condition, when auditory information is used to navigate the road, cooperative interactions between the two networks can help performance. Conversely, we found trend toward a negative correlation between integrated information and performance during the split task (Fig. 6*B*; r = –0.4, P = 0.22), suggesting that interactions between the two networks might hinder, rather than improve, performance in this case.

Finally, we hypothesized that the subjects who would be best able to switch between high integrated information between the driving and listening networks during the integrated task and low integrated information during the split task would be best at maintaining a consistently high performance across tasks. As shown in Fig. 6*C*, a within-subjects analysis shows that a high differential in integrated information between the integrated and split tasks predicted high sustained performance in both tasks (significant correlation of r = 0.8 with P = 0.0031). These results held true after controlling for individual average frame-wise displacement (14, 15) (Table S4). Measures of functional connectivity or network activity did not show such a correlation with performance (Fig. S6).

Discussion

We developed a driving while listening paradigm aimed at inducing a functional split-brain condition in healthy human subjects. We assessed multivariate functional connectivity and integrated information between brain networks involved in driving and listening during an integrated task, when subjects drove following GPS instructions, and during a split task, when they drove while listening to a radio show. We found that the integration between the two networks, assessed through a multivariate measure of functional connectivity based on coordinated shifts of multivoxel patterns across time, was higher in the integrated task compared with the split task. Furthermore, the integration of information between the two networks, assessed by the improvement in prediction accuracy of the joint dynamics of the two networks over their independent dynamics, was high in the integrated task and zero in the split task. Finally, subjects who were better at switching between high and low integrated information depending on the task had a better overall driving performance.

Because our aim was to characterize changes in between-network interactions, we ensured that behavioral performance and brain activation did not differ between the integrated and split tasks by choosing relatively easy tasks; long, continuous performance reproducing daily life situations; and highly trained subjects (*SI Discussion*). We did not ceil the performance or use any other way to equate the driving performance artificially between tasks. Under different conditions, fMRI studies have

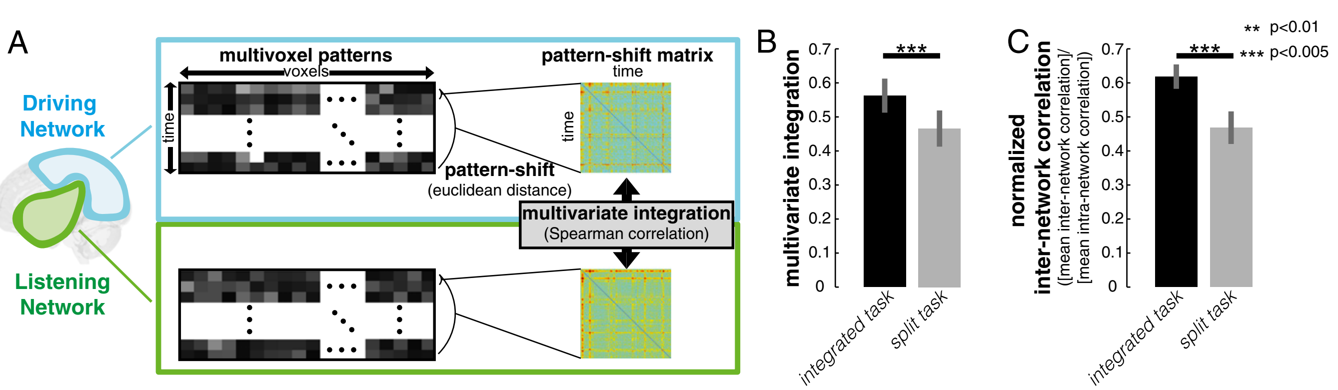

Fig. 4. Multivariate integration. (*A*) Dissimilarity of multivoxel patterns across time points was calculated to obtain a pattern-shift matrix for each network. The similarity of the two pattern-shift matrices of the driving and listening networks provided a measure of between-network multivariate integration. (*B*) Multivariate integration was significantly higher in the integrated task than in the split task. (*C*) Mean pairwise correlation between networks normalized by within-network correlation (internetwork over intranetwork mean correlation, or normalized internetwork correlation) was also significantly higher in the integrated task than in the split task.

