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# Association between real-world experiential diversity and positive affect relates to hippocampal–striatal functional connectivity

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**Experiential diversity promotes well-being in animal models. Here, using geolocation tracking, experience sampling and neuroimaging, we found that daily variability in physical location was associated with increased positive affect in humans. This effect was stronger for individuals who exhibited greater functional coupling of the hippocampus and striatum. These results link diversity in real-world daily experiences to fluctuations in positive affect and identify a hippocampal–striatal circuit associated with this bidirectional relationship.**

Experiential diversity confers substantial benefits for cognitive and affective function[1]. Animals able to roam freely within 'enriched' environments that offer diverse and variable experiences exhibit greater affective well-being than those reared in standard laboratory environments[1]. In rodents, exposure to enriched environments facilitates play[2], social affiliative behavior[3], optimistic evaluative biases[4] and stress resilience[5]. Each of these behavioral phenotypes in rodent models is characteristic of positive affective states in humans[6], underscoring the benefits of experiential diversity for psychological well-being. The behavioral effects of environmental enrichment are paralleled by pronounced changes in brain structure and function across a number of regions[7]. In particular, plastic synaptic changes in the hippocampus and striatum of animals reared in complex environments[7] highlight these brain regions as potential mediators of the beneficial consequences of experiential diversity.

Increased exposure to novelty may be a central mechanism through which enriched environments promote positive affect. While the increased physical activity and social interaction afforded by enriched environments facilitate positive behavioral outcomes[7], environmental novelty alone is sufficient to produce many benefits of enrichment[8]. Behavioral and neural data suggest that exposure to novelty has subjectively rewarding and reinforcing properties[9,10]. For example, novel stimuli can effectively reinforce action[10], elicit activity in reward-sensitive dopaminergic neurons[9] and promote a preference for the contexts in which they are encountered[11]. The same hippocampal–striatal circuit implicated in the effects of environmental enrichment is also centrally involved in novelty detection, as well as the encoding of reward and positive affective states[9,10,12]. Collectively, these empirical findings corroborate a long-standing theoretical proposal that novel experiences may function as intrinsic rewards and generate positive affect[13]. However, no study to date has examined whether variation in real-world experiential diversity is associated with positive affective states in humans.

Because humans live in a complex and dynamic environment, daily living ostensibly affords limitless opportunity for experiential diversity. However, exposure to novel experiences, and their rewarding effects, depends on the degree to which individuals exploit this opportunity by exploring their environment. Roaming entropy (RE), which indexes the variability in an individual's physical location over the course of a day, is a quantitative, location-derived metric of experiential diversity[14]. In rodents, increased levels of RE reproduce the key neural and cognitive effects of environmental enrichment[14]. In the present study, we examined whether daily RE might serve as an ecologically valid measure of experiential diversity in humans and, accordingly, whether day-to-day variation in RE might relate to fluctuations in positive affect.

We conducted geolocation tracking on a sample of 132 human participants (90 females; aged 18–31 years, mean (s.d.) age = 23 (3.4) years) recruited in three cohorts in New York and Miami. Participants' locations were tracked continuously for 3–4 months (mean (s.d.) = 104.6 (22.1) d). During geolocation tracking, participants were prompted to provide assessments of positive affect (PA) and negative affect (NA) via a questionnaire sent to their mobile phones. Affect assessments were delivered at random times every other day. Ten participants who responded to fewer than 20 ecological momentary assessments (EMAs) were excluded (Supplementary Fig. 1), leaving 122 participants (84 female; mean (s.d.) age = 22.75 (3.36) years) for inclusion.

