



Distinct patterns of functional brain connectivity correlate with objective performance and subjective beliefs

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P. Barttfeld, B. Wicker, P. Mcaleer, P. Belin, Y. Cojan, et al.. Distinct patterns of functional brain connectivity correlate with objective performance and subjective beliefs. Proceedings of the National Academy of Sciences of the United States of America, 2013, 110 (28), pp.11577-11582. 10.1073/pnas.1301353110 . hal-02014979

HAL Id: hal-02014979

<https://hal.science/hal-02014979>

Submitted on 11 Feb 2019

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pNAS

interoception | metacognition | resting-state | partial-report-paradigm

Interoception (generally defined as the ability to detect subtle changes in bodily systems, including muscles, skin, joints, and viscera) (17), is closely related to metacognition of agency (18, 19). We reasoned that this may more generally reflect a partially overlapping system regulating attention to internal states, including interoception (focus on body systems) and metacognitive ability

PNAS | July 9, 2013 | vol. 110 | no. 28 | 11577–11582

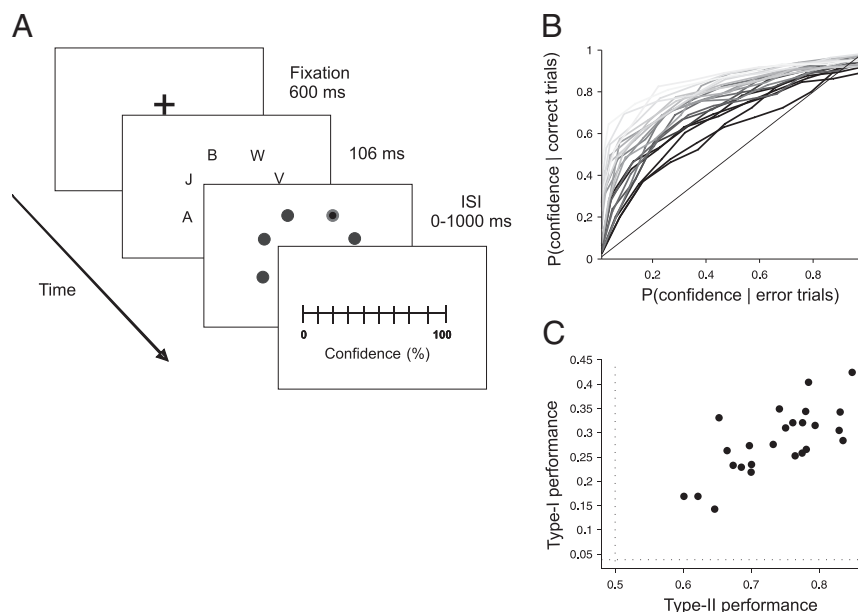


Fig. 1. (A) Subjects performed a partial report task experiment identifying a letter in a cued location of a cluttered field (3) and subsequently indicating the degree of confidence in their response in a continuous scale. (B) Individual ROC curves reflect a broad variability in metacognitive accuracy. (C) Type-I and type-II performance show a significant correlation across individuals, but with sufficient dispersion to perform a reliable bivariate regression to both factors. Dotted lines mark random type-I (1/26) and type-II (0.5) performance.

is referred as functional connectivity. To investigate connectivity changes associated with type-I and type-II performance, we conducted an across-subjects bivariate linear regression, between each entry of the correlation matrix $C_{s,p}$ and type-I and type-II performances of the subject in the PR task. This led to six matrices of beta (β) values, $B_{s,r(i,j)}$, one per attentional state s and regression r to type-I or type-II performance (Fig. S2). As an example, a positive value of $B_{resting,type-I}(i,j)$ indicates that connectivity between ROI(i) and ROI(j) increases with type-I performance for networks measured in the resting state.

For visualization purposes, we projected $B_{s,r}(i,j)$ values exceeding a threshold of 3 SDs into glass brains (Fig. 2 *A* and *B*).

For type-I performance (Fig. 24), the vast majority of values were positive, showing a marked tendency of increased connectivity with type-I performance. On the contrary, $B_{s,r}(i,j)$ values indexing how connectivity varies with type-II performance— $B_{s,type-II}(i,j)$ —showed different patterns across states (Fig. 2B). For networks measured in the exteroceptive and resting states, the vast majority of values were negative, indicating a marked tendency of decrease in connectivity with type-II performance. This pattern was different for networks measured in the interoceptive state. The regression revealed a dense distribution of positive $B_{interoceptive,type-II}$ values for ROIs localized within the frontoparietal system and negative $B_{interoceptive,type-II}$ values within

