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Real-life behavioral and neural circuit markers of physical activity as a compensatory mechanism for social isolation

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Social isolation and loneliness pose major societal challenges accelerated by the coronavirus disease 2019 pandemic, especially for mental health. In this cohort study using accelerometry, electronic diaries and neuroimaging in a community-based sample of 317 young adults, we show that people felt affectively worse when lacking social contact, but less so when engaging in physical activity. This putative compensatory mechanism was present even at small physical activity doses and was pronounced in individuals with higher brain functional connectivity within the default mode network signaling risk for depression. Social-affective benefits of movement were higher in people showing exacerbated loneliness and were replicated throughout the pandemic. These findings extend the state of knowledge on the dynamic interplay of social contact and physical activity in daily life identifying an accessible protective strategy to mitigate the negative effects of social isolation, particularly among at-risk individuals, which comes with the potential to improve public health in the post-pandemic world.

Social isolation and loneliness increase human mortality like known health risk factors such as obesity, alcohol consumption or smoking 15 cigarettes per day[1]. Lack of social contact also impairs momentary affective well-being[2], impacts the structural and functional integrity of emotion regulatory brain networks[3,4] and is a potent risk factor for mood disorders[5]. Social distancing directives during the coronavirus disease 2019 (COVID-19) pandemic have exacerbated this public health problem and highlighted the importance of finding remedial strategies[6]. One promising strategy to mitigate the negative affective consequences of lack of social contact is physical activity, a known protective factor for affective well-being and mental health[7] with neural mechanistic links to emotion regulatory brain regions[8]. However, the everyday relevance and biological basis are unknown. In this study, we hypothesized that physical activity can compensate for the negative

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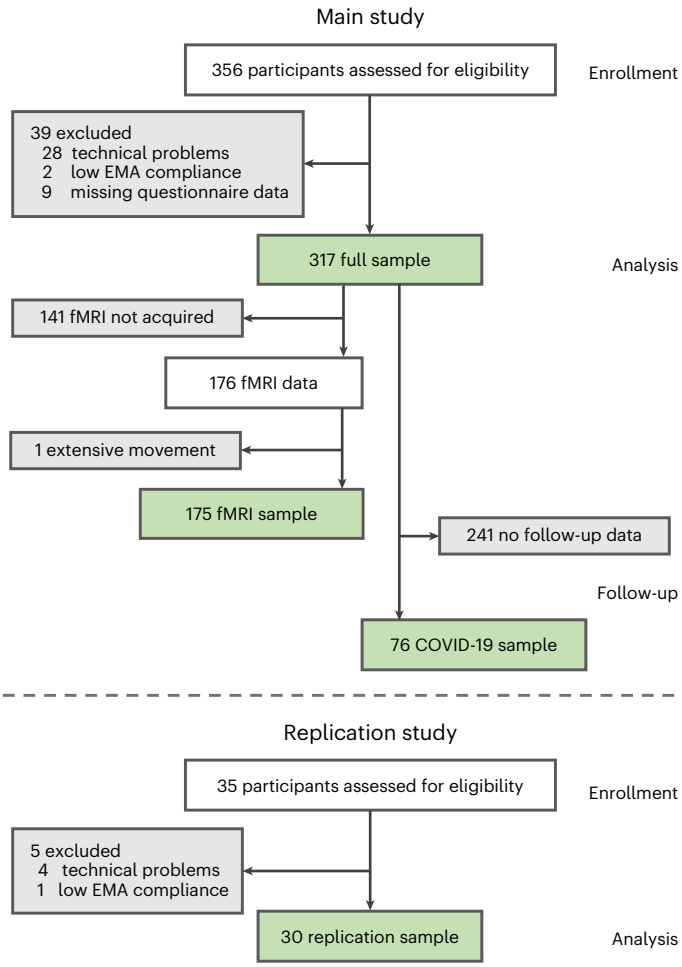

Fig. 1 | Participant flowchart. Participant numbers according to study stage. EMA, ecological momentary assessment.

affective effects of lacking social contact in daily life and that individuals at increased neural[4] and psychological[9] risk for depression benefit most from this compensatory mechanism.

