RESEARCH PAPER

Reconstruction of behavior-relevant individual brain activity: an individualized fMRI study

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Received March 26, 2019; accepted May 5, 2019

Different patterns of brain activity are observed in various subjects across a wide functional domain. However, these individual differences, which are often neglected through the group average, are not yet completely understood. Based on the fundamental assumption that human behavior is rooted in the underlying brain function, we speculated that the individual differences in brain activity are reflected in the individual differences in behavior. Adopting 98 behavioral measures and assessing the brain activity induced at seven task functional magnetic resonance imaging states, we demonstrated that the individual differences in brain activity can be used to predict behavioral measures of individual subjects with high accuracy using the partial least square regression model. In addition, we revealed that behavior-relevant individual differences in brain activity transferred between different task states and can be used to reconstruct individual brain activity. Reconstructed individual brain activity retained certain individual differences which were lost in the group average and could serve as an individual functional localizer. Therefore, our results suggest that the individual differences in brain activity contain behavior-relevant information and should be included in group averaging. Moreover, reconstructed individual brain activity shows a potential use in precise and personalized medicine.

individual difference, brain function, behavior, prediction, fMRI

INTRODUCTION

Traditional studies focusing on identification of common processing mechanisms of the human brain have made fruitful progresses in understanding the brain function and human behavior; however, the individual differences in brain activity and human behavior are commonly observed across different subjects in various domains (McNab and Klingberg, 2008; Tom et al., 2007; Wig et al., 2008). Understanding these individual differences is a major challenge in modern human neuroscience, as it provides a way of linking brain function to human cognition and behavior and facilitates the realization of precise and personalized medicine (Wang and Zhou, 2017).

These individual differences in brain activity are often considered to be sources of "noise" in scientific investigations of neural functions and are usually discarded through data averaging using a group of subjects (Kanai and Rees, 2011; Van Horn et al., 2008). However, growing evidences indicate that the variable brain organizations across different subjects are stable individual signatures (Gordon et al., 2017a; Gordon et al., 2017b), and several studies suggest that researchers should pay more attention to the importance of these individual differences to boost the translational potential of neuroimaging findings (Dubois and Adolphs, 2016; Seghier and Price, 2018). Tavor et al. (2016) investigated the possibility that the individual differences in brain activity are inherent features of individuals and discovered that these individual differences in brain activity could be predicted by the resting state functional connectivity, demonstrating that the individual differences in brain activity are independent of volatile factors to a considerable degree. However, brain functions assessed by functional magnetic resonance imaging (fMRI) are derived from the blood oxygen-level-dependent (BOLD) signal, which is an indirect measure of neural activity and is thus biased by the vascular structure (Kim and Ogawa, 2012), resulting in less direct interpretation (Logothetis, 2008; Logothetis and Wandell, 2004). The careful consideration of the neurovascular variability in the BOLD signal presents a specific challenge in the individual assessment of neural function with fMRI (Dubois and Adolphs, 2016). Therefore, the extent to which the variability in BOLD signal can reflect the actual variability in the underlying neural function remains obscure (Logothetis, 2008).

Previous studies indicate that variability in neural substrates shapes individual differences in human behaviors (Bogdan et al., 2012; Hariri, 2009). Based on the assumption that human behavior is deeply rooted in the underlying brain function, we speculated that individual differences in the brain activity are also reflected in the individual differences in human behaviors. In this study, we investigated the extent to which the individual differences in brain activity contained behavior-relevant information, and we aimed to show that despite the existence of neurovascular variability, the behavior-relevant individual differences in brain activity can still be extracted to facilitate the inference of brain function at the individual level.

Specifically, we used the partial least square regression (PLSR) model to characterize the relationship between the brain activity induced at each of the seven task states and 98 behavioral measures in a single integrated analysis (Figure 1). Instead of predicting the 98 behavioral measures one at a time, we included all the 98 behavioral measures in the prediction model in a holistic manner. This kind of integrated analysis allowed us to capture as many as possible individual differences in brain activity that were also reflected in the individual behaviors. The behavior-relevant individual differences in brain activity extracted from the prediction model would later be used to reconstruct the brain activity of an individual subject.