Each day with adequate geolocation data (Supplementary Figs. 2 and 3) was downsampled to 1-min temporal resolution and converted into a measure of daily RE, previously used to quantify rodent exploratory behavior[14]:

$$RE = \sum_{j=1}^{n} (p_{ij} \times (\log_2 p_{ij}))/\log(n)$$

In this equation, $p_{ij}$ is the within-day historical probability that location $j$ was visited by participant $i$ (that is, the proportion of the day spent in each unique location), and $n$ is the total number of unique locations in the environment, at a GPS resolution of four-decimal degrees. Thus, RE is higher for days in which one visits a greater number of locations and exhibits greater uniformity in the time distribution across visited locations. A minimum RE value would be achieved by spending all day in a single location, whereas maximum RE would, theoretically, be achieved by

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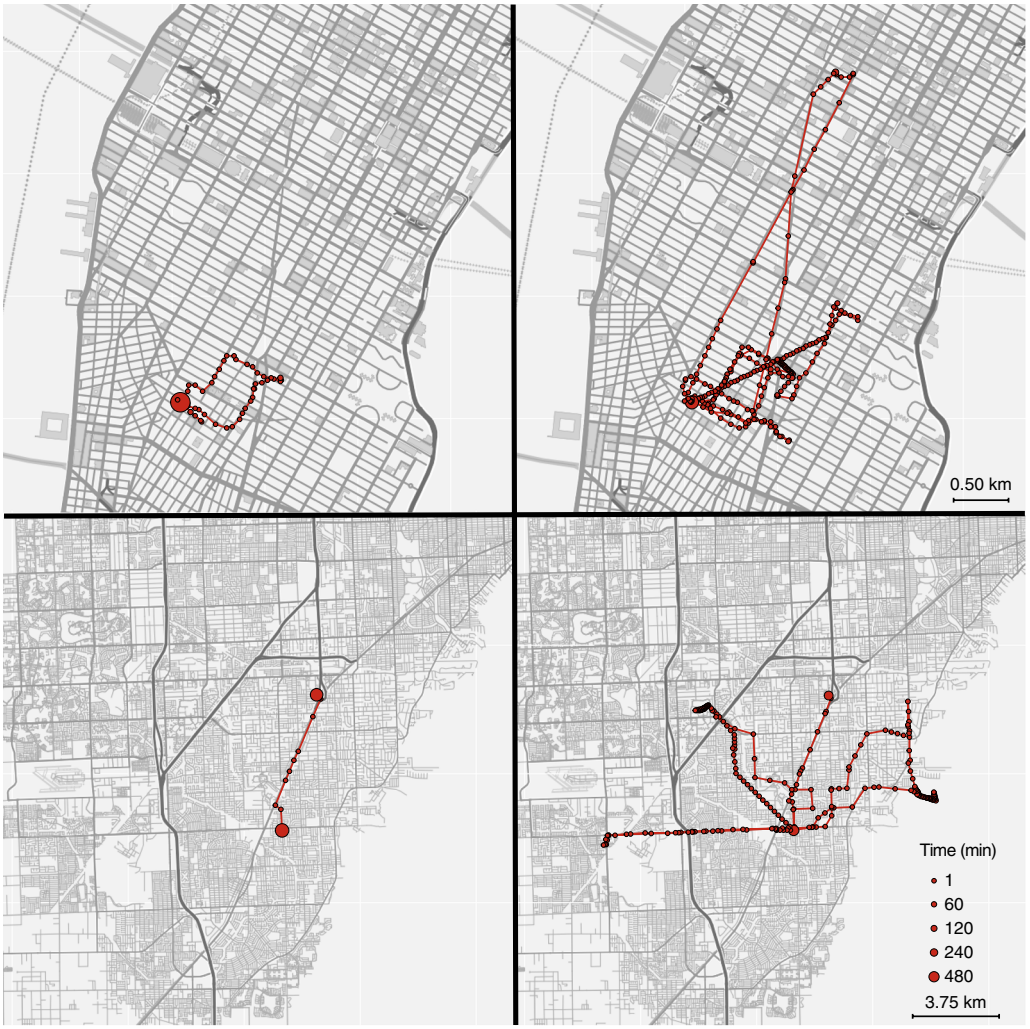


**Fig. 1 | Geolocation tracking in New York and Miami.** Representative days with low (left column) and high (right column) RE from one participant in New York (top row) and one participant in Miami (bottom row). Map tiles by Stamen Design, under CC BY 3.0. Map data by OpenStreetMap.org contributors.

spending an equal proportion of the day in each unique location in an environment (Fig. 1).