Results

The physical activity of individuals (Fig. 1 and Table 1) significantly moderated the known relationship[2] between momentary social isolation and decreased affective valence in everyday life ($\beta = 0.01$; 95% confidence interval (CI) = 0–0.02; $P = 0.020$; Supplementary Table 2). Specifically, higher physical activity significantly decreased the reduction in affective well-being associated with the lack of social contact (Fig. 2a–c). According to our data, about 349 milli-g (g/1,000) physical activity across 1 h (for example, walking approximately three miles per hour) are necessary to fully compensate for the lack of affective well-being in everyday life (Supplementary Results 1). We successfully replicated this effect in the second sample we studied during the COVID-19 pandemic ($\beta = 0.03$; 95% CI = 0.02–0.04; $P < 0.001$; Fig. 2c, study 2; Supplementary Table 8). At the neurobiological level, individuals with higher resting-state functional connectivity within the default mode network (DMN), a risk phenotype for loneliness[4] and depression[10], compensated best for this momentary 'social-affective deficit' through physical activity ($\beta = 0.14$; 95% CI = 0.01–0.26; $P = 0.029$; Fig. 3b and Supplementary Table 3). Moreover, we observed similar benefits of physical activity at the between-individual level and related it to established psychological risk factors for mental health. First, participants with small social networks and high habitual physical activity levels exhibited lower trait loneliness compared to those with low levels of habitual physical activity ($\beta = 0.05$; 95% CI = 0.001–0.092, $P = 0.046$; Fig. 2d and Supplementary Table 4). Second, individuals with a pronounced compensatory mechanism were less likely to frequently feel lonely during the first COVID-19 lockdown (odds ratio (OR) = 0.92; 95% CI = 0.85–0.99; $P = 0.021$; Supplementary Table 5). Further exploratory analyses showed that offsetting the social-affective deficit with physical activity was effective even under pandemic-like constraints (curfews, closed gyms), for example, when only light physical activity ($\beta = 0.04$; 95% CI = 0–0.8; $P = 0.040$; Supplementary Table 6) and physical activity at home ($\beta = 0.08$; 95% CI = 0.01–0.15; $P = 0.032$; Supplementary Table 6) are considered.

Discussion

Our intensive e-diary and accelerometer-based longitudinal data suggest that physical activity can effectively and reproducibly compensate for the loss of affective well-being associated with lack of social contact in real life. While social contact and physical activity are well-known protective resources for mental health[1,5,7], previous studies have predominantly examined these factors using questionnaires or individually in the real world[2,8]. Our naturalistic study extends the state of knowledge by showing a dynamic interplay of both factors impacting human affective well-being in everyday life. Our data further show that about 1 h of walking at a speed of three miles per hour can compensate for the 'social-affective deficit' in everyday life and that this beneficial effect even persists when physical activity is performed at lower doses and only at home. This indicates a considerable potential of physical activity to counteract the negative affective consequences of social isolation in everyday life. Importantly, the effect was larger in people at higher neural risk for affective disorders. These included people from the general population with risk-related changes in DMN brain connectivity[4,10], smaller social networks[11] and frequently perceived loneliness under the regulatory constraints of the COVID-19 pandemic. Thus, our data not only suggest an effective and accessible strategy to mitigate the negative effects of social isolation and loneliness in everyday life, but also contribute to the identification of probable responders and enrich existing evidence-based recommendations for the preventive management of affective dysfunction in the post-pandemic world[6,9].

Limitations

We captured affective valence via an established scale specifically developed and validated for investigating mood in everyday life[12,13]. Therefore, our study provides insights into mood changes provoked by physical activity and social interaction. However, given the ongoing discussions on mood assessments in the field, future studies should examine the effects of physical activity in the context of lacking social contact on specific emotions (for example, anxiety, anger). Moreover, although our real-life observational data have high ecological validity, they do not allow for causal inferences. In particular, our findings show correlations and the temporal directionality of effects, but we cannot rule out potential influences of undiscovered third variables. Future studies should address the causality question by incorporating experimental manipulations such as just-in-time adaptive interventions into their real-life investigations.

