NeuroImage 244 (2021) 118587

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Similarity and stability of face network across populations and throughout adolescence and adulthood

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ARTICLE INFO

Keywords:
Canonical connectivity profile
Change
Adolescence
Psychopathology
fMRI

ABSTRACT

The ability to extract cues from faces is fundamental for social animals, including humans. An individual's profile of functional connectivity across a face network can be shaped by common organizing principles, stable individual traits, and time-varying mental states. In the present study, we used data obtained with functional magnetic resonance imaging in two cohorts, IMAGEN ($N = 534$) and ALSPAC ($N = 465$), to investigate - both at group and individual levels - the consistency of the regional profile of functional connectivity across populations (IMAGEN,

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https://doi.org/10.1016/j.neuroimage.2021.118587.
Received 3 August 2021; Received in revised form 15 September 2021; Accepted 16 September 2021
Available online 21 September 2021.

ALSPAC) and time (Visits 1 to 3 in IMAGEN; age 14 to 22 years). At the group level, we found a robust canonical profile of connectivity both across populations and time. At the individual level, connectivity profiles deviated from the canonical profile, and the magnitude of this deviation related to the presence of psychopathology. These findings suggest that the brain processes faces in a highly stereotypical manner, and that the deviations from this normative pattern may be related to the risk of mental illness.

1. Introduction

The face is a rich source of social signals that provide information about individuals' identity, as well as their mental and emotional states (Mandal and Awasthi, 2015). This information is essential for social species, including humans, for their survival as it allows them to adjust behaviors according to social contexts. Humans are born with a preference for faces (Slater and Quinn, 2001). Nonetheless, response properties and functional connectivity of brain regions supporting face perception and processing continue to mature throughout childhood and adolescence until early adulthood (Behrmann et al., 2016; Cohen Kadosh et al., 2011; Pascalis et al., 2011). Regardless of developmental changes and individual variations, extensive research has shown that extracting and processing information from a face requires the coordinated engagement of a similar set of brain regions. These regions can be divided into a core system, which includes occipitotemporal regions (*e.g.*, fusiform face area) mediating the visual analysis of faces and consistently involved in different face-related tasks (Allison et al., 2000; McCarthy et al., 1997), and an extended system comprised of neural systems that are involved in various cognitive processes depending on stimuli and task requirements (Adolphs, 2002; Fusar-Poli et al., 2009; Haxby et al., 2000). This model provides a neuronal framework of face processing, and indicates a potential canonical structure of the network shared across populations and ages (Fairhall and Ishai, 2007; Gobbini and Haxby, 2007). In principle, this canonical structure of the face network can be seen as a specific instantiation of the "inter-subject synchronization" whereby brains of different individuals respond in a highly similar manner to a dynamic stream of naturalistic (visual) stimuli (Hasson et al., 2010, 2004).

While different brains may perceive and process faces in a similar manner, there is considerable interest in understanding how the face network varies across individuals, whether healthy or diagnosed with various psychiatric disorders. Hypo- or hyper- "connectivity" in the face network have been found to be associated with depression, anxiety, and autism (Brühl et al., 2014; Kleinhans et al., 2008; Stuhrmann et al., 2011). While there are some consistent findings across these studies, other reports are rather inconsistent. For example, one study found that patients with social anxiety exhibited lower connectivity between the amygdala and the rostral anterior cingulate cortex when viewing fearful faces (Prater et al., 2013), but such "disconnection" was absent in another study (Demenescu et al., 2013). One of the factors that contribute to the inconsistent findings is idiosyncrasy in patients with mental diseases, which means both higher and lower connectivity can exist in a given clinical group, as compared with healthy controls. Regardless the direction of such differences, alterations in specific connections within functional networks can lead to an overall distortion of an inter-regional pattern of functional connectivity relative to the typical, canonical template (Hahamy et al., 2015). Thus, comparing individual connectivity profiles to a typical - canonical - profile may allow one to identify possible deviations in brain functioning in relation to mental illness.

Another factor that contributes to the inconsistent findings is the stability of a functional network over time and during development. The ability to extract cues from faces may vary from time to time depending on factors such as observers' attentions (Pessoa et al., 2002) or their emotional states (Attwood et al., 2017). For instance, the amygdala has greater response to fearful faces than neutral faces only when sufficient attentional resources are available to process those faces (Pessoa et al., 2002). Findings from several studies also suggest that brain regions, such as the amygdala, can respond to faces differently from one session to another (Johnstone et al., 2005; Plichta et al., 2012; Van Den Bulk et al., 2013). These findings of intra-individual variations in the response of a region within the distributed face-processing network lead us to predict that intra-individual variations will be present – over time - in the overall profile of connectivity in the face network. In this report, we use the term "profile" to refer to a relative strength of "functional connectivity" across all pairs (edges) of brain regions (nodes) constituting a network; the connectivity strength is indexed by a correlation between time series of functional magnetic resonance imaging (fMRI) signals recorded in region A and B. On a group level, it has been observed that such profiles of functional connectivity across the whole brain network are highly stable across time and tasks, suggesting existence of an "intrinsic" standard architecture of functional brain organization (Cole et al., 2014; Geerligs et al., 2015). By stability we mean the consistency of connectivity profiles across time. Between-subject averaging may, however, obscure patterns of brain organization specific to each individual and, in turn, lead to an underestimation of within-subject variations across time. Indeed, on individual level, the connectivity profiles during the same task range from stable to unstable over time, depending on task, imaging quality, scan duration and developmental stages of participants (Breukelaar et al., 2020; Dufford et al., 2021; Geerligs et al., 2015; Horien et al., 2019, 2018; Vanderwal et al., 2021, 2017; Waller et al., 2017). Furthermore, it has been shown that the degree of individual stability varies as a function of performance (Ousdal et al., 2020) and psychiatric illness (Kaufmann et al., 2018).