We examined whether RE was associated with day-to-day variation in self-reported positive affect and negative affect (Supplementary Figs. 4 and 5), with the following potentially confounding factors included in the model: distance traveled for that day, city (Miami or New York), day of the week, time of day that the EMA was completed, and temperature and precipitation at the modal location for that day. Across participants, self-reported positive affect was higher on days when RE was greater ($B = 0.79$, $t(3{,}834) = 2.464$, $P = 0.014$; Supplementary Table 1). The RE metric corresponded closely to the number of unique locations visited in a day (mean within-individual correlation, 0.85; Supplementary Note 1 and Supplementary Fig. 6), and both RE and this simpler metric were significantly predictive of positive affect. Of the other variables in the model, only day of the week was significantly associated with positive affect (Supplementary Table 1), with positive affect lower during the early to middle part of the week as compared to the weekend (Extended Data Fig. 1). There was no significant relationship between RE and negative affect ($B = -0.19$, $t(3{,}835) = -0.66$, $P = 0.509$; Supplementary Table 2).

These findings suggest that increased diversity in one's daily spatial environment is associated with greater positive affect. We next sought to test whether this relationship might reflect increased exposure to novel and diverse experiences on days with higher RE. Our limited geolocation tracking period did not allow us to determine whether an individual had ever previously visited a specific location or the location was truly novel. However, we derived a putative measure of location novelty by calculating the number of unique locations an individual visited each day that had not previously been visited during the tracking period. The number of novel locations correlated positively with RE ($B = 0.0005$, $t(9{,}697) = 141.03$, $P < 0.001$; mean within-individual correlation, 0.79) and was also significantly associated with positive affect ($B = 1.60$, $t(3{,}473) = 4.676$, $P < 0.001$). Moreover, when both RE and the number of novel locations were included in the model, the latter remained associated with positive affect ($B = 2.44$, $t(3{,}472) = 4.40$, $P < 0.001$), whereas RE was no longer significantly associated with positive affect ($B = -1.06$, $t(3{,}472) = -1.94$, $P = 0.053$). These analyses suggest that increases in RE may indeed be associated with heightened exposure to novelty and that daily novelty exposure is associated with positive affect. However, given our limited temporal window of observation, this result should be corroborated in a study in which absolute location novelty can be accurately determined.

We next tested whether RE is associated with diversity in specific dimensions of the experiences that an individual has in a given day. We extracted US Census Bureau data capturing the sociodemographic features of each location visited by a participant, for example, population density, median age, total businesses, educational attainment, unemployment rate, race and gender (Supplementary