Conclusion

Our multimodal epidemiological cohort study shows that physical activity is reproducibly linked to better affective well-being in people lacking social contact in daily life, especially in persons at neural and psychological risk for affective disorders. These data suggest an effective and accessible strategy to mitigate the negative effects of social isolation and loneliness that can improve public health and enrich existing evidence-based recommendations for the preventive management of social isolation in the post-pandemic world.

Table 1 | Demographic and psychological characteristics, ambulatory assessment and neuroimaging parameters of study 1

Measure	Full sample *n*=317			fMRI sample *n*=175			COVID-19 sample *n*=76		
	Mean	s.d.	*n*[a]	Mean	s.d.	*n*[a]	Mean	s.d.	*n*[a]
Demographic variables									
Age (years)	23.08	2.83	317	23.19	2.75	175	22.6	2.7	76
Sex, female/male	181/136	–	317	80/95	–	175	42/34	–	76
Education (years)	12.24	1.17	304	12.35	1.01	168	12.41	1.00	73
Nationality, German/other	297/20	–	317	163/12	–	175	71/5	–	76
Body mass index (kg m^{-2})	23.20	4.54	317	23.24	3.5	175	23.12	5.41	76
Smoking, nonsmoker/smoker	239/74	–	313	134/39	–	173	61/15	–	76
Household size (no. individuals)	2.65	1.33	316	2.69	1.31	175	2.53	1.21	76
Household income (€ per month)[b]	2,305	1,035	269	2,225	2,260	151	2,012.5	1,042.5	65
Psychological variables									
Socioeconomic status	14.31	3.30	317	14.31	3.30	175	14.16	3.47	76
Physical activity (h per week)	5.08	3.63	280	5.03	3.35	159	4.73	3.42	67
Social network size (individuals)	18.98	8.01	192	18.95	8.22	174	19.27	8.17	72
Trait neuroticism (NEO-FFI-30-N)[c]	1.31	0.77	316	1.20	0.72	174	1.19	0.73	76
UCLA Loneliness Scale	1.59	0.5	315	1.57	0.77	174	1.57	0.52	76
Trait anxiety (STAI-T)[d]	36.07	9.45	316	35.17	8.43	174	35.54	8.93	76
Schizotypal traits (SPQ)[e]	4.04	3.56	304	3.6	3.26	166	4.34	3.79	73
Ambulatory assessment									
Movement acceleration intensity (milli-g min^{-1})[f]	68.82	22.09	317	69.77	21.77	175	66.41	19.69	76
E-diary prompts per day	12.31	2.65	317	12.39	2.6	175	12.28	2.64	76
Compliance (%)	80.90	24.37	317	81.19	24.13	175	81.76	44.14	76
Affective valence	71.31	11.48	317	71.67	11.10	175	72.54	12.32	76
Intraclass correlation coefficient: affective valence[g]	0.35	–	317	0.35	–	175	0.42	–	76
fMRI data quality									
Number of valid scans	–	–	–	208.2	3.1	175	–	–	–
Mean frame-wise displacement (mm)	–	–	–	0.15	0.06	175	–	–	–

[a]*n* is the number of individuals for which the information for a given sample and variable was available. [b]We assessed monthly household income after taxes in 13 ordinal categories: (1) less than €500; (2) €500–749; (3) €750–999; (4) €1,000–1,249; (5) €1,250–1,499; (6) €1,500–1,749; (7) €1,750–1,999; (8) €2,000–2,249; (9) €2,250–2,499; (10) €2,500–2,999; (11) €3,000–3,999; (12) €4,000–4,999; and (13) more than €5,000. For the descriptive comparison of the two samples in this table, we assigned category means to individuals, for example, a value of €624.5 to a participant reporting a category. [c]Trait neuroticism: six self-rated items (five-point-scale)[19]. [d]Schizotypal traits: 22 self-rated items (yes/no; 1 point for yes)[20]. [e]Trait anxiety: 20 self-rated items (response options 1–4)[21]. [f]Values were averaged across participants and the study week, respectively. [g]We used intraclass correlation coefficients to calculate the variance estimates of our outcome variables: in the study, 35.0% of the variance in affective valence can be attributed to within-individual variation. NEO-FFI-30-N, 30-item short version of the NEO Five-Factor Inventory; SPQ, Schizotypal Personality Questionnaire; STAI-T, State-Trait Anxiety Inventory; UCLA, University of California, Los Angeles.