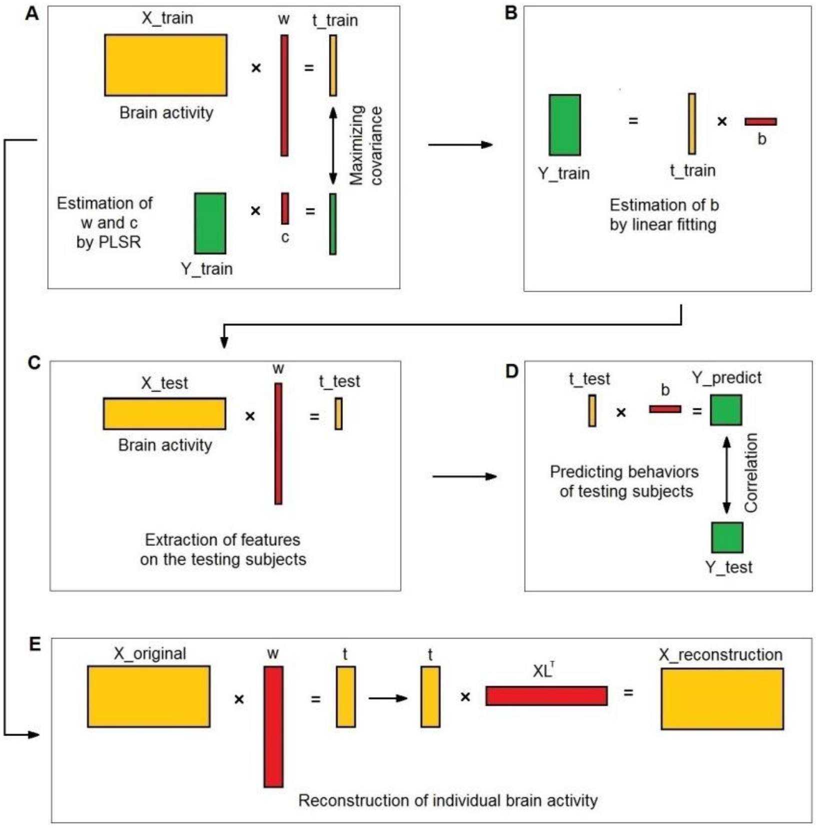

Figure 1 Flowchart of the PLSR and reconstruction procedure. A, Optimization of the PLSR procedure. B, Training procedure to fit the behaviors. C, Extraction of brain activity features from new subjects. D, Prediction of behaviors from new subjects. E, Reconstruction of individual brain activity.

RESULTS

Exploratory analysis of the individual differences in brain activity

We performed exploratory analysis to investigate the magnitude and spatial distribution of the individual differences in brain activity. We visualized the group average and standard deviation of the brain activity across all subjects (Figure S1 in Supporting Information). A large variation in individual brain activation commonly existed across the cortex in both the activated and non-activated regions. For example, the inferior frontal junction exhibited a small mean activation but a large variation in language tasks. The inferior parietal lobe and medioventral occipital cortex presented large mean activations in working memory and relational tasks, respectively, but they also showed substantial variations. To investigate whether the individual specific brain activity at a task state contained behavior-relevant information, we presented the correlation between the brain activation and specific behavioral measures in Figure S2 in Supporting Information. The individual differences in brain activity were related to multiple behavioral measures. Figure S3 (Supporting Information) shows the correlation structure of all behaviors. Some behaviors within the same domain were highly correlated and thus showed similar correlation relationships with the brain activity. These results indicated that the averaging process neglected a number of individual specific brain activities related to multiple behavioral measures.

Prediction of behavioral measures using individual differences in brain activity

Next, we utilized the individual differences in brain activity to predict all behavioral measures by virtue of the PLSR model in a holistic manner. We averaged the prediction accuracy of behavioral measures that belonged to the same category and presented the result of cognitive behaviors in Figure 2. The predicted behaviors featured a smaller range than the actual behaviors, but the original range of the behaviors was still preserved to a certain degree. Table S1 (Supporting Information) provides the raw prediction accuracy of each behavioral measure and the statistical testing results. Most of the prediction accuracies were statistically (P<1×10^{-6}) better than random control models under two-sample t-tests. We observed that the prediction accuracy presented non-significant (r<0.1; P>0.2) correlation to the variability of behaviors. The prediction accuracy reflected the generalization capability of the relationship between behavioral measures and brain activity, and could be used to assess the extent to which behavior the individual differences in brain activity were most relevant.