Here, we use data obtained in two cohorts, namely IMAGEN (Schumann et al., 2010) and ALSPAC (Boyd et al., 2013; Fraser et al., 2013), to investigate the similarity and stability of connectivity profiles of the face network at group and individual levels. Based on previous research described above, we expected to find a canonical profile of functional connectivity in the face network that presents consistently across populations and ages at group level. When diving into the individual level, we first assessed the extent to which each participant deviates from the canonical profile. Then, we asked whether such deviations relate to the degree of (global) psychopathology reported by each individual. Lastly, we used three sets of fMRI data acquired at 14, 19, and 22 years of age in IMAGEN to investigate to what extent individual connectivity profiles are stable from adolescence to adulthood.

2. Method

2.1. Participants

The IMAGEN Study is a longitudinal study that, at baseline, recruited a community-based sample of 2000 adolescents, 13–15 years of age, at eight sites located in England (London, Nottingham), France (Paris), Ireland (Dublin), and Germany (Berlin, Dresden, Hamburg, Mannheim) (Schumann et al., 2010). Supplementary Table S1 provides distribution of participants at each site, as well as their demographics. Further details are available at https://imagen-europe.com/standard-operating-procedures/. We used data from 534 participants (female = 310, male = 224) with good quality of imaging data at all three visits: Visit 1, Visit 2 and Visit 3 at age of 14 years (14.46 ± 0.39), 19 years (19.15 ± 0.78) and 22 years (22.02 ± 0.64) respectively.

The ALSPAC (Avon Longitudinal Study of Parents and Children) study is a birth cohort based in Bristol, United Kingdom (Boyd et al., 2013; Fraser et al., 2013). For this report, we used imaging data obtained in a sample of young men (N = 507, around 19 years of age). After performing quality control of their fMRI images, 465 participants (19.62 ± 0.84 years of age) from ALSPAC with good quality fMRI were included in this analysis (details of quality con-

trol procedures are outlined in Supplementary Fig. S1). Please note that the study website contains details of all the data that are available through a fully searchable data dictionary and variable search tool (http://www.bristol.ac.uk/alspac/researchers/our-data/). Ethical approvals for the IMAGEN and the ALSPAC studies were given by the Local Research Ethics Committees.

2.2. MRI acquisition and processing

In IMAGEN, high-resolution T1-weighted images and functional images were obtained at eight European sites with 3-Tesla MRI systems by different manufacturers (Siemens: five sites, Philips: two sites, General Electric: one site). The MR protocol and cross-site standardization of the IMAGEN study are described in Schumann et al. (Schumann et al., 2010) and IMAGEN Github (https://github.com/imagen2). Briefly, T1-weighted anatomical images were acquired using 3D MPRAGE sequences, (slice thickness = 1.1 mm; TR = 2300 ms; TE = 2.8 ms), and functional images were acquired with GE-EPI sequences (resolution = 3.4 × 3.4 mm; slice thickness = 2.4 mm; TR = 2200 ms; TE = 30 ms). In ALSPAC, scanning was performed on a General Electric 3-Tesla MRI systems, with T1-weighted anatomical images acquired using 3D FSPGR sequences (slice thickness = 1 mm; TR = 7.9 ms, TE = 3.0 ms), and functional images acquired using GE-EPI sequences (resolution = 3.4 × 3.4 mm; slice thickness = 2.4 mm; TR = 3000 ms, TE = 35 ms). Quality control, preprocessing of anatomical and functional data were performed, respectively, using MRIQC 0.15.0 (Esteban et al., 2017), fMRIPrep 1.3.2 (Esteban et al., 2019) and FSL_regfilt 5.0.9. The same preprocessing procedures were applied to the IMAGEN dataset and the ALSPAC dataset. Details can be found in Supplements (Supplementary Methods) and our previous study (Liao et al., 2021).

During the fMRI session, participants viewed passively short videoclips displaying ambiguous facial expressions (with face movements such as nose twitching, opening mouth, blinking eyes), angry facial expression or non-biological control stimuli (consisting of black- and white- concentric circles of various contrasts, expanding and contracting at various speeds; details can be found in the initial report describing this paradigm (Grosbras and Paus, 2006)). The three viewing conditions were organized into 19 blocks of 18 s duration each (5 Ambiguous, 5 Angry, 9 control, each face block contains 7,8 video clips) for a single 6 min fMRI run. The same face-task paradigm was used in both ALSPAC and IMAGEN. Note that in IMAGEN Visit 2 and Visit 3, an additional happy-face condition was added in the task; for this reason, there were 4 blocks for each face condition and 12 blocks for the control.

2.3. Regions of interest and network definition

Regions of interest (ROIs) that are relevant to face processing and constitute the face network in this study were defined by a probabilistic map computed in a subsample of adolescents (n = 1,110) of the IMAGEN dataset, as reported in Tahmasebi et al. (2012). In this probabilistic map, 25 ROIs included the following brain regions: amygdala (AmygdalaL, AmygdalaR), cerebellum (CerebellumL, CerebellumR), putamen (PutamenL, PutamenR), rhinal sulcus (RhinalSulcusL, RhinalSulcusR), anterior superior temporal sulcus (AntSTSL, AntSTSR), posterior temporal sulcus (PostSTSL, PostSTSR), fusiform face area (FFAL, FFAR), lateral occipital cortex (LOCL, LOCR), V2-V3 (V2V3L, V2V3R), premotor cortex (PMCL, PMCR), mid ventrolateral frontal cortex (MVLFCL, MVLFCR), mid dorsolateral frontal cortex (MDLFCL, MDLFCR) in both left and right hemisphere, and presupplementary motor area (PreSMAR) (see detailed information in Supplementary Table S2). The probabilistic maps computed previously (Tahmasebi et al., 2012) were used to extract mean blood-oxygen-level-dependent (BOLD) signal time series within each of the 25 ROIs. Subsequently, we obtained the BOLD signal time-series for each face condition by concatenating the mean-centered and detrended signal from the corresponding blocks, shifted by 2 TRs to accommodate for the rise in the hemodynamic response. Fisher z-transformed Pearson correlation coefficients between mean BOLD signal time-series of each possible pair of the 25 ROIs were calculated and used to construct a 25 × 25 symmetrical connectivity matrix (or network), where each element represents a connection strength, or edge, between two ROIs (nodes). In the following text, we referred to the connectivity matrix with the 25 ROIs as the “face network”. This was done for each participant at each visit, and for each face condition (angry and ambiguous face) separately, such that each participant had two matrices reflecting connectivity profiles during viewing of angry and ambiguous faces, respectively.