Methods

The cohort study was conducted in accordance with ethical guidelines for medical research compliant with the Declaration of Helsinki 2013 version. All participants provided written informed consent for a study protocol approved by the institutional review board of Heidelberg University. Medical Faculty Mannheim (medical ethics committee II) at the Ruprecht-Karls-University in Heidelberg approved both studies (study 1: approval no. 2014-555N-MA; study 2: approval no. 2019-733N). Participants received monetary compensation for their effort. The flowchart depicts how the study size was arrived at in both the main (study 1) and the replication study (study 2); see Fig. 1.

Study population and measures

We studied a community-based cohort of 317 healthy young adults aged 18–28 years (57.09% females), recruited from September 2014 to November 2018, for 7 days during everyday life (Table 1 and Supplementary Table 1). We further studied a replication sample of 30 healthy adults aged 18–63 years, recruited from December 2019 to July 2022, for 6 months during everyday life during the COVID-19 pandemic in Germany (Supplementary Table 7). The biological sex of participants was determined using a questionnaire.

Participants wore accelerometers on their hip (study 1) or wrist (study 2) to measure their physical activity, and repeatedly reported their real-life social contact and affective valence using smartphone-based e-diaries (Fig. 2a). Established multilevel reliability measures (Spearman–Brown[14]) yielded sound coefficients of $\rho = 0.80$ (within-individual level) and $\rho = 0.94$ (between-individual level) in our sample and for the two affective valence variables assessed (that is, unwell to well and content to discontent). Moreover, within and between person correlations of the two items applied yielded positive correlations ($r_{within} = 0.66$; $r_{between} = 0.88$), which indicates convergent validity for the affective valence assessment instrument applied. Participants additionally completed a battery of psychological questionnaires[11,15], and we continuously tracked their geographical locations and situational contexts as described previously[2] (Fig. 2b and Supplementary Information 1). A total of 175 participants from study 1 additionally underwent a resting-state functional magnetic resonance imaging (fMRI) scan

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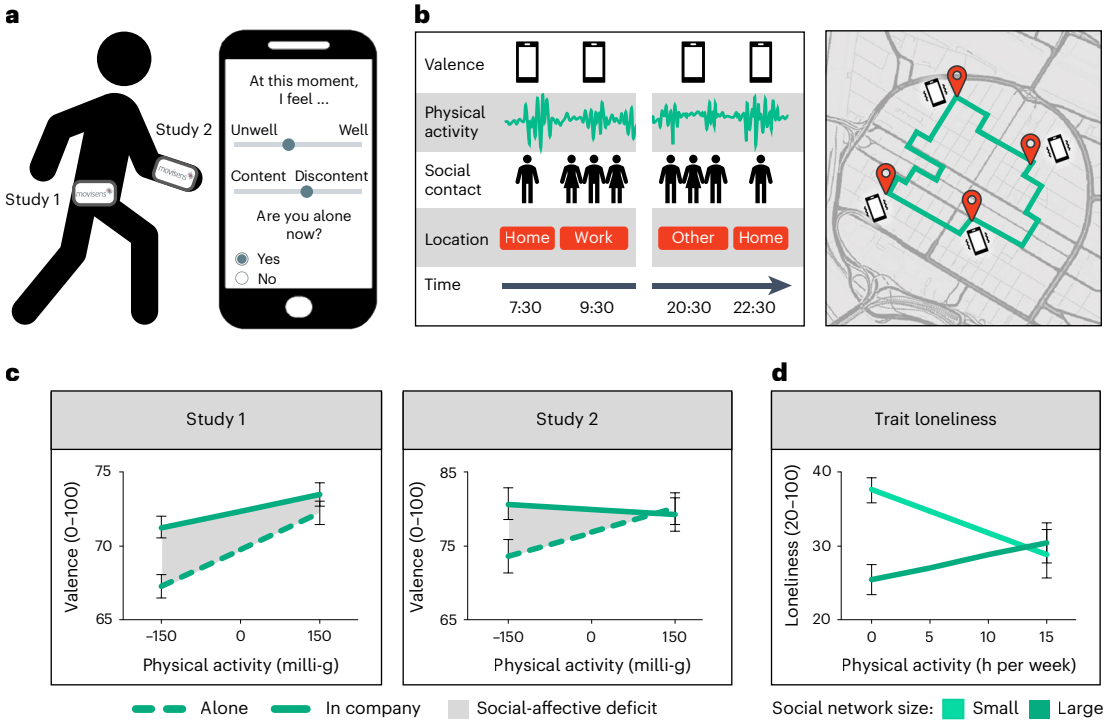