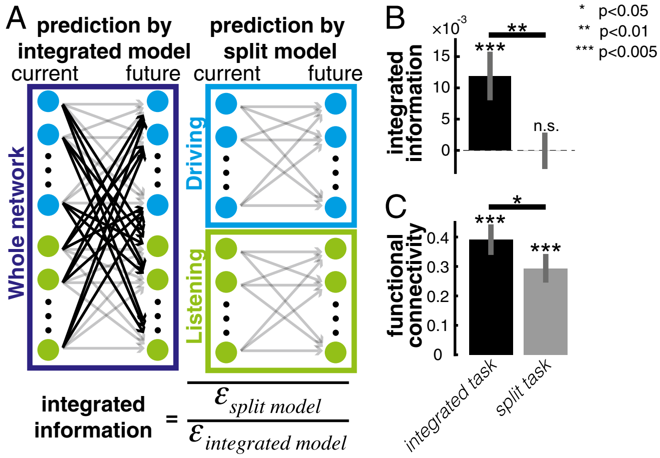

Fig. 5. Integrated information. (*A*) Index of integrated information was obtained by comparing how current activity patterns (filled circles) from the whole system can predict future states better than using the driving and listening networks separately predicting themselves. Note that the comparison between the split and integrated models was performed for both the integrated and split tasks to compute integrated information. (*B*) Integrated information values for the integrated task and the split task. The group mean integrated information was significantly higher than zero in the integrated task, but not in the split task (n.s.). Integrated information was also significantly higher in the integrated task compared with the split task. (*C*) Average functional connectivity values in the integrated versus split task conditions.

revealed changes in brain activation, such as reduced activity in driving networks when driving while performing a sentence comprehension task (16, 17). Similarly, under more challenging conditions, driving while listening to someone speak can induce a decrease in driving accuracy (16), reminiscent of the decrease in performance in cross-modal tasks when stimuli are incongruent (18). Such an effect of congruency on task performance has also been found during working memory and Stroop tasks (19).

To compare neural interactions during the integrated driving/listening task compared with the split version, we designed a measure that would be sensitive to correlated multivariate state shifts between the two networks. Previous studies used correlations in whole-brain multivariate activity patterns to identify temporally clustered brain states, such as the presence of microstates in the EEG (20) or task-positive/negative states in whole-brain fMRI (21, 22). The method used here differs from previous attempts by measuring correlated changes in network multivariate patterns (MVPs) over time (pattern shifts) to quantify between-network functional integration. As predicted, the multivariate correlation between activity patterns in the two networks was higher in the integrated task compared with the split task. This result held true when frontal, parietal, and occipital anatomical subdivisions of the driving network were considered separately. Between-network univariate correlations were also higher in the integrated task than in the split task, suggesting that task-dependent integration is robust. In line with these results, previous studies using univariate measures have shown, for example, that the functional connectivity between default and attention networks increases in a memory recollection task (23) or during creative thinking (24) compared with an external attention task. Altogether, the finding of decreased functional connectivity between driving and listening networks in our split task is consistent with the decreased functional connectivity between the two hemispheres observed in human patients with a split brain (9), as well as in monkeys and rats after surgical callosotomy (10, 11).

We further determined that in the integrated task, the driving and listening networks were "informationally integrated"; that is, the whole system predicted its future states better than its parts separately. By contrast, during the split task, the driving and listening networks were "informationally split"; the whole system did not predict itself better than the sum of its parts. For both the integrated and split tasks, integrated information was defined as the ratio between the prediction error obtained with the driving or listening subsystem separately predicting itself over the prediction error obtained with both the driving and listening systems jointly predicting themselves. The same number of time course features was used in the prediction algorithm for both the integrated and split task conditions (Figs. S7 and S8 and *SI Discussion*). In essence, integrated information captures how much better the system, as a whole, can predict itself compared with the sum of its parts. Unlike measures of correlation and integration, measures of integrated information are insensitive to common input and are, instead, sensitive to the information value of neural activity patterns in predicting their own time course. Differences between integrated information and informational connectivity measures (25, 26) are discussed in *SI Discussion*.

In the split task condition, average functional connectivity values were decreased to the range observed in anatomical split brains (0.3 correlation mean) (9). Ultimately, however, integrated information was the only measure that both revealed a functional split between networks in the split condition and correlated with behavior. We found that highly integrated information predicted an optimal performance during the integrated task. Moreover, the ability of individual subjects to reorganize between high and low information integration states across tasks was correlated with the individual subject's ability to maintain a consistently high driving performance. In contrast, correlation-based measures and network activity levels did not predict performance. A possible caveat is that derivatives of Granger causality, such as the LASSO prediction algorithm used here, could be affected by regional differences in the hemodynamic response function (27). However, it is unlikely that neurovascular coupling would differ between the integrated and split tasks.