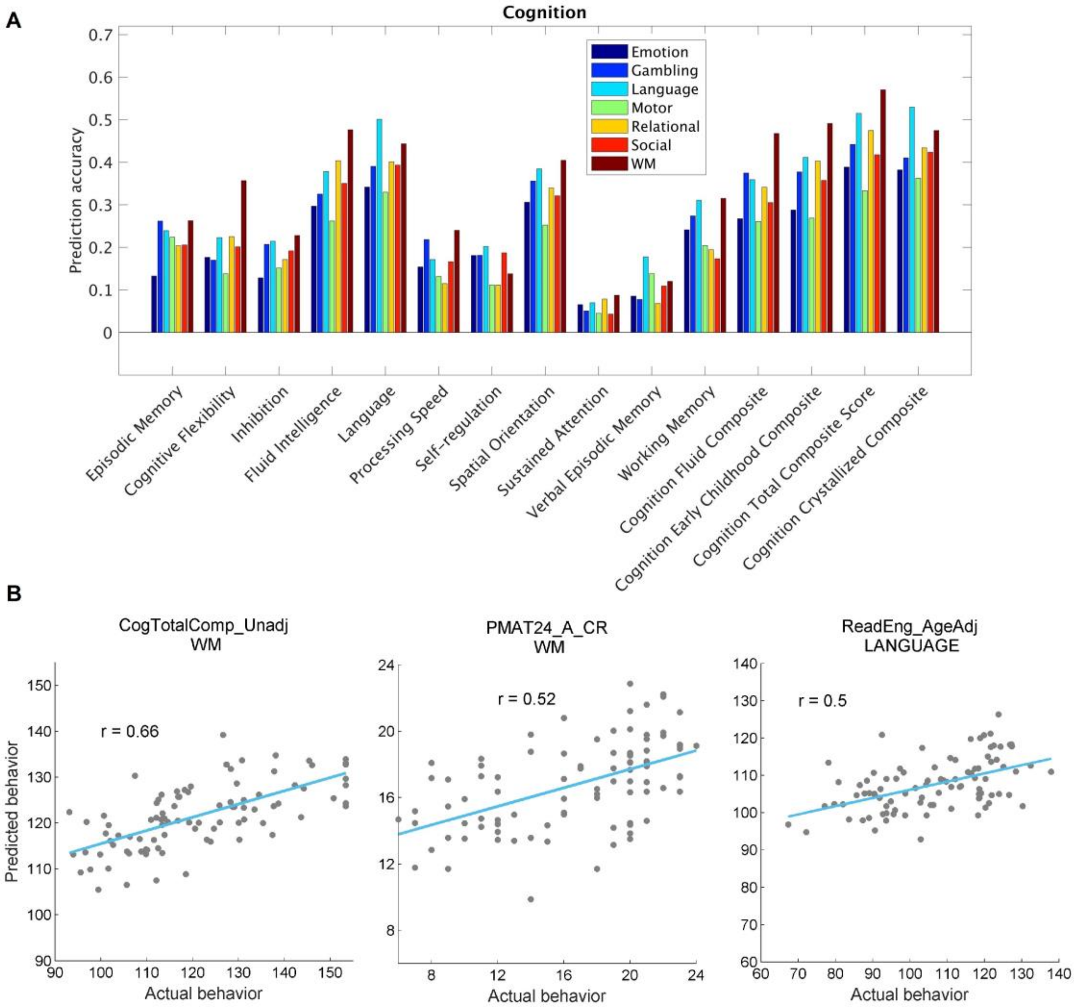

Figure 2 Prediction accuracy of behavioral measures in the cognitive domain. A, Prediction accuracies of different behavioral categories are presented in the bar plot. Different colors represent the brain activity induced at different task states. B, Examples of several predicted and actual behavioral measures are shown, with P<1×10^{-6}.