To expand our findings beyond the face network, we repeated the similarity and stability analyses using a 120-node whole-brain network defined by the Automated Anatomical Labelling (AAL, version 2) atlas (Rolls et al., 2015; Tzourio-Mazoyer et al., 2002). The AAL atlas is one of the most widely used parcellations in network neuroscience; it comprises 94 cortical and subcortical regions and 26 cerebellar parcels (the atlas is available at https://www.gin.cnrs.fr/en/tools/aal/) (Rolls et al., 2015). Similar to the procedures used for creating the face network, we obtained two whole-brain networks (angry and ambiguous face conditions) for each participant at each visit by extracting, mean-centering and detrending the BOLD signal time-series, and calculating Fisher z-transformed Pearson correlation coefficients between mean BOLD signal time-series of each possible pair of the 120 regions of interest. Since the face network is based on the probabilistic map of the brain response to faces (population probability higher than 0.5), the BOLD time series used for creating the face network should be less noisy than those for the whole-brain network. Furthermore, it should be reiterated that the BOLD signal time-series used to calculate both the face and whole-brain networks have the same origin, namely these were acquired while participants were viewing faces.

2.4. Psychopathology scores

In IMAGEN participants, psychiatric symptoms were assessed with the validated Development and Wellbeing Assessment interview (DAWBA, www.dawba.com) at each visit (namely, Visit 1, Visit 2, Visit 3). Based on participants’ answers to the DAWBA questions, a computer algorithm assigns an individual to one of six ordered-categorical diagnostic “probability bands” (*i.e.*, from < 0.1% likely to > 70% likely). There are 15 psychiatric disorders assessed, such as conduct disorders, generalized anxiety, and depression. All 15 disorders were assessed in Visit 1, 11 disorders were assessed in Visit 2, and 10 disorders were assessed in Visit 3. We derived an overall psychopathology score by first summing up disorder probability bands for each visit, and then averaged the sum from the three visits. Thus, the overall psychopathology score indicated the overall severity of psychiatric symptoms across adolescence to adulthood (detailed descriptions for the sum of disorder probability bands for each visit can be found in Supplementary Fig. S2). A total of 451 IMAGEN participants completed DAWBA at all three visits. Note that there was no measure of psychopathology available in ALSPAC at the MRI visit.

2.5. Statistics analysis

We hypothesized that there is a canonical profile of functional connectivity in the face network that is similar across populations and ages. To test this hypothesis, for each of the two face conditions, we first calculate group-averaged face networks for each cohort and each visit (namely, ALSPAC, IMAGEN Visit 1, IMAGEN Visit 2 and IMAGEN Visit 3). Pearson correlation coefficients were then calculated between a given pair of face networks, with high correlation values indicating a high similarity between the two networks. The similarity across populations was evaluated using the ALSPAC dataset and the Visit-2 IMAGEN dataset, which were acquired in participants of similar ages (*i.e.*, 19 years). The similarity across time was evaluated by comparing the

group-averaged face networks acquired in IMAGEN at Visit 1, Visit 2 and Visit 3.

We then investigated to what extent individual profiles of functional connectivity match (or deviate from) the canonical profile of the face network. To quantify the deviation/similarity between individual profiles of functional connectivity and the canonical profile, we calculated Pearson correlation coefficients between each participant's profile and the (group-averaged) canonical profile. We refer to such similarity between the individual profile and the canonical profile as the "individual-canonical similarity" in the text below. We also calculated – for each participant - the mean of the individual-canonical profile similarity across the three visits (namely, Visit 1, Visit 2, Visit 3) to obtain the overall individual-canonical similarity scores. Thus, a high overall similarity indicates that an individual's connectivity profile is similar to the canonical profile from adolescence to young adulthood. To expand our findings (canonical profile and similarity) beyond the face network, we calculated group-averaged networks (for each cohort and each visit) and the individual-canonical similarity for the 120-node whole-brain network. A paired *t*-test and a linear-regression model were used to evaluate the differences in the similarity between the face and the whole-brain networks.

Furthermore, we asked whether such deviations from the canonical profile relate to the degree of psychopathology. A linear mixed-effect model with Restricted Maximum Likelihood (REML) was used to investigate the relationship between the individual-canonical similarity and the psychopathology score. In this model, we used the overall individual-canonical similarity for the face network as the independent variable of interest. The psychopathology score was the dependent variable, and the scan site was the random effect (intercept). Since psychopathology might be related to sex and head motion (Kebets et al., 2019), we included sex, the mean of framewise displacements across each visit (indicator of head motion during scans) and the squared mean of framewise displacements (to account for possible nonlinear relationship) in the model as confounders. In addition, given that we observed a positive correlation between the similarity of the face network and that of the whole-brain network (Supplementary Fig. S5), we ran a second model that included the individual-canonical profile similarity based on the whole-brain network as an additional confounder.

To investigate the stability of functional connectivity at individual level, Pearson correlations between the connectivity profiles obtained at Visit 1, Visit 2 and Visit 3 were calculated for each participant in IMAGEN, with high values indicating high stability of the connectivity profiles between two different sessions (ages). The repeated measures ANOVA and the paired *t*-test (post hoc) with a false discovery rate (FDR) correction were used to test whether the stability of connectivity profiles for the face network changes across time. We then derived the overall stability of the individuals' connectivity profiles over the three visits by averaging – for each participant - the stability of the connectivity profiles across the three pairs of visits (namely, Visit 1-Visit 2, Visit 1-Visit 3 and Visit 2-Visit 3); high values of the averaged between-visit stability indicate high stability of connectivity profiles from adolescence to young adulthood. In the text below, we refer to this measure as "stability". Note that we also calculated the stability measure based on the whole-brain network, and used the paired *t*-test and a linear-regression model to explore the differences in the stability between the face and whole-brain networks. Next, we tested if individuals with a high *stability* of functional connectivity across time also have a high *similarity* of their individual profiles to the canonical one by assessing the relationship between the stability of connectivity profiles and the individual-canonical similarity using a mixed-effect model that included sex, the mean framewise displacement and squared mean framewise displacement as confounders, and the scan site as the random factor. Given the close relationship between stability and similarity, we further explored whether the relationship between the individual-canonical similarity and the psychopathology remains after including the individual-level stability in the mixed effect model. All analyses were done with R (version 4.0.5) and "lme4" and "lmerTest" package (Bates et al., 2015; Kuznetsova et al., 2017), with significant threshold for p-value is 0.05 (two sided).