An intriguing question is what happens to consciousness when driving while listening in the split condition. Is there a single conscious stream, with attention deployed primarily to a dominant task, typically listening, and much less to driving? Alternatively, does driving become unconscious, as on autopilot? Or, does a normally integrated conscious stream split into two separate conscious streams that coexist within the same brain, as indicated by studies of patients with an anatomically split brain? Integrated information is thought to be essential for consciousness (28), and the reduction of integrated information demonstrated here is at least compatible with a split in consciousness. Moreover, the finding that patients with a split brain can perform split tasks better than normal individuals when the two tasks are independent (6, 7) is similar to our finding that a

Table 1. Robustness of integrated information estimates over time lags

	Integrated task		Split task	
Time-lag (TR)	*t* scores	*P* values	*t* scores	*P* values
1	3.525	0.0024***	1.177	0.132
2	1.762	0.0529⁺	0.7121	0.2456
3	1.9794	0.0367*	−1.3975	0.9051
4	2.8673	0.0077**	−3.2532	0.9962
5	2.2944	0.0212*	−1.3969	0.905
6	2.6356	0.0116*	−0.1526	0.5592
7	3.2519	0.0039***	0.6029	0.2794
8	3.2543	0.0038***	0.6251	0.2723
9	2.3938	0.0178*	0.4314	0.3372
10	2.3137	0.0205*	0.9631	0.1781

Statistical significance for integrated information between the driving and listening networks, estimated using 1–10 TR time lags.
$^{+}P < 0.1$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.005$.

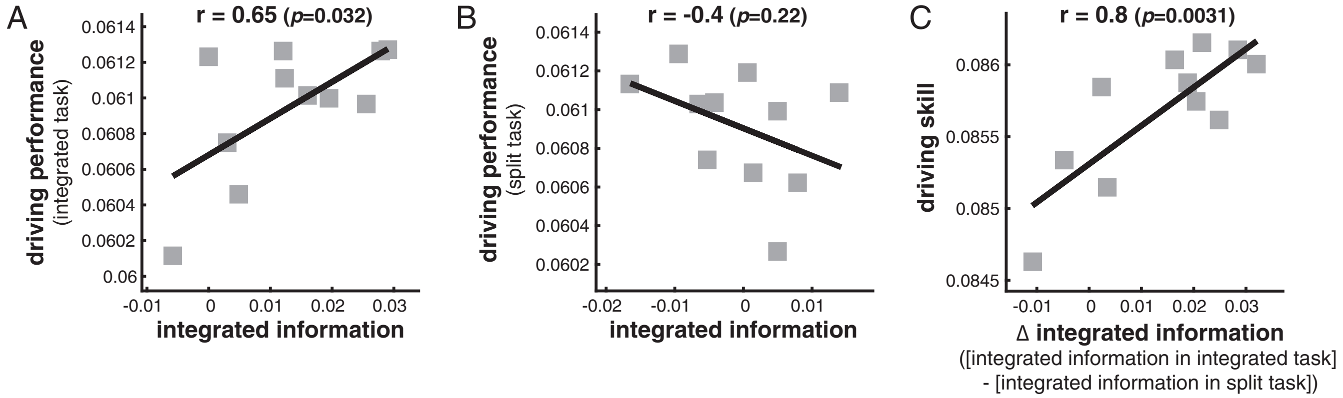

Fig. 6. Correlation between integrated information and driving performance. Although a positive correlation was found in the integrated task (*A*), a trend toward a negative correlation was observed in the split task (*B*). (*C*) Significant correlation between the overall driving performances across tasks, which we call "driving skill," with difference in integrated information between tasks (Δ integrated information).

functional split between the driving and listening networks favors performance in the split task, whereas functional integration impairs it. Future work will examine whether, as predicted by theoretical considerations about the substrate of consciousness, the functional split brain observed in the split task is associated with a transition from one to two maxima of integrated information, and thus from one to two streams of consciousness (28).