Reconstruction of behavior-relevant individual brain activity

The number of components varied across tasks (from 40 to 60). We visualized the first three components to investigate the spatial distributions of the individual differences in brain activity that contributed to the prediction of behavioral measures (Figure 3). The first component was similar to the group average and may represent the common neural substrates across subjects. The following components recruited regions that were inactivated in the group average and may represent individual specific neural substrates. We further used the extracted components to reconstruct the individual brain activity in Figure 4. The reconstructed brain activity exhibited smoothed patterns, as numerous individual differences in brain activity that were irrelevant to the behaviors were disregarded. However, as indicated by the red circle, specific individual differences in brain activity were still retained by the reconstruction procedure, whereas the behavior-relevant individual differences were lost in the group average. We also quantitatively determined that the reconstructed brain activity retained the individual specific signature of the original brain activity (Figure S4 in Supporting Information). The quantitative average similarities (evaluated by correlation) between the reconstructed and original brain activities for the seven tasks were as follows: EMOTION 0.43, GAMBLING 0.48, LANGUAGE 0.48, MOTOR 0.47, RELATIONAL 0.39, SOCIAL 0.40, and working memory (WM) 0.42. These similarities vanished (below 0.01) when we randomly changed the patterns of behavior-relevant individual differences.

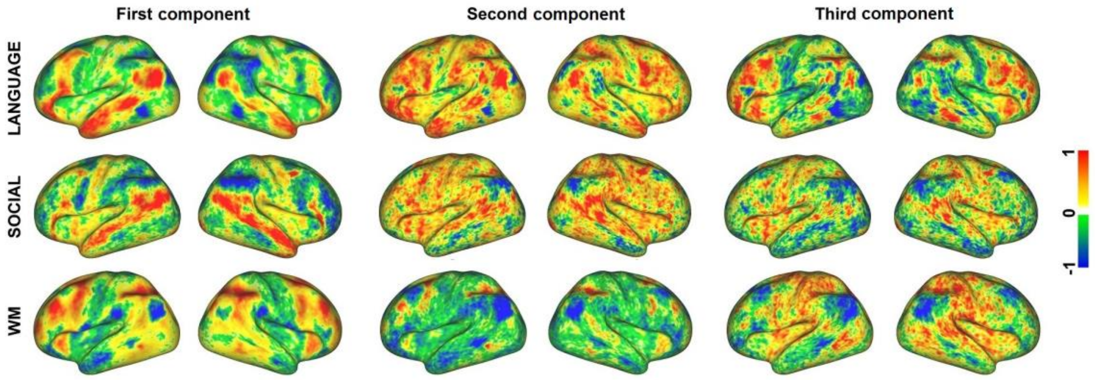

Figure 3 Visualization of the patterns of behavior-relevant individual differences. The first three components of behavior-relevant individual differences induced at three task states are shown. We mapped the 98 percentiles of the most positive and negative data values to 1 and –1.

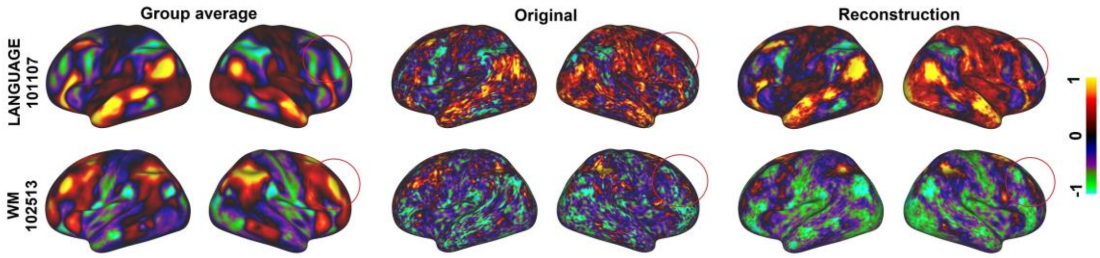

Figure 4 Reconstruction of individual brain activity from behavior-relevant individual differences. We selected several tasks and visualized the brain activity of different subjects. We mapped the 98 percentiles of the most positive and negative data values to 1 and –1. The red circles indicate that certain behavior-relevant individual differences were retained in the reconstructed individual brain activity but lost in the group average brain activity.