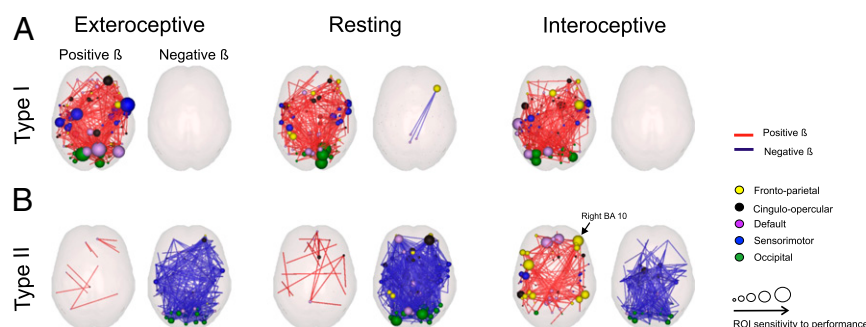


Fig. 2. Dependence of functional brain connectivity with type-I and type-II performance measured by a bivariate regression of connectivity to both factors. Red links denote positive beta (β) values (connectivity increases with performance). Blue links negative β -values (connectivity decreases with performance). For visualization purposes only β whose absolute value exceeded 3 SDs were depicted. For each ROI, the size of the sphere denotes the number of connections exceeding 3 SDs. Color indicates the functional system to which the ROI belongs. (A) β -Values for type-I performance. ROIs whose connectivity varies positively with type-I performance were mostly located in medial and posterior brain regions. The four ROIs with the highest rank in the number of connections exceeding a threshold (for networks measured under exteroceptive state, the state with the highest average β -value) are in dorsal frontal cortex ([60, 8, 34]), occipital cortex ([−16, −76, 33]), the precuneus ([11, −68, 42]) and parietal cortex ([−26, −8, 54]) (see Table 1 for the top 15 ROIs), which is consistent with previous findings of connectivity in the resting state predicting visual performance (11). (B) β -Values for type-II performance. The spatial distribution of ROIs whose connectivity increases for increasing type-II performance was mostly located in frontal regions in the FP and DBN. The 4 ROIs with the highest rank in the number of connections exceeding a threshold (for networks measured under interoceptive state, the state with the highest average β -value) are in the ventromedial prefrontal cortex ([−11, 45, 17] and [9, 51, 16]), the dorsal frontal cortex [−42, 7, 36] and the anterior prefrontal cortex [42, 48, −3] (see Table 2 for the top 15 ROIs).

confidence becomes a worse indicator of future recall (because both high and low confidence elements are recalled). Thus, participants with high interoceptive accuracy have worse metacognitive accuracy of future recall during the systole. This leads to a negative correlation between type-II performance and introspective ability, which may seem at odds with our finding that only networks measured in the interoceptive state show connections increasing with type-II performance. However, there is no intrinsic contradiction between these results: a partial overlap on brain circuitry of interoception and metacognitive ability may reveal itself as a competition between these processes, yielding results similar to those found by Garfinkel and colleagues (34). In the following paragraphs we argue how these arguments can be sketched for specific predictions of interactions between the systems of metacognitive ability and interoception. More generally, our work on functional brain networks and Garfinkel et al.'s behavioral studies (34), are only the first steps to understanding what may be a complex pattern of interactions between the systems of metacognitive ability and interoception. This may help bridge the fertile but largely disconnected literature of metacognitive ability (2, 35–37) and interoception (17, 32, 33, 38).

Beyond the results described in this study, other predictions derive from the hypothesis of partially overlapping systems of metacognitive ability and interoception: (i) Training interoception—for instance with interventions of mindfulness—may be a vehicle to partially improve metacognitive ability in a broad and nonspecific manner. (ii) Psychiatric disorders with deficits of interoception (such as depersonalization disorders; ref. 39), should reflect a specific deficit in type-II performance without affecting type-I performance. (iii) Synchronic expression of introspective and interoceptive tasks may reflect a bottleneck and hence interference. As in ref. 2, concurrent performance with an interoceptive task may impair (or delay, or interact with) type-II, but not type-I performance. (iv) Finally, a more speculative and theoretically provoking thought is that metacognitive ability and interoception may share a fundamental role in cementing conscious experience. In several psychological theories, metacognition is considered a process of second-order (meta) representation of first-order processes, which is constitutive of consciousness (see ref. 36 for a review). Similarly, interoceptive sensitivity has often been identified as a precursor of consciousness, although of a different kind: awareness of one's body, which is intimately linked to self-identity and self-consciousness (40). Hence a further prediction that can be examined empirically is that manipulations affecting conscious state (through sleep or mild sedation for instance) should show a correlated fade out of interoceptive and metacognitive abilities.