Table 1
Similarity between the connectivity profiles of the group-averaged face network and individuals' face networks for each visit and population. Visits 1–3 are from the longitudinal IMAGEN dataset.

		Mean	SD	Min	Max
Angry	Visit 1	0.517	0.136	0.087	0.780
	Visit 2	0.493	0.130	0.145	0.812
	Visit 3	0.495	0.130	0.107	0.785
	ALSPAC	0.531	0.118	0.152	0.830
Ambiguous	Visit 1	0.540	0.127	0.146	0.827
	Visit 2	0.536	0.126	0.093	0.802
	Visit 3	0.541	0.126	0.141	0.795
	ALSPAC	0.553	0.108	0.093	0.784

3. Results

3.1. Canonical profile of functional connectivity

To test the hypothesis that there is a canonical profile of functional connectivity of the face network that would be present across populations and ages, for each of the two face conditions, we first calculated group-averaged matrices for each cohort and each visit separately (ALSPAC, IMAGEN Visit 1, IMAGEN Visit 2, and IMAGEN Visit 3), and tested to what extent these profiles were similar to each other. We found that the group-averaged (i.e., across-participant mean) matrices of ALSPAC (19 years of age) and IMAGEN Visit 2 (19 years of age) were highly similar to each other in both angry and ambiguous face conditions (Angry: $r = 0.965$, $p < 0.001$, Fig. 1; Ambiguous: $r = 0.963$, $p < 0.001$, Supplementary Fig. S3), supporting the existence of a canonical connectivity profile of the face network across populations. In IMAGEN dataset, the group-averaged profiles of the face network acquired at Visit 1 (14 years of age), Visit 2 (19 years of age) and Visit 3 (22 years of age) were highly similar to each other in both face conditions (Angry: Visit 1-Visit 2, $r = 0.991$, $p < 0.001$; Visit 1-Visit 3, $r = 0.983$, $p < 0.001$; Visit 2-Visit 3, $r = 0.991$, $p < 0.001$, Fig. 1. Ambiguous: Visit 1-Visit 2, $r = 0.989$, $p < 0.001$; Visit 1-Visit 3, $r = 0.976$, $p < 0.001$; Visit 2-Visit 3, $r = 0.988$, $p < 0.001$, Supplementary Fig. S3). Thus, on the group level, the canonical profile of functional connectivity of the face network appears highly stable between adolescence and young adulthood. In addition, we observed that the group-averaged profile of the whole-brain network was invariant across populations and ages (Supplementary Fig. S4).

3.2. Individual-canonical profile similarity

As between-subject averaging may obscure patterns of functional organization specific to each individual, we next explored to what extent individuals' connectivity profiles of the face network match the canonical profile (Fig. 2).

We found that – across the 300 edges in the face network – correlations of each individual profile with the canonical profile range between ~0.1 and ~0.9 (mean r ~0.5 across all samples and conditions; Table 1). Note that the individual-canonical profile similarity obtained for the face network was similar to that based on the whole-brain network (Supplementary Table S4, Fig. S5). These findings suggest that there is a large range in how similar individuals' connectivity profiles are to the canonical profile.

Next, we tested our prediction that individuals with connectivity profiles of the face network that deviate from the canonical profile may report more symptoms of various psychiatric conditions (i.e., more psychopathology). Using the linear mixed effects model, we tested whether the overall presence and severity of psychiatric symptoms correlates