Transfer reconstruction of behavior-relevant individual brain activity

We also used the behavior-relevant individual differences in brain activity induced at one task state to reconstruct the individual brain activity induced at another task state and compared this transfer reconstruction to the normal reconstruction. Figure 5 shows an example of the transfer reconstruction result, and Table 1 lists the quantitative analysis results. The transfer reconstruction was similar to the normal reconstruction, but this similarity vanished when we randomly changed the patterns of behavior-relevant individual differences in brain activity. This condition only became possible when behavior-relevant individual differences in brain activity induced at one task state were also reflected in another task state. Therefore, the brain activities induced at different task states shared specific common patterns of behavior-relevant individual differences.

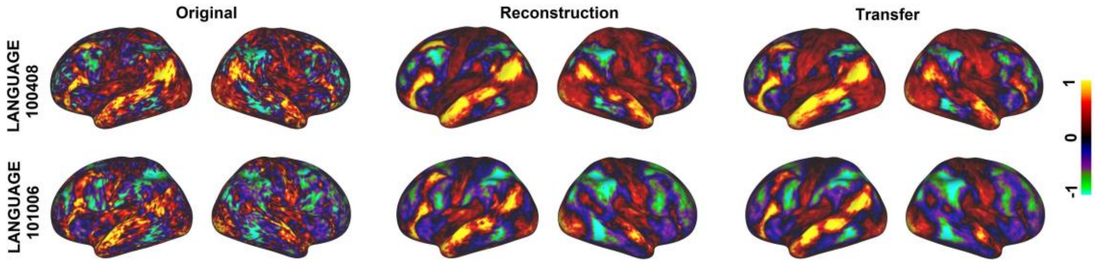

Figure 5 Transfer reconstruction of the individual brain activity. We showed the transfer reconstruction of the brain activity at the language state from behavior-relevant individual differences extracted at the working memory state. The transfer reconstruction was highly similar to the normal reconstruction.

DISCUSSION

In this study, we investigated the strategy to extract individual differences in brain activity that featured behavior-relevant meanings. We demonstrated that individual differences in brain activity induced at task state were closely related to multiple behavioral measures and could be used to predict the behavioral measures of individual subjects with high prediction accuracy. We also reconstructed the individual brain activity from the behavior-relevant individual differences that transferred between different task states and revealed a behavior-relevant individual brain activity that was otherwise neglected in the group average. In a word, we provided a way of linking behavior to individual brain function that unraveled the functional substrates of human behaviors and proposed a strategy for characterizing individual brain activity.

Our exploratory analysis documented that the individual brain activation varied widely across subjects throughout the cortex and might differ from the group average activation. This finding was also shown in a previous study (Seghier and Price, 2016), which indicated that the group-level inference is not always valid at the individual level, as a significant group effect may be driven by a few subjects, whereas a non-significant group effect may reflect heterogeneity in the population. Therefore, a complement analysis of the group average is necessary for inferring brain functions. For example, the variability in the individual brain activation has been utilized to disassociate brain functional networks (Kherif et al., 2009; Seghier and Price, 2009), and the threshold-weighted overlap map was invented to visualize the inter-subject variability in brain activation (Seghier and Price, 2016). Our research differed from these studies in terms of characterizing the individual brain activation by linking the variability in the individual brain function to behaviors.

The strategy of linking individual brain function to behaviors is commonly applied and deeply rooted to the close relationship between human behavior and brain function, which has been validated by previous studies (Sadaghiani and Kleinschmidt, 2013; Smith et al., 2015). A number of increasing evidences indicate that the individual differences in brain activity are associated with the variability in important cognitive ability and behaviors (Cole et al., 2012; Miller and Van Horn, 2007; Samanez-Larkin et al., 2010; van den Heuvel et al., 2009). Previous studies have also established a framework for predicting behavioral measures from the functional connectivity (Beaty et al., 2018; Finn et al., 2015; Greene et al., 2018; Rosenberg et al., 2016; Shen et al., 2017). These works focused on predicting a specific behavioral measure from the brain activity induced at a certain state or determining the best brain state that is suitable for predicting behaviors. Our study differs from the previous works in that we aimed to find the individual differences in brain activity that may be reflected in different behaviors in a holistic manner. Smith et al. (2015) conducted a similar holistic multivariate analysis using canonical correlation analysis and showed that a specific pattern of functional connectivity is associated with a positive–negative behavioral axis. Our study explored deeper by utilizing the specific pattern of behavior-relevant individual differences to reconstruct individual brain activities.