Materials and Methods

Participants. Thirteen healthy male (22–34 y of age) experienced drivers participated in the study. All subjects provided informed consent following the procedures approved by the Health Sciences Institutional Review Board of the University of Wisconsin–Madison. Before the experiments, subjects practiced in a driving simulator until driving performance became stable. Subjects performed the same simulated driving task used in the fMRI experiment with the goal of minimizing the deviation from the simulated track centerline.

Experimental Paradigm. All subjects completed fMRI sessions consisting of two tasks of interest and three localizer tasks. During the tasks of interest, subjects were asked to drive (*i*) while following GPS instructions (integrated task) or (*ii*) while listening to a radio show (split task). The three localizer tasks were designed to identify brain regions separately involved in driving versus listening. Subjects (*iii*) played the simulator alone (driving task), (*iv*) listened to GPS instructions alone (GPS task), or (*v*) listened to radio show alone (radio task). All tasks were first performed steadily for 5 min (steady-state design) and then repeated in five additional sessions consisting of five 1-min task periods separated by 30-s resting periods (block design). The block design tasks were performed in a semirandomized order. First of all, all patients performed the single driving task. Half of the subjects then performed the split task, the integrated task, and then the radio show and GPS conditions. The other half performed the integrated task, the split task, and then the GPS and radio show conditions.

Stimuli. A two-lane highway track without junctions or other vehicles was used (Racer; www.racer.nl/). Subjects were instructed to change lanes when being directed by the GPS in the integrated task or when passing designated objects (road signs and call boxes) at sides of the track in the split and driving-alone tasks. The number of lane switches was set to be the same among all tasks.

All auditory stimuli were prepared by recording the same female voice. The narrative GPS guidance stimuli consisted not only of directions to make subjects switch lanes but also directions calling attention to the objects on the track. The radio show scripts were made of samples extracted from online articles, and included various topics unrelated to the driving task.

Behavioral Measures. Subjects reported task difficulty and drowsiness after each task condition. In addition, listening comprehension tests consisting of 10 questions were completed after task conditions involving auditory stimuli to confirm that the concurrent execution of driving did not affect listening comprehension. Two behavioral measures were quantified for the driving task. First, the driving performance was defined as the difference between the mean deviation from the track centerline compared with a theoretical upper bound. Second, the subjects' overall driving skill was defined as the first principal component of the driving performance (explaining over 96% of total variance) across the split and integrated tasks. The driving performance of one subject was not used in the analysis due to a failure of storing the driving record.

fMRI Data Acquisition. The fMRI time series were acquired using a 3-T GE MR scanner. Multislice T2*-weighted fMRI images [repetition time (TR) = 1,100 ms, echo time (TE) = 14 ms, 29 slices, with a slice thickness of 4 mm and an interslice gap of 1 mm] and a structural T1-weighted sequence were acquired in each subject. A time series of 300/437 volumes was acquired for each condition of steady task/block task design. A high-resolution T1 image (parameters: TR = 8.16 ms, TE = 3.18 ms, inversion time (TI) = 450 ms, 156 slices, with a slice thickness of 1 mm) was also acquired in each volunteer at the end of the whole experiment for coregistration to the functional data. During data acquisition, subjects wore earphones in combination with earplugs and remained in a comfortable supine position.

fMRI Data Preprocessing. All fMRI images were motion-corrected, slice timing-corrected, and spatially smoothed (FWHM = 5 mm) using the SPM8 package (Wellcome Department of Imaging Neuroscience, Wellcome Trust Centre for Neuroimaging, London, United Kingdom). A frame-wise displacement over 0.15 mm was used to identify spike events. The dataset of one subject was excluded from further analyses because 38% of fMRI data samples in the integrated task were diagnosed as spike events. For other subjects, identified spike events in each condition were less than 15%.

Network Selection. We identified the driving and listening networks as the voxels activated in at least one condition involving a driving or a listening task. For the driving network, contrast images were computed (*i*) for the activation compared with baseline in the isolated driving task, (*ii*) for the increased activation in the split task compared with the isolated radio task, and (*iii*) for the increased activation in the integrated task compared with the isolated GPS task. For the listening network, contrast images were computed (*i*) for the activation compared with baseline in the isolated radio task, (*ii*) for the activation compared with baseline in the isolated GPS task, (*iii*) for the increased activation in the split task compared with the isolated driving task, and (*iv*) for the increased activation in the integrated task compared with the isolated driving task. For each network, a random effects analysis then tested for any activation under the global null hypothesis. Network constituents were then defined as all voxels surviving $P < 0.05$ corrected using voxel-wise, family-wise error. A small number of voxels overlapping between the driving and listening networks were discarded from further analyses. We used a two-sample t test to compare average activation values in the driving and listening networks during the integrated versus split task block designs. Throughout this study, parametric t test analyses were confirmed by nonparametric permutation tests (reported in Table S1).