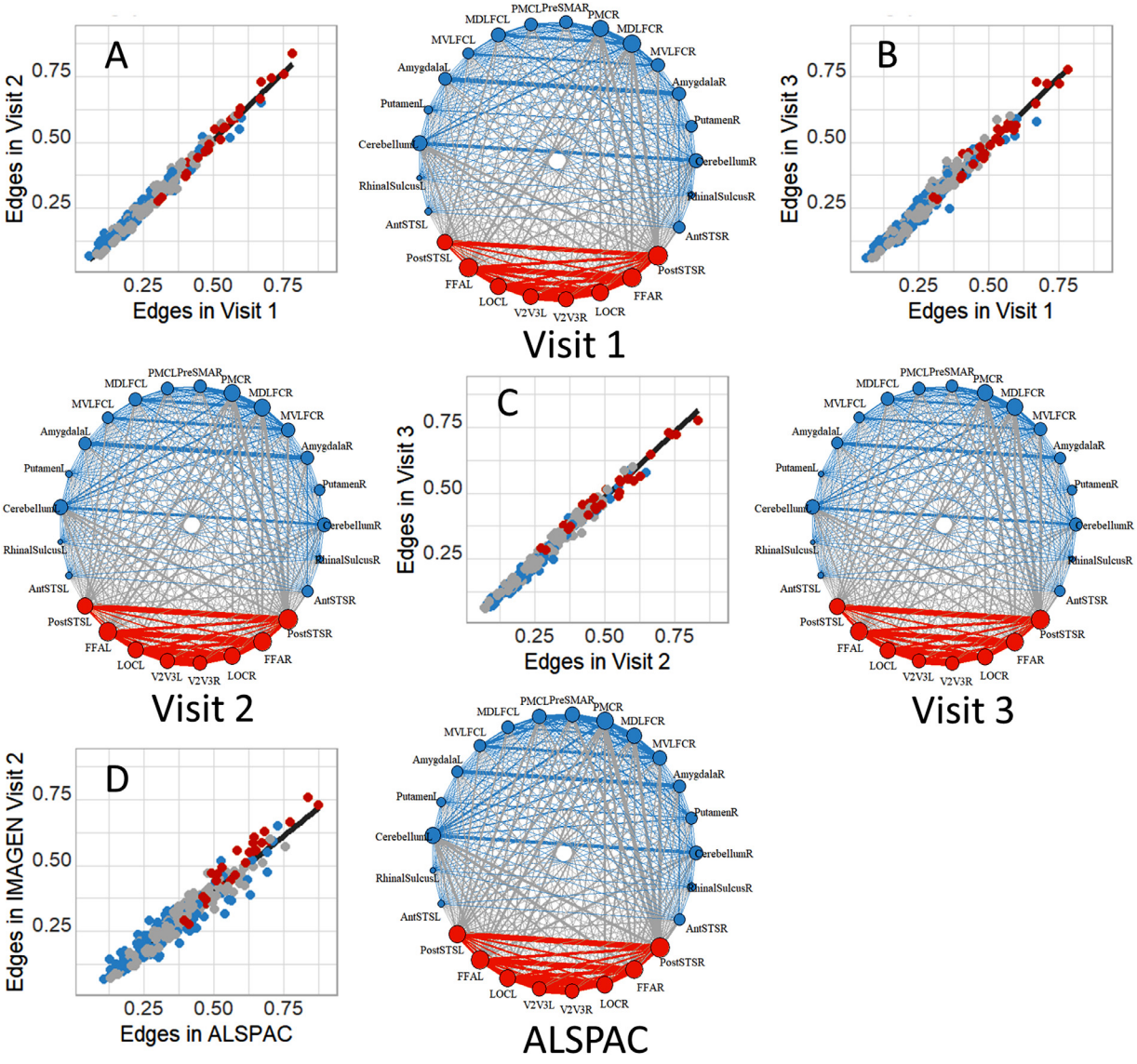

Fig. 1. Group-averaged connectivity profiles of the face network are highly stable across ages and similar across populations: correlation between edges from (A) IMAGEN Visit 1 and IMAGEN Visit 2; (B) IMAGEN Visit 1 and IMAGEN Visit 3; (C) IMAGEN Visit 2 and IMAGEN Visit 3; (D) ALSPAC and IMAGEN (Visit 2). We categorized the 25 ROIs into "core regions" and "extended region" according to the model in Haxby and Gobbini's paper (Haxby et al., 2000). Red nodes in the network plots represent the core regions that mediate the visual analysis of faces. Red links in the network plots and red points in the correlation plots represent functional connections between core regions. Blue nodes in the network plots represent the extended regions that are relevant for processing meaning of information gleaned from faces. Blue links in the network plots and blue points in the correlation plots represent functional connections between extended regions. Gray links in the network plots and gray points in the correlation plots represent functional connections between the core and extended regions. Only figures for angry faces are shown here; results for ambiguous faces can be found in Supplement Fig.S3. Edge values of each group-averaged network can also be found in Supplement Table S3 (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

with the overall individual-canonical similarity of the face network. The overall psychopathology score indicates an overall symptom severity across adolescence to adulthood. Our results showed a negative correlation between the psychopathology scores and the individual-canonical profile similarity for the angry face (estimated coefficient = −1.652, SE = 0.535, df = 411.670, t = −3.085, p = 0.002), but not for the ambiguous face (estimated coefficient = −0.561, SE = 0.571, df = 408.023, t = −0.983, p = 0.326). The relationship between the psychopathology scores and the individual-canonical similarity remained significant-in the Angry condition - after accounting for the individual-canonical similarity based on the whole-brain network (Angry: estimated coefficient = −1.568, SE = 0.605, df = 400.776, t = −2.592, p = 0.010. Ambiguous: estimated coefficient = −0.463, SE = 0.637, df = 406.667, t = −0.728, p = 0.467). Note that, in the same model, no relationship was observed between the psychopathology scores and the similarity based on the whole-brain network (Angry: estimated coefficient = −0.237, SE = 0.809, df = 425.741, t = −0.293, p = 0.769. Ambiguous: estimated coefficient = −0.288, SE = 0.818, df = 431.662, t = −0.352, p = 0.725). Note also that the negative correlations between the overall individual-canonical similarity for angry face and psychopathology scores from each of the three visits were found when psychopathology scores at each of the three visits were correlated with the profile similarity separately (Supplementary Table S5).

3.3. Intra-individual stability of connectivity profiles of face network over years

At an individual level, many factors may affect the perception and processing of faces, and lead to different brain response from one session to another (Johnstone et al., 2005; Pessoa et al., 2002). Therefore,

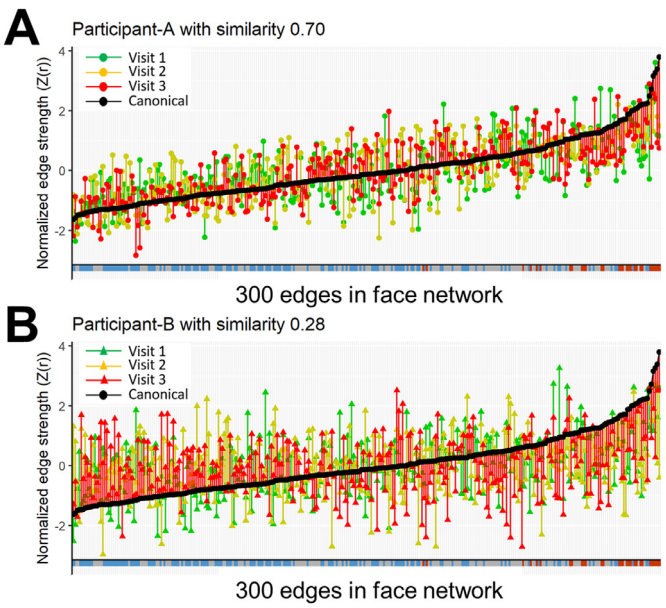

Fig. 2. Individual-canonical similarity of connectivity profiles of the face network. Canonical profile of the face network for angry face (black line), and individual profiles from three visits (color symbols) of a participant with high similarity (A), and for a participant with low similarity (B). Strength of edges are normalized within a connectivity profile. The edges are arranged based on edge strength in the canonical face network (left to right: weakest to strongest edge). The colors on the x-axis (red, blue, and gray) represent functional connections within the core regions, within the extended regions, and between the core and extended regions, respectively (same color scheme as used in Fig. 1) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