Our results extend the reach of the covariations of connectivity of previous studies to the domain of metacognition and highlight that mental states of interoceptive, resting, and exteroceptive attention convey different information about future objective performance and accuracy of subjective beliefs. Beyond the specific consequences for the domain of metacognition, our results indicate how information about individual traits may be enriched when based on a set of functional brain networks obtained from different mental states.

Materials and Methods

Participants. Twenty-five subjects (12 male; mean age = 25.06 y) with normal or corrected-to-normal vision, no report of history of psychiatric or neurological

disorders, and no current use of any psychoactive medications, gave their written consent to participate in the experiment. The study was conducted in accordance with the Declaration of Helsinki and approved by the institutional ethics committees of the Fundación para la Lucha contra las Enfermedades Neurológicas de la Infancia (Argentina) and Glasgow university (UK). Sixteen subjects were from Buenos Aires and 9 from Glasgow, Scotland. Both groups showed a very similar pattern of results in the main observations of this study (Fig. S3) and hence were pooled together to increase the statistical power.

Partial Report (Behavioral) Experiment. Several days after the fMRI recordings, participants performed a PR experiment, identifying a letter in a cued location of a cluttered field (3). Participants were asked to report, using a standard keyboard, the letter presented in the position cued by the red circle, which remained on screen until the subject's response. Random performance is 1/26, because for each trial, subjects had to choose 1 of 26 possible letters. Subsequently, participants indicated the degree of confidence in their response in a continuous scale (Fig. 1A). Performance in the objective task (reporting the letter, or type-I performance) and performance in the subjective task (reporting confidence on response, or type-II performance) were used as linear regressors for functional MRI connectivity. To explore how much of the total variance in the fMRI data was explained by the two behavioral regressors, we calculated the R-square value (Fig. S5).

fMRI Recordings and Analysis. Functional images from Buenos Aires were acquired on a GE HDx 3.0T MR system with a conventional eight-channel head coil. Twenty-four axial slices (5 mm thick) were acquired parallel to the plane connecting the anterior and posterior commissures and covering the whole brain [repetition time (TR) = 2,000 ms, echo time (TE) = 35 ms, flip angle = 90°]. To aid in the localization of functional data, high-resolution structural T1 image [3D Fast inversion recovery spoiled gradient echo (SPGR-IR), inversion time 700 ms; flip angle (FA) = 15°, field of view (FOV) = 192 × 256 × 256 mm; matrix 512 × 512 × 168; slice thickness 1.1 mm] was also acquired. Images from Glasgow were acquired on a 3-T Siemens MRI system (Magnetom Vision; Siemens Electric) with the same parameters.

Subjects underwent three functional runs lasting 7 min 22 s each for the Buenos Aires dataset and 12 min for the Glasgow dataset. We ran the experiment in Glasgow with longer time series to assure that the functional networks measured with 7 min 22 s were stable and close to convergence to a stationary value (Fig. S4). Subjects were instructed to keep their eyes closed without falling asleep. Random sequences of tones with the same distribution of duration (200 ms), pitch (400 Hz), and oddball frequency (pitch 410 Hz every 15 tones) were presented every 400 ms during the three blocks at very low volume. In the interoceptive attention run, participants were instructed to focus on their respiration cycle, perceiving the air flowing in and out. In the exteroceptive attention, participants were informed that they would hear a series of sounds and should focus on it. In the resting block, subjects were instructed to relax, not to do any mental effort and not to fall asleep. After the recordings we asked subjects whether they heard the beeps in the other runs. None of the subjects reported noticing the tones in the resting state or interoceptive attention, indicating that in absence of directed attention the tones were camouflaged within the noise of the scanner. Conversely, all subjects reported a consistent approximate number of odd tones during the exteroceptive attention run. As the goal of our study was simply to direct subjects' attention to different states, we did not measure auditability but sounds were presented with exactly the same parameters in all three states.

ACKNOWLEDGMENTS. The authors thank Alejo Salles, Ariel Zylberberg and Simon van Gall for useful suggestions for the manuscript. This work is funded by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), the Secretaría de Ciencia y Técnica de la Universidad de Buenos Aires (UBACYT), and by the Human Frontiers Science Program. M.S. is sponsored by the James McDonnell Foundation 21st Century Science Initiative in Understanding Human Cognition – Scholar Award. B.W. is supported by the Centre National de la Recherche Scientifique. P. Barttfeld was supported by a fellowship from the Consejo Nacional de Investigaciones Científicas y Técnicas and a Human Frontiers Science Program research grant.

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