Fig. 2 | Ambulatory assessment and behavioral study findings. **a**, Accelerometry was used to measure physical activity, while affective valence and social contact were assessed through ecological momentary assessment. **b**, Exemplified sampling scheme: geolocations were continuously tracked and assigned using an advanced day reconstruction method (for example, at home, work). E-diaries were either location-based or triggered at random times. **c**, Study 1 (n = 317; Table 1). Physical activity engagement (x axis) offsetting the social-affective deficit (y axis) associated with the absence of real-life social contact as illustrated by the gray-shaded area between the solid (in company) and dashed (alone) green lines. The regression lines, derived from the multilevel interaction analyses (outcome: affective valence; predictor: real-life social contact; moderator: physical activity centered within-individual), demonstrate that the more participants had been physically active before an e-diary assessment, the less affective loss they experienced when being alone. Physical activity values to the very left of the x axis refer to sedentary behavior such as sitting, while values to the very right depict moderate activities such as walking. Study 2 (n = 30; Supplementary Table 7). Replication of the compensatory effect of physical activity during the COVID-19 pandemic. P values for the beta coefficients are two-sided and were derived from the t-statistics of the multilevel model. The error bars indicate the s.e. of the respective estimated mean valence scores. **d**, Trait loneliness. Participants with small social networks (light green) who engaged in high habitual levels of physical activity reported lower trait loneliness compared to those engaging in low habitual levels of physical activity (Supplementary Table 4). P values are two-sided and were derived from the t-statistics of the multiple linear regression. The error bars indicate the s.e. of the respective estimated mean loneliness scores. Credit: **a**, smartphone icon, Elisa Riva, Pixabay.com. Map in **b** created using OpenStreetMap.

after the ambulatory study week to quantify DMN connectivity (Supplementary Results 2), a neural risk marker for social isolation and depression[4,10]. In 76 participants from study 1, we additionally assessed individuals' perceptions of loneliness during the ongoing first wave of the COVID-19 pandemic (Supplementary Results 4).

Power analysis

Because statistical power analyses of multilevel models strongly depend on a host of assumptions (for example, on random slopes, covariance structure) that cannot be drawn in the absence of the final dataset[16], we estimated whether our final sample size of n = 317 was suitable to detect the expected effects referring to the most recent simulation studies[17]. According to these simulation studies, a sample size of n = 200 was necessary to detect the minimum detectable effect size (0.08) in a level-1 direct effect analysis given a level-1 sample size of at least 30 at a power of 80%, which provides evidence for the sufficient power of our analysis.

Data analysis

All statistical analyses were performed with SAS v.9.4. Brain imaging data were analyzed using the CONN toolbox v.19c in MATLAB v. 9.8 (R2020a). Study 1: within participants (main model), we analyzed the main and interaction effects of momentary social contact (predictor: alone versus in company) and momentary physical activity (moderator: mean of milli-g in the 60 min before an e-diary prompt) on momentary affective valence (outcome) using multilevel models with time of day, time of day squared, current location (level 1), sex, age and body mass index (level 2) as covariates. Between participants, we predicted trait loneliness (outcome) with the main and interaction terms of social network size[11] (predictor) and habitual physical activity level (moderator: hours per week). In addition, we predicted the frequency of perceived loneliness during the first COVID-19 lockdown (outcome) by extracting random slopes from the multilevel interaction of social contact and physical activity on affective valence (predictor: from the main model) and fitting an ordinal logistic regression model assuming proportional odds. At the neural level, we computed DMN connectivity estimates from the participants' resting-state fMRI data (Fig. 3) and introduced them as an additional moderator into our main model, resulting in a three-way multilevel interaction analysis. In study 2, we used the main model of study 1 to replicate the findings during the ongoing COVID-19 pandemic (see Supplementary Information for more details).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