we expected relatively low (compare with group level) intra-individual stability of connectivity profiles of face network over years. Data obtained in IMAGEN participants who completed all three visits were used to investigate to what extend the individual connectivity profile of face network change over years. We found the individual stability of connectivity profiles ranged from −0.11 to 0.77 (Fig. 3A). For the angry face condition, mean (±SD) stability (correlation coefficients) for Visit 1-Visit 2, Visit 1-Visit 3 and Visit 2-Visit 3 were 0.294 ± 0.131, 0.288 ± 0.127, 0.285 ± 0.127, respectively. For the ambiguous face, mean (±SD) stability for Visit 1-Visit 2, Visit 1-Visit 3 and Visit 2-Visit 3 were 0.328 ± 0.132, 0.323 ± 0.131, 0.342 ± 0.132, respectively. We observed no (angry faces) or a subtle (ambiguous faces) change in the stability of connectivity profiles for the face network from adolescence to adulthood (repeated measures ANOVA, angry: $F = 1.086$, $p = 0.338$, generalized eta squared = 0.001; ambiguous: $F = 4.346$, $p = 0.013$, generalized eta squared = 0.004. Fig. 3A). Note that the stability obtained for the face network was similar to that based on the whole-brain network (Supplementary Table S6, Fig. S6). These results indicate that, at the individual level, there is a considerable inter-individual variation in the stability of connectivity profiles across time.

Next, we asked if individuals with high *stability* of functional connectivity across time also have a high *similarity* of their individual profiles to the canonical one. We assessed the relationship between stability of connectivity profiles and the individual-canonical profile similarity with scan site, sex and mean framewise displacements controlled. Strong positive correlations between the stability and similarity were found for both face conditions (Angry: estimate = 0. 991, SE = 0.027, df = 471.172, $t = 36.483$, $p < 0.001$. Ambiguous: estimate = 1.041, SE = 0.030, df = 529, $t = 35.062$, $p < 0.001$, Fig. 3B).

Finally, given this relationship between stability and similarity, we have tested whether the relationship between individual-canonical similarity and psychopathology described above remains after including individual-level stability in the model. We observed that the relationship between individual-canonical similarity and psychopathology (angry faces) was still present (estimated coefficient = −2.762, SE = 1.038, df = 443.326, $t = -2.660$, $p = 0.008$).

4. Discussion

When evaluated at a group level, the inter-regional profile of functional connectivity while viewing faces is highly similar across populations and development, from adolescence to young adulthood. Such an invariance of the canonical profile suggests that – on average – our brains respond to faces in a rather stereotypical manner. When studied at an individual level, however, it is clear that not everyone displays this canonical profile, with individuals deviating from it to a different degree. We found that such deviations from the canonical profile explain, to some extent, inter-individual variations in the presence of psychopathology (the more deviation, the more psychopathology).

To what extent different brains operate in a similar manner? In 2004, a pioneering study reported that human brains show a significant tendency “to act in unison” while viewing a movie (Hasson et al., 2004). Such “inter-subject synchronization” between different brains suggests a possible canonical pattern of functional connectivity shared across individuals. This is consistent with several published reports of notable similarity of the spatial patterns of functional connectivity across populations and mental states (Cole et al., 2014; Geerligs et al., 2015). In line with these observations, we found a canonical profile of functional connectivity in the face network that is shared across populations and ages. The canonical network architecture is characterized by strong “connections” within occipitotemporal regions, and may reflect an invariant (obligatory) engagement of these regions (and their interactions) in mediating visual analysis of faces. Our exploratory analyses also showed that individual profiles of the core system in the face network were more similar to the canonical profile than the extended system (Supplementary Fig. S8). These findings are consistent with the fundamental role of these core regions in the hierarchical structure of core-extended systems for face perception (Haxby et al., 2000), where the core regions are required to cooperate with the extended regions to process different information carried by faces.

Even though the average connectivity pattern may be invariant across populations and developmental stages, it may vary depending on personal traits or mental states of individuals. Here we showed that the spatial correlation between the canonical network and each individual’s network showed only a moderate similarity regardless of which network-the face network or the whole-brain network - was used. This may be due to inter-individual variations in perceptual and cognitive processes engaged while viewing faces, such as implicit recognition of facial expressions or overt attention to different parts of the face, such as the eyes or mouth (Jiang et al., 2017; Pessoa et al., 2002). There is extensive research that identified differences in the perception or recognition of faces between patients with various mental disease and healthy controls (Bourke et al., 2010; Marsh and Blair, 2008; Nomi and Uddin, 2015). There are also multiple reports of differences in the brain response to faces throughout the brain in clinical groups, as compared with healthy controls. Both “hypo-“ and “hyper- connectivity” were found in patients with mental illness in specific parts of face network (Brühl et al., 2014; Kleinhans et al., 2008; Stuhrmann et al., 2011). Indirectly, these studies suggest that the overall pattern of functional connectivity is likely to deviate from the typical, or “canonical”, pattern. A direct comparison of an individual connectivity profile to a typical - canonical - profile may provide a parsimonious way to detect “atypical” brain function in individuals and, in turn, ask whether it relates to psychopathology. A handful of studies found such deviations from a canonical (typical) profile of the resting-state functional connectivity in patients with autism spectrum disorder (Hahamy et al., 2015; Nunes et al., 2019). In these studies, the magnitude of the deviation