Our strategy for characterizing individual brain activity compromises between the group-average brain activity and original individual brain activity. The group average method treats the variability in the individual brain activity as a source of noise and identifies common brain activities among a group of subjects. This process of averaging enhances the signal-to-noise ratio and provides a reliable group-level inference, but numerous individual differences are also precluded (Dubois and Adolphs, 2016). On the other hand, although the original brain activity retains all the individual differences, it also contains many structured noises and may also be biased by the neurovascular variability in the BOLD signal (Dubois and Adolphs, 2016); hence, individual differences in original brain activity are notably difficult to interpret. Our strategy involves retaining the individual differences in brain activity that are only related to behavioral measures under the hypothesis that behavior-relevant individual differences are more likely to reflect the actual variability in neural functions. The good generalization capability to predict behavioral measures of individual subjects ensures that the retained individual differences in brain activity are not the consequences of over fitting. Thus, the reconstructed brain activity is more likely to reflect the actual underlying variation in neural functions. Our reconstructed individual brain activity serves as a reference to the original individual brain activity, as it describes the extent to which the individual differences present behavior-relevant meanings and retains certain behavior-relevant individual differences that are lost in the group average. Therefore, our reconstructed individual brain activity suggests a brain function inference that is suitable at the individual level. The transfer reconstruction of the brain activity enables the inference of individual brain functions belonging to another domain. Therefore, the utilization of our strategy is flexible and is not restricted to the seven tasks adopted in our study.

In conclusion, we identified individual differences in brain activity that may serve as functional substrates underlying certain behaviors. Our results provide important insights into how brain functions give rise to behaviors at the individual level. Our proposed strategy of reconstruction also shows practical potentials in the field of translational neuroscience. This strategy provides a method for inferring reliable individualized functional localizer due to its generalization capability in reconstructing individual brain activities. The behavior-relevant individual differences may also be related to the impaired cognitive and behavioral functions in patients with neurological diseases. The revealed atypical pattern of brain function in patients may also help us understand the mechanisms of neurological diseases.

MATERIALS AND METHODS

Imaging and behavioral data of the Human Connectome Project (HCP)

We used the minimally pre-processed data (Glasser et al., 2013) provided by the HCP. Acquisition parameters, processing, and task designs are described in detail in several publications (Barch et al., 2013; Smith et al., 2013; Sotiropoulos et al., 2013; Ugurbil et al., 2013). We used the task fMRI data that were projected into 2 mm standard Connectivity Informatics Technology Initiative (CIFTI) grayordinates space, and the multimodal surface matching (MSM) algorithm (Robinson et al., 2014) based on multiple areal features (MSMAll) was used for an accurate inter-subject registration. The brain activity at each task state was defined as the *z*-score statistic of each task fMRI contrast. The task fMRI contained 86 contrasts from seven task domains, and we selected one representative contrast for each task domain for further analysis. The selected contrasts were listed as follows: EMOTION FACES-SHAPES, GAMBLING PUNISH, LANGUAGE STORY-MATH, MOTOR AVG, RELATIONAL REL-MATCH, SOCIAL TOM-RANDOM, and WM 2BK-0BK.

We used the unrestricted behavioral measures from five domains, including cognition, emotion, motor, personality, and sensory, which can be accessed from the HCP database website (http://humanconnectome.org/data). The behavioral measures were defined as the performance on the HCP behavioral tests (Barch et al., 2013). Table S1 (Supporting Information) lists all the 98 behavioral measures. We first selected all the subjects from the S1200 release and then retained 922 subjects that featured all the seven task fMRI data and all the 98 behavioral measures.