Multivariate Integration: Correlation of MVP Shifts. Recent studies have shown that consistent multivoxel activity patterns (MVPs) are present with the same task stimuli (29, 30). Thus, task-related transient state changes in a network should be reflected by a temporal shift in MVP. We defined a multivariate measure of functional integration (MVP shift similarity) based on the correlation of MVP shifts within the driving and listening networks during each task. Before calculating the index, the signals from white matter and ventricle regions of interest (ROIs), six motion-correction parameters, spike regressors, a linear trend, and a vector of mean signal intensity were removed from voxel-wise signals. After linear regression, all time series were band-pass–filtered (0.01–0.45 Hz). For each network, we then calculated a state-shift matrix whose elements are Euclidian distances of MVPs between any different time points during a task (Fig. 4*A*). By calculating the 2D correlation between those matrices, we obtained the pattern-wise similarity of state shifts between driving and listening networks in each condition. After converting these values to *z*-scores using the Fisher transform, group means of pattern-shift similarity were compared using a t test between the integrated and split task conditions.

To quantify average voxel-wise connectivity between networks further, the mean zero-lag cross-correlation of all pairs of voxels between driving and listening networks was divided by the mean zero-lag cross-correlation of all pairs of voxels within these ROIs (normalized internetwork correlation; Fig. 4*C*). This measure was applied on the same voxel-wise signals used for multivariate connectivity analysis. After converting these values to *z*-scores using the Fisher transform, group means of the normalized internetwork correlation were compared using a *t* test between integrated and split tasks.

Integrated Information Analysis. Integrated information is the information content specified by a system above and beyond its parts (31). Here, we used as a practical measure of integrated information the increased ability for the whole system to predict its own future behavior compared with the prediction obtained using only its parts. High values of integrated information require both high integration and high differentiation (32). Previous practical measures of integrated information (33, 34), based on mutual information, can be biased toward mainly capturing correlation in the presence of a limited number of data time points, which is necessarily the case with fMRI. In this study, we thus developed an index of integrated information based on multivariate prediction.

Before multivariate prediction, a linear trend and a vector of mean signal intensity were linearly removed from voxel-wise signals, and coarse-graining was performed using a functional brain atlas (35). We then used a LASSO algorithm, implementing L1-norm regularization to allow further feature extraction, to maximize the accuracy of prediction. Further details of integrated information computation are reported in *SI Materials and Methods*.

We used fivefold cross-validation to estimate prediction accuracy robustly: Each task condition dataset was divided into five separate subsamples. The model fitting was then conducted in a row-wise manner, by adding the L1-regularizing term on each row of the equation. For example, the *k*th row of the integrated model becomes:

$$X_{k,t} = \sum_{j=1}^{n} A_{kj} X_{j,t-\tau} + \lambda_{ikp} \sum_{j=1}^{n} \left| A_{kj} \right| + \varepsilon_{ik}.$$

The optimization of the equation was conducted through a coordinate descent algorithm provided by Glmnet (web.stanford.edu/~hastie/glmnet_matlab/). The regularization coefficient λ_{ikp} generating the minimum cross-validation error for each condition was selected for final analysis. The time lag τ was varied from 1 to 10 fMRI TRs. The mean value of integrated information over all time lags was computed for group analysis. Post hoc *t* tests were then performed on integrated information values for each time lag.

Correlation with Behavior. We computed the Pearson correlation between the overall activation values, univariate and multivariate connectivity values, and integrated information measures on one side and the driving performance on the other side, in the integrated task condition versus split task condition. Before this analysis, a d'Agostino–Pearson test ensured the normality of data point distribution. We also computed the correlation between changes in functional measures between conditions (for activation, connectivity, and integrated information) and the first principal component of driving performance (driving skill) across the split and integrated task conditions. Correlation results were considered significant at $P < 0.05$ in each condition.

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