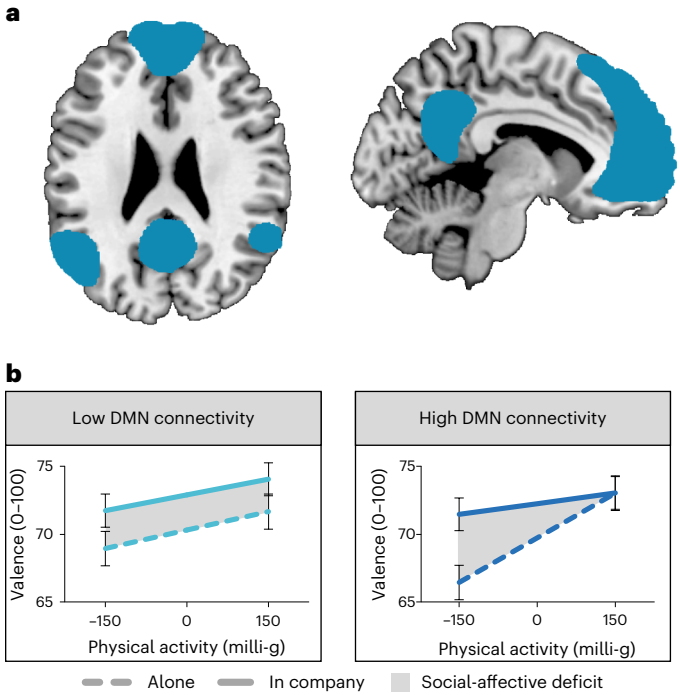

Fig. 3 | DMN and study findings at the neural level. a, According to the neuronal signatures seen in 'lonely brains', we analyzed the within-network connectivity of the DMN based on the 100-region, 7-network Schaefer–Yeo parcellation atlas[18]. **b**, Participants with higher within-DMN connectivity, a neuronal signature repeatedly found in lonely individuals and associated with affective disorders, showed a pronounced compensation of the momentary 'social-affective deficit' through physical activity (Supplementary Table 3). *P* values for the beta coefficients are two-sided and were derived from the *t*-statistics of the multilevel model. The error bars indicate the s.e. of the respective estimated mean valence scores.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request. Figures 1, 2 and 3 have associated raw data. For the neuroimaging analysis we used a 100-region, 7-network parcellation atlas[18]: https://github.com/ThomasYeoLab/CBIG/tree/master/stable_projects/brain_parcellation/Schaefer2018_LocalGlobal/Parcellations/MNI.

Code availability

The custom code used for the analyses of this study is available from the corresponding author upon reasonable request.

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Author contributions

A.B. and M.R. contributed equally to the study. A.M.-L. and H.T. were co-senior authors. M.R., U.E.-P., A.M.-L. and H.T. conceived and designed the study. A.B., M.R., O.B. and A.M. acquired the data. A.B., M.R., M.G., I.T. and I.R. analyzed the data. A.B., M.R., A.M.-L. and H.T. drafted the paper. A.B., M.R., M.G., I.T., I.R., C.N., O.B., A.M., C.v.d.G., U.B., U.E.-P., A.M.-L. and H.T. participated in interpreting the data and developing further stages and the final version of the paper.