Partial least square regression model

The PLSR (Abdi, 2003) is performed to simultaneously decompose X and Y to find components that explain the maximum covariance between X and Y. Figure 1 shows a flowchart of the method used in our study. The model can be mathematically formalized as follows: $Y_{\mathrm{n}\times\mathrm{d}}$ represents the behavioral measures included in our model, n refers to the number of subjects, and d denotes the total number of behavioral measures. $X_{\mathrm{n}\times\mathrm{m}}$ represents the brain activity induced at a certain task state, m specifies the dimension of the 2 mm standard CIFTI grayordinates space (91282); the PLSR finds the unit vectors $\mathrm{w}_{\mathrm{m}\times 1}$ and $\mathrm{c}_{\mathrm{d}\times 1}$ to maximize the covariance between $t_{\mathrm{n}\times 1} = X_{\mathrm{n}\times\mathrm{m}} * \mathrm{w}_{\mathrm{m}\times 1}$ and $u_{\mathrm{n}\times 1} = Y_{\mathrm{n}\times\mathrm{d}} * \mathrm{c}_{\mathrm{d}\times 1}$ ($*$ represents the matrix multiplication). The expression $\mathrm{w}_{\mathrm{m}\times 1}$ describes how much each vertex contributes to the component $t_{\mathrm{n}\times 1}$ and represents the spatial pattern of the behavior-relevant individual difference (i.e., component $t_{\mathrm{n}\times 1}$). Then, we can use t as a new independent variable to predict Y in a linear model, after which t is subtracted from both X and Y, and the residues are treated as new X and Y to reiterate the process until X becomes a null matrix. At the end of the procedure, we obtained a sequence of t_{i}

and $\mathrm{w_i}$, where i represents the number of iterations. The procedure ensures that different t_{i} and t_{j} are orthogonal. Therefore, different components contribute independently to the prediction of behavioral measures. Practically, we used the plsregress command implemented in Matlab.

Model training and evaluation

We randomly separated the 922 subjects into training and testing groups by a ratio of 9:1, i.e., 830 and 92, respectively. Before proceeding to the formal analysis, we estimated the means of X_{train} and Y_{train} and subtracted them from $X_{\mathrm{train(830\times m)}}$ and $Y_{\mathrm{train(830\times d)}}$, respectively. This step was similarly conducted for $X_{\mathrm{test(92\times m)}}$ and $Y_{\mathrm{test(92\times d)}}$, but the means were estimated from the training data instead of the testing data. We fed the $X_{\mathrm{train(830\times m)}}$ and $Y_{\mathrm{train(830\times d)}}$ into the PLSR model to obtain $t_{\mathrm{train(830\times 1)}} = X_{\mathrm{train(830\times m)}} * \mathrm{w_{train(m\times 1)}}$ and used $t_{\mathrm{train(830\times 1)}}$ to fit $Y_{\mathrm{train(830\times d)}}$ in a linear model as $Y_{\mathrm{train(830\times d)}} = t_{\mathrm{train(830\times 1)}} * \mathrm{b_{train(1\times d)}} + \mathrm{e}$, where $\mathrm{b_{train(1\times d)}}$ represents how much each component contributes to the fitting of $Y_{\mathrm{train(830\times d)}}$, and e denotes the residue. Then, we used $X_{\mathrm{test(92\times m)}}$ to achieve $t_{\mathrm{test(92\times 1)}} = X_{\mathrm{test(92\times m)}} * \mathrm{w_{train(m\times 1)}}$, and finally we obtained the prediction of $Y_{\mathrm{test(92\times d)}}$ as $Y_{\mathrm{predict(92\times d)}} = t_{\mathrm{test(92\times 1)}} * \mathrm{b_{train(1\times d)}}$. We evaluated the prediction accuracy by calculating the correlation between $Y_{\mathrm{test(92\times d)}}$ and $Y_{\mathrm{predict(92\times d)}}$ for each behavioral measure. This process was repeated 100 times with different random separations, and the prediction accuracies were averaged to acquire the final evaluation of the prediction model. To specify the number of components in the model, we calculated the variance in behavioral measures that each component could explain independently. A truncation was adopted after the variance decreased an order of magnitude (10 times) as to the maximum value. This method is intuitive given the reasonability of dropping the “less informative” components. We used the correlation coefficient (*r*) instead of the mean squared error (MSE) or mean absolute error (MAE) to assess the prediction accuracy, because unlike MSE and MAE, which are non-standardized and un-bounded across different behavioral measures, *r* is standardized and bounded between 0 and 1 and thus suitable for comparison between different behavioral measures.