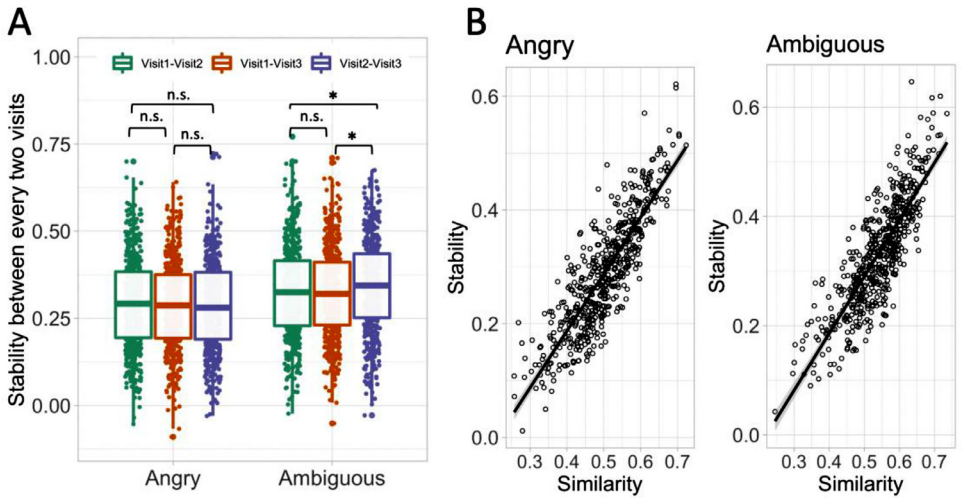

Fig. 3. (A) Stability of the individual profile of the face network from one visit to another in IMAGEN; the higher the value, the higher the stability. Results of the paired *t*-test suggest that the stability changes very little (ambiguous faces) or not at all (angry faces) from adolescence to adulthood ("n.s.": non-significant, $p > 0.05$; "*": $0.05 >= p > 0.01$). (B) Relationships between the overall individual-canonical profile similarity and the overall stability for angry and ambiguous faces, respectively. The overall individual-canonical profile similarity is the mean of the three individual-canonical profile similarities in the three visits (namely, Visit 1, Visit 2, Visit 3). The overall stability is derived by averaging the stability of the connectivity profiles for the three pairs of visits (namely, Visit 1-Visit 2, Visit 1-Visit 3 and Visit 2-Visit 3).

correlated with behavioral symptoms of autism spectrum disorder. Our results suggest that the degree of a deviation from the canonical profile of the face network is informative even in a non-clinical community-based sample. Altogether, these findings suggest that a canonical profile shared across typical healthy populations might be used as a benchmark for detecting abnormalities in functional connectivity in people at risk of mental disorders. Note, however, that the relationship between the individual-canonical deviation and the psychopathology was significant only in the angry (not ambiguous) face condition, and only in the case of the face (not whole-brain) network.

At an individual level, we found that the connectivity profiles of the face network and the whole-brain network changed from one time point to another. Furthermore, it appears that – across individuals – the stability and similarity of the profiles are inter-related: individuals with more stable profiles (across time) possess profiles that are more similar to the canonical profile. In other words, it seems that an individual's connectivity profile fluctuates around the canonical profile over time: individuals with substantial deviation of their profiles from the canonical one tend to have different profiles at different time points. Previous studies found a universal "intrinsic" network architecture that shared across the resting-state and many brain states. This intrinsic network architecture, however, can be moderated by task demands (Cole et al., 2014; Geerligs et al., 2015). With greater demands for cognitive processing, networks might adopt a more efficient but also more costly workspace configuration; with lower demands, brain networks might 'relax' into a more clustered and less costly configuration (Kitzbichler et al., 2011). Thus, we speculate that the canonical profile may represent a stable, fundamental structure of face network, which could be constraint by brain structure and shaped by a trade-off between minimizing costs and maximizing adaptative values to meet cognitive demands. Individual connectivity profiles can deviate from the canonical profile depending on cognitive demands, but those profiles with substantially deviation may be of high cost and/or low efficiency, and thus, unstable and vulnerable to the influences of (internal and external) environment factors.

The changes of network within individuals have been reported previously across different paradigms (Breukelaar et al., 2020; Geerligs et al., 2015; Horien et al., 2019; Vanderwal et al., 2017). Several factors, including but not limited to developmental changes and mental states, can contribute to such temporal variations in the profile of functional connectivity of the face network. While some evidence suggests that the network structure of face processing is mature by adolescence, modification of the functional connectivity could extend into adulthood (Cohen Kadosh et al., 2011; Joseph et al., 2012; Zhang et al., 2019). Fluctuations in mental states, which could originate from internal and external environments, can also contribute to changes in connectivity profile of the face network. As participants were only asked to view face videoclips passively, and with more than three years between successive scans, it is unlikely that learning effects or habituation effect would contribute to the changes in functional connectivity of the face network (Telzer et al., 2018). At the same time, as there is no active task to maintain attention, factors from internal and external environments, such as emotion states and scanner environments, may influence participants' perception and processing of facial expressions, and contribute to the (in)stability of connectivity profiles. Previous studies have found that different mental states, such as attention (Pessoa et al., 2002), anxiety state (Bishop et al., 2004), cognitive emotion regulation (Belden et al., 2014), can contribute to variations of brain response to faces in extended regions, including amygdala, prefrontal cortex as well as in parietal and temporal lobe region. Moreover, due to the aversive features of MRI scan (e.g., confinement and noise), people may experience anxiety during MRI, especially at the first time (Chapman et al., 2010). State-related variations in the level of alertness and arousal are accompanied by variations in non-specific modulatory systems, such as dopaminergic and noradrenergic projections to the cerebral cortex (Glowinski, 1984), and these systems may, in turn, induce apparent "coupling" of regions receiving the same modulatory input. Given the distribution of these projections, such effects might be more pronounced in association cortices. Consistent with this possibility, we observed that profiles of functional connectivity of the extended regions constituting the face network were less stable across time, as compare with the core regions (Supplementary Fig. S7).

Taken together, this study highlights the existence – at a group level – of a canonical profile of functional connectivity in the face network, which is invariant across populations and time. Individuals who deviate from this canonical profile report higher load of psychopathology, which appears to be limited to the angry-face condition. In principle, this finding suggests that a canonical profile shared across general populations might be used as a benchmark for detecting possible abnormalities in functional connectivity in individuals at risk of mental illness. Studies carried out with different facial expressions and/or different task paradigms could shed more light on the generalizability of this notion.