Competing interests

A.M.-L. has received consultant fees from the Daimler and Benz Foundation, EPFL Brain Mind Institute, Fondation FondaMental, Hector II Foundation, Invisio, Janssen-Cilag GmbH, Lundbeck A/S, Lundbeckfonden, Lundbeck Neuroscience Foundation, Neurotorium, MedinCell, The LOOP Zürich, University Medical Center Utrecht, University of Washington, the Mental Wellbeing Association and the von Behring-Röntgen Foundation; speaker fees from Ärztekammer Nordrhein, Caritas, Clarivate, the German Society for Neuroscientific Assessment, Gentner Verlag, the State Medical Association Baden-Württemberg, LWL Bochum, Northwell Health, Ruhr University Bochum, Penn State University, the Society of Biological Psychiatry, the University Prague and Vitos Klinik Rheingau; and editorial or author fees from the American Association for the Advancement of Science, the European College of Neuropsychopharmacology, Servier Int. and Thieme Verlag. U.E.-P. reports consultancy for Boehringer Ingelheim and speaker honorarium from Angelini Pharma. The other authors declare no competing interests.

Additional information

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Software and code

Policy information about availability of computer code

Data collection	Study 1: movisensXS, version 0.6.3658 (movisens GmbH, Germany, https://xs.movisens.com); Geocoder software 1.0 (movisens GmbH, Germany,www.movisens.com) Study 2: movisensXS, version 1.5-INDICATE (movisens GmbH, Germany, https://xs.movisens.com)
Data analysis	SAS software version 9.4, SAS Institute Inc., Cary, NC, USA; CONN-toolbox v.19c (http://web.mit.edu/swg/software.htm); SPM12 (www.fil.ion.ucl.ac.uk/spm); DataAnalyzer, version 1.6.12129 (movisens GmbH, Germany, www.movisens.com); MATLAB version 9.8 (R2020a), The MathWorks, Inc., Natick, Massachusetts, USA

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The data that support the findings of this study are available from the corresponding author upon reasonable request. The Figures 1, 2 and eFigure 1 have associated raw data. The custom code used for the analyses of this study is available from the corresponding author upon reasonable request.

For the neuroimaging analysis we used a 100 regions 7 networks parcellation atlas21: https://github.com/ThomasYeoLab/CBIG/tree/master/stable_projects/brain_parcellation/Schaefer2018_LocalGlobal/Parcellations/MNI

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	sex
Reporting on race, ethnicity, or other socially relevant groupings	nationality
Population characteristics	We studied a community-based cohort of 317 healthy young adults aged 18 to 28 years (57.09 % females) for 7 days in everyday life (study 1). We further studied a replication sample (study 2) of 30 healthy adults aged 18 to 63 years (50% females) for 6 months in everyday life during the COVID-19 pandemic in Germany.
Recruitment	Study 1: Based on a two-stage proportionally layered procedure (stratified by age, sex, and nationality), participants were randomly selected from population registries at the Psychiatric-Epidemiological Center at the Central Institute of Mental Health (CIMH; Mannheim, Germany) between September 2014 and October 2018. To the best of our knowledge, there was no self-selection bias. Study 2: Participants were recruited from the local community by advertisement between December 2019 and July 2022.
Ethics oversight	The Medical Faculty Mannheim (medical ethics committee II) at the Ruprecht-Karls-University in Heidelberg approved both studies.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☒ Behavioural & social sciences ☐ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	In this cohort study using accelerometry, electronic diaries and neuroimaging in a community-based sample of 317 young adults, we show that people felt worse when lacking social contact, but less so when engaging in physical activity.
Research sample	Since we were interested in resilience mechanisms for mental health we studied a community-based cohort of 317 healthy young adults aged 18 to 28 years (57.09 % females), recruited from September 2014 to November 2018, for 7 days in everyday life. According to our sampling strategy we consider the sample to be representative.
Sampling strategy	Based on a two-stage proportionally layered procedure (stratified by age, sex, and nationality), participants were randomly selected from population registries at the Psychiatric-Epidemiological Center at the Central Institute of Mental Health (CIMH; Mannheim, Germany) between September 2014 and October 2018. To the best of our knowledge, there was no self-selection bias.
Data collection	Study 1: Participants wore a triaxial accelerometers (Move II or Move III; movisens GmbH, Germany) for 7 consecutive days during waking hours on the right hip. Study 2: Participants wore a triaxial accelerometers (Move 4; movisens GmbH, Germany) on their non-dominant wrist.