Reconstruction of individual brain activity

As estimating the mean of $X_{\mathrm{n\times m}}$ costs one degree of freedom and m is normally much larger than n, one can estimate $\mathrm{n-1}$ independent components from the PLSR at most, i.e., $t_{\mathrm{n\times(n-1)}} = X_{\mathrm{n\times m}} * \mathrm{w_{m\times(n\text{-}1)}}$. If we let $XL_{\mathrm{m\times(n-1)}} = X^{\mathrm{T}}_{\mathrm{n\times m}} * t_{\mathrm{n\times(n-1)}}$, where T represents the matrix transposition, then $t_{\mathrm{n\times(n-1)}} * XL^{\mathrm{T}}_{\mathrm{m\times(n-1)}}$ recovers 100% of variance in $X_{\mathrm{n\times m}}$. If we select the first k components, then $t_{\mathrm{n\times k}} * XL^{\mathrm{T}}_{\mathrm{m\times k}}$ is the partial least square approximation to $X_{\mathrm{n\times m}}$. The reconstruction procedure can be understood as projecting the original individual brain activity on a set of orthogonal bases composed of the behavior-relevant individual differences, which amount to keeping the behavior-relevant individual differences and discarding the others. In our study, we observed the first k (determined by the method described above) components of behavior-relevant individual differences, and they were used to reconstruct the individual brain activity.

Permutation analysis

We performed 100 random permutations to test the performance of the prediction model statistically. The random models were trained and evaluated in the same manner, but the pairings between each subject's brain activity feature and behavioral measures were shuffled. Then, we tested whether the prediction accuracy of the original model was statistically better than the prediction accuracy of the random model under a two-sample *t*-test for each behavioral measure.

The author(s) declare that they have no conflict of interest. The HCP project involving human subjects was approved by the ethical committee of NIH, and conformed with the Helsinki Declaration of 1975 (as revised in 2008) concerning Human Rights, and followed out policy concerning Informed Consent as shown on Springer.com.

This work was partially supported by the Natural Science Foundation of China (91432302, 31620103905, 81501179). Data were provided by the Human Connectome Project, WU-Minn Consortium (Principal Investigators: David Van Essen and Kamil Ugurbil; 1U54MH091657) funded by the 16 NIH Institutes and Centers that support the NIH Blueprint for Neuroscience Research.

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Tables

	EMOTION	GAMBLING	LANGUAGE	MOTOR	RELATIONAL	SOCIAL	WM
EMOTION		0.73 (0.10)	0.71 (0.09)	0.72 (0.12)	0.69 (0.07)	0.67 (0.08)	0.70 (0.07)
GAMBLING	0.70 (0.08)		0.72 (0.09)	0.73 (0.09)	0.68 (0.08)	0.66 (0.09)	0.70 (0.09)
LANGUAGE	0.70 (0.09)	0.74 (0.09)		0.72 (0.13)	0.67 (0.08)	0.66 (0.08)	0.69 (0.08)
MOTOR	0.71 (0.09)	0.74 (0.10)	0.72 (0.09)		0.68 (0.09)	0.67 (0.10)	0.70 (0.10)
RELATIONAL	0.71 (0.10)	0.72 (0.08)	0.69 (0.08)	0.70 (0.11)		0.66 (0.08)	0.70 (0.09)
SOCIAL	0.70 (0.08)	0.72 (0.09)	0.70 (0.10)	0.71 (0.09)	0.68 (0.09)		0.69 (0.09)
WM	0.70 (0.07)	0.73 (0.10)	0.70 (0.09)	0.71 (0.10)	0.69 (0.07)	0.66 (0.09)	

Table 1 Similarity analysis of the transfer reconstruction results. The capitalized letter refers to the abbreviation of the seven tasks, with E for EMOTION, G for GAMBLING, L for LANGUAGE, M for MOTOR, R for RELATIONAL, S for SOCIAL, and W for WM. The row represents the source task state from which the behavior-relevant individual differences are extracted, whereas the column represents the target task state from which the individual brain activity is reconstructed. The off-diagonal values outside the bracket represent the similarities between the transfer and original reconstructions and are significantly (P<1×10^{-6}; two-sample *t*-test) larger than the random results in the bracket.

SUPPORTING INFORMATION

Figure S1 Individual specific functional information was lost in the group average process.
Figure S2 Individual differences in brain activity were related to multiple behavioral measures.
Figure S3 Correlation structure of all behavioral measures.
Figure S4 Similarity between the actual and reconstructed individual differences.
Table S1 Raw prediction accuracy of behavioral traits.