Credit authorship contribution statement

Zhijie Liao: Conceptualization, Formal analysis, Visualization, Writing – original draft. **Tobias Banaschewski:** Conceptualization, Project administration, Funding acquisition. **Arun L.W. Bokde:** Conceptualization, Project administration, Funding acquisition. **Sylvane Desrivières:** Conceptualization, Project administration, Funding acquisition. **Herta Flor:** Conceptualization, Project administration, Funding acquisition. **Antoine Grigis:** Conceptualization, Project administration, Funding ac-

quisition. **Hugh Garavan:** Conceptualization, Project administration, Funding acquisition. **Penny Gowland:** Conceptualization, Project administration, Funding acquisition. **Andreas Heinz:** Conceptualization, Project administration, Funding acquisition. **Bernd Ittermann:** Conceptualization, Project administration, Funding acquisition. **Jean-Luc Martinot:** Conceptualization, Project administration, Funding acquisition. **Marie-Laure Paillère Martinot:** Conceptualization, Project administration, Funding acquisition. **Eric Artiges:** Conceptualization, Project administration, Funding acquisition. **Frauke Nees:** Conceptualization, Project administration, Funding acquisition. **Dimitri Papadopoulos Orfanos:** Conceptualization, Project administration, Funding acquisition. **Luise Poustka:** Conceptualization, Project administration, Funding acquisition. **Sarah Hohmann:** Conceptualization, Project administration, Funding acquisition. **Sabina Millenet:** Conceptualization, Project administration, Funding acquisition. **Juliane H. Fröhner:** Conceptualization, Project administration, Funding acquisition. **Michael N. Smolka:** Conceptualization, Project administration, Funding acquisition. **Henrik Walter:** Conceptualization, Project administration, Funding acquisition. **Robert Whelan:** Conceptualization, Project administration, Funding acquisition. **Gunter Schumann:** Conceptualization, Project administration, Funding acquisition. **Tomáš Paus:** Conceptualization, Project administration, Funding acquisition, Writing – review & editing, Supervision.

Acknowledgments

We are extremely grateful to all the families who took part in this study the whole ALSPAC team, which includes midwives, interviewers, computer and laboratory technicians, clerical workers, research scientists, volunteers, managers, receptionists and nurses. The UK Medical Research Council and Wellcome (Grant ref: 102215/2/13/2) and the University of Bristol provide core support for ALSPAC. A comprehensive list of grants funding is available on the ALSPAC website (http://www.bristol.ac.uk/alspac/external/documents/grant-acknowledgements.pdf). This research was specifically funded by Wellcome Trust and MRC (076467/Z/05/Z). IMAGEN received support from the following sources: the European Union-funded FP6 Integrated Project IMAGEN (Reinforcement-related behavior in normal brain function and psychopathology) (LSHM-CT- 2007–037286), the Horizon 2020 funded ERC Advanced Grant 'STRATIFY' (Brain network based stratification of reinforcement-related disorders) (695313), Human Brain Project (HBP SGA 2, 785907, and HBP SGA 3, 945539), the Medical Research Council Grant 'c-VEDA' (Consortium on Vulnerability to Externalizing Disorders and Addictions) (MR/N000390/1), the National Institute of Health (NIH) (R01DA049238, A decentralized macro and micro gene-by-environment interaction analysis of substance use behavior and its brain biomarkers), the National Institute for Health Research (NIHR) Biomedical Research center at South London and Maudsley NHS Foundation Trust and King's College London, the Bundesministeriumfür Bildung und Forschung (BMBF grants 01GS08152; 01EV0711; Forschungsnetz AERIAL 01EE1406A, 01EE1406B), the Deutsche Forschungsgemeinschaft (DFG grants SM 80/7–2, SFB 940, TRR 265, NE 1383/14–1), the Medical Research Foundation and Medical Research Council (grants MR/R00465X/1 and MR/S020306/1), the National Institutes of Health (NIH) funded ENIGMA (grants 5U54EB020403–05 and 1R56AG058854–01). Further support was provided by grants from: - the ANR (ANR-12-SAMA-0004, AAPG2019 – GeBra), the Eranet Neuron (AF12-NEUR0008–01 – WM2NA; and ANR-18-NEUR00002–01 – ADORe), the Fondation de France (00081242), the Fondation pour la Recherche Médicale (DPA20140629802), the Mission Interministérielle de Lutte-contre-les-Drogues-et-les-Conduites-Addictives (MILDECA), the Assistance-Publique-Hôpitaux-de-Paris and INSERM (interface grant), Paris Sud University IDEX 2012, the Fondation de l'Avenir (grant AP-RM-17–013), the Fédération pour la Recherche sur le Cerveau; the National Institutes of Health, Science Foundation Ireland (16/ERCD/3797), U.S.A. (Axon, Testosterone and Mental Health during Adolescence; RO1 MH085772–01A1), and by NIH Consortium grant U54 EB020403, supported by a cross-NIH alliance that funds Big Data to Knowledge Centres of Excellence. We thank Steven Tilley for his help in analyzing image data with MRIQC and fmriPrep. We also thank Daniel Vosberg for his help in proofreading. This research was supported by a grant from the National Institutes of Health (R01MH085772 to T. Paus). This publication is the work of the authors and T. Paus will serve as guarantors for the contents of this paper and does not necessarily represent the official views of the National Institutes of Health. Z. Liao is supported by China Scholarship Council Award (201806380177).

Disclosures

Dr. Banaschewski served in an advisory or consultancy role for Lundbeck, Medice, Neurim Pharmaceuticals, Oberberg GmbH, Shire. He received conference support or speaker's fee by Lilly, Medice, Novartis and Shire. He has been involved in clinical trials conducted by Shire & Viforpharma. He received royalties from Hogrefe, Kohlhammer, CIP Medien, Oxford University Press. The present work is unrelated to the above grants and relationships. The other authors report no biomedical financial interests or potential conflicts of interest.

Data and code availability

Data are available upon request via ALSPAC: http://www.bristol.ac.uk/alspac/researchers/access/, and IMAGEN: https://imagen-europe.com/resources/imagen-project-proposal/. The R code used to compute the individual-canonical similarity and stability is available at https://github.com/Zhijie31/Similarity_stability.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2021.118587.

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