	Besides the researcher, research assistants were present during data collection, but not aware of the specific research question.
Timing	Study 1: Participants were recruited from September 2014 to November 2018, for 7 days in everyday life. Study 2: Participants were recruited from December 2019 to July 2022, for 6 months in everyday life during the COVID-19 pandemic in Germany.
Data exclusions	Following established procedures, we excluded participants if the following criteria applied: (i) severe technical problems with the accelerometer such as a prematurely terminated measurement (N = 28), (ii) e-diary compliance below 30% (N = 2), or (iii) missing questionnaire data (N = 9). The final sample consisted of 317 healthy participants (57.09 % females) with a mean age of 23.08 years (SD = 2.83).
Non-participation	No participants dropped out/declined participation.
Randomization	Randomization was not relevant because we conducted an observational and no intervention study.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☐	☒ MRI-based neuroimaging

Plants

Seed stocks	*Report on the source of all seed stocks or other plant material used. If applicable, state the seed stock centre and catalogue number. If plant specimens were collected from the field, describe the collection location, date and sampling procedures.*
Novel plant genotypes	*Describe the methods by which all novel plant genotypes were produced. This includes those generated by transgenic approaches, gene editing, chemical/radiation-based mutagenesis and hybridization. For transgenic lines, describe the transformation method, the number of independent lines analyzed and the generation upon which experiments were performed. For gene-edited lines, describe the editor used, the endogenous sequence targeted for editing, the targeting guide RNA sequence (if applicable) and how the editor was applied.*
Authentication	*Describe any authentication procedures for each seed stock used or novel genotype generated. Describe any experiments used to assess the effect of a mutation and, where applicable, how potential secondary effects (e.g. second site T-DNA insertions, mosiacism, off-target gene editing) were examined.*

Magnetic resonance imaging

Experimental design

Design type	Resting-state (duration: 6:52 minutes, 206 whole-brain scans).
Design specifications	Participants were instructed to relax, not engage in any particular mental activity during the scan and to keep their eyes open, while a gray background with a fixation cross was presented.
Behavioral performance measures	During resting-state fMRI measurements participants do not perform any behavioral tasks.

Acquisition

Imaging type(s)	functional magnetic resonance imaging
Field strength	3 Tesla
Sequence & imaging parameters	Functional data were acquired with an echo-planar-imaging sequence with the following parameters: echo time (TE) 30 ms, 28 oblique slices oer volume, 4 mm slice thickness, 1 mm slice distance, repetition time (TR) 2000 ms, 80° flip angle,

192 mm field of view (FOV) and 64 x 64 matrix.

Area of acquisition: whole-brain

Diffusion MRI ☐ Used ☒ Not used

Preprocessing

Preprocessing software: SPM12 (www.fil.ion.ucl.ac.uk/spm); CONN-toolbox v.19c (http://web.mit.edu/swg/software.htm).

Normalization: Direct normalization to the MNI template (T1-weighted).

Normalization template: Montreal Neurological Institute (MNI) space with resampling to 2 × 2 × 2 mm voxels.

Noise and artifact removal: CompCor approach (White Matter and CSF ROIs, 6 motion parameters + 6 first-order temporal derivatives).

Volume censoring: Scrubbing of movement-related outlier scans with a framewise displacement > 0.9 mm or global BOLD signal changes > 5 standard deviations.

Statistical modeling & inference

Model type and settings: The extraction of resting-state functional connectivity values does not require any statistical model.

Effect(s) tested: n/a

Specify type of analysis: ☐ Whole brain ☒ ROI-based ☐ Both

Anatomical location(s): All nodes of the default mode network (specifically, regions 38 – 50 and 90 – 100 of the atlas) as defined by the Schaefer-Yeo 100 regions parcellation.

Statistic type for inference: n/a

(See Eklund et al. 2016)

Correction: n/a

Models & analysis

n/a	Involved in the study
☐	☒ Functional and/or effective connectivity
☒	☐ Graph analysis
☒	☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity: Functional connectivity was calculated by computing pairwise Pearson correlations between the time series of two DMN regions of interest as defined by the Schaefer-Yeo 100 regions parcellation.