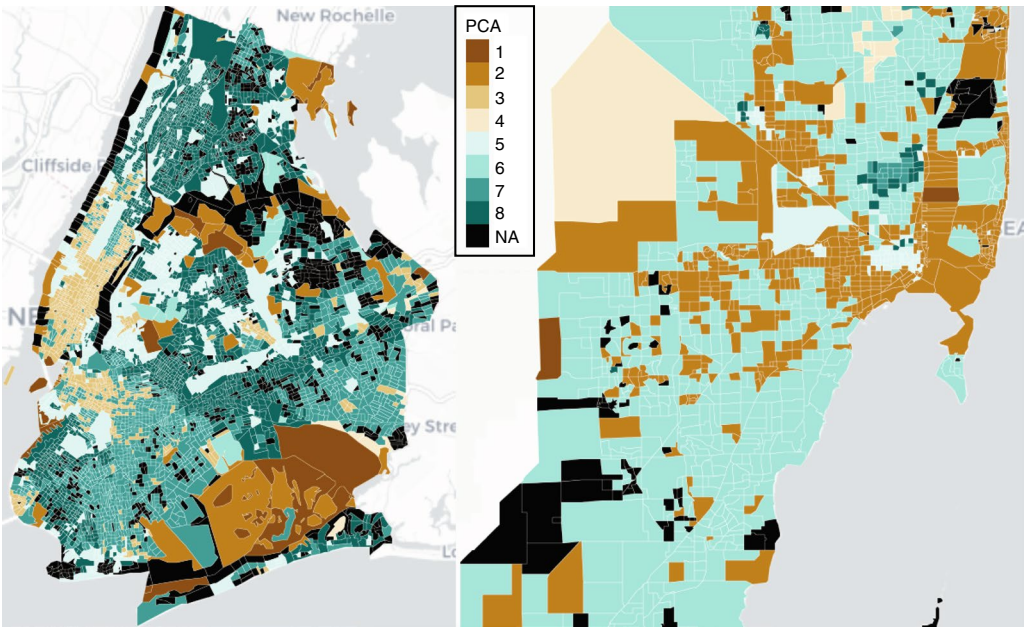


**Fig. 2 | Physical location transformed into sociodemographic feature space.** Maps depicting the sociodemographic feature space of New York (left) and Miami (right) at the spatial resolution of a block group. Colored locations represent positions in this sociodemographic feature space derived from our discretized PCA. Daily entropy over this sociodemographic feature space was associated with $PA_t$ ($n = 122$, independent human participants). Map tiles by CARTO under CC BY 4.0. Map data by OpenStreetMap.org contributors. NA, not assessed.

Appendix 1). We used principal-component analysis (PCA) to reduce the dimensionality of the data (Supplementary Table 3). We discretized the values for the first three components into high and low values, and we recoded each location as one of eight possible locations in this 2 × 2 × 2 (PC1 (low/high) × PC2 (low/high) × PC3 (low/high)) sociodemographic feature space. Consistent with our hypothesis that RE might be associated with greater diversity in one's daily experiences, RE was significantly correlated with entropy over this sociodemographic feature space ($B = 5.55$, $t(9{,}697) = 78.56$, $P < 0.001$). As large spatial extents of both New York and Miami contain a limited range of values in this sociodemographic space (Fig. 2), this correlation is not a trivial consequence of each visited GPS location having a unique location in the PCA-derived sociodemographic feature space. Greater entropy over sociodemographic environmental features was also associated with increased positive affect ($B = 1.14$, $t(3{,}834) = 3.48$, $P = 0.0005$; Supplementary Table 3). Moreover, when both RE and sociodemographic feature entropy were included in the model, the latter remained significantly associated with positive affect ($B = 0.94$, $t(3{,}833) = 2.21$, $P = 0.027$), whereas RE was no longer associated with positive affect ($B = 0.35$, $t(3{,}833) = 0.870$, $P = 0.384$). Collectively, these analyses suggest that the RE measure of location variability is associated with exposure to diverse sociodemographic features of the environment and that increases in such experiential diversity, above and beyond location variability, are associated with day-to-day variation in positive affect.

While it is possible that the novel and diverse experiences associated with high-RE days facilitate positive affect, another possibility is that individuals are more motivated to explore their environments during days in which they feel better. To examine the potential directionality of our observed effect, we conducted analyses of the temporal relationship between RE and positive affect. We first tested whether the previous day's RE influenced positive affect on a given day. When including the RE for both the previous ($RE_{t-1}$) and current ($RE_t$) day in a model predicting the current day's positive affect ($PA_t$), only $RE_t$ significantly predicted $PA_t$ ($B = 0.87$, $t(3{,}367) = 2.498$, $P = 0.0125$), whereas $RE_{t-1}$ did not ($B = 0.31$, $t(3{,}367) = 0.957$, $P = 0.339$). We also examined whether $PA_t$ predicted RE on the following day ($RE_{t+1}$); no significant relationship existed between $PA_t$ and $RE_{t+1}$ ($B = 0.0008$, $t(3{,}396) = 1.029$, $P = 0.3037$) in a model that also included $RE_t$.

Next, we repeated these temporal analyses with the measures of daily novelty exposure and sociodemographic experiential diversity, each of which was more strongly related to positive affect than RE itself. The number of novel locations for both the concurrent ($B = 1.66$, $t(3{,}031) = 4.476$, $P < 0.001$) and previous ($B = 0.73$, $t(3{,}031) = 2.121$, $P = 0.034$) day and the sociodemographic entropy for the concurrent ($B = 1.12$, $t(3{,}367) = 3.219$, $P = 0.0013$) and previous ($B = 0.61$, $t(3{,}367) = 2.085$, $P = 0.037$) day significantly predicted a given day's positive affect. We also observed a significant effect in the opposite temporal direction, such that a given day's positive affect significantly predicted both the following day's number of novel locations ($B = 0.003$, $t(3{,}079) = 3.477$, $P = 0.0005$) and entropy over sociodemographic features of the environment ($B = 0.002$, $t(3{,}396) = 3.066$, $P = 0.002$), with the concurrent day's value for each variable included in the models. These analyses suggest a bidirectional and temporally extended interaction in which novelty and experiential diversity are associated with greater subsequent positive affect, which in turn is associated with more novel and diverse experiences on the subsequent day. This is consistent with theoretical proposals that behaviors promoting positive emotions can engender self-reinforcing 'upward spirals' (ref. [15]), fostering subsequent repetition of those same behaviors. Nonetheless, future studies that directly manipulate positive affect, or exposure to novel and diverse experiences, will be critical to provide causal evidence for such bidirectional effects.

To better understand the neural mechanisms associated with the relationship between RE and positive affect, we performed a resting-state functional magnetic resonance imaging (rs-fMRI) scan in approximately half of the participants ($n = 58$) at the end of the geolocation tracking period. We used the random-effects estimates from the multilevel model for each individual as an index of the strength of coupling between RE and positive affect. We defined an anatomical seed region in the ventral striatum, an area widely

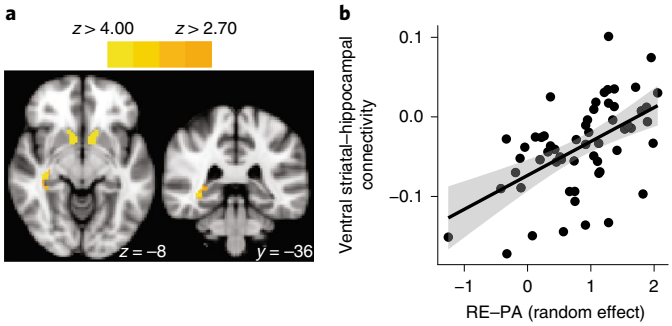


**Fig. 3 | Entropy–affect association is linked to hippocampal–ventral striatal connectivity. a**,**b**, Resting-state functional connectivity between (**a**) a ventral striatal seed and the posterior hippocampus (**b**) correlates positively with individual differences in the degree to which RE is associated with positive affect. The shaded band represents the 95% confidence interval on the best-fitting regression line ($n = 58$ participants).

associated with the subjective experience of positive affect, as well as the processing of reward and novelty[12]. We conducted a whole-brain analysis, corrected for multiple comparisons, to identify regions of the brain in which resting-state functional connectivity with the ventral striatum was associated with a stronger relationship between RE and positive affect (controlling for mean PA, RE and frame-wise displacement, and cohort; Fig. 3). This analysis identified a cluster within the right posterior hippocampus ($[x = 34, y = -24, z = -8]$, $B = 0.08$, $t(52) = 4.51$, $P < 0.001$; Supplementary Table 5 and Supplementary Fig. 7). This finding suggests that functional integration of the striatum and the hippocampus, regions that are centrally implicated in the processing of reward and environmental novelty, is associated with the strength of the relationship between experiential diversity and positive affect.

Our findings demonstrate that objectively measured increases in the diversity of one's physical environment are associated with increases in positive affect and link connectivity within a hippocampal–striatal circuit to the strength of this effect. The hippocampus is centrally implicated in both the representation of spatial location and the detection of novelty[9,10]. Exposure to novel spatial environments elicits hippocampal activity that drives dopamine release in the nucleus accumbens via glutamatergic projections[9,10]. These projections play a necessary role in the formation of associations between spatial locations and primary rewards[16] and are also proposed to underpin the rewarding properties of novelty[9,10]. Consistent with this proposal, individuals with greater hippocampal–ventral striatal tract strength also exhibit higher levels of novelty-seeking traits[17]. Collectively, this literature suggests that hippocampus–nucleus accumbens functional connectivity might influence the degree to which novelty and diversity in one's spatial environment are experienced as subjectively rewarding, which in turn may promote subsequent exploratory or novelty-seeking behavior. While these data do not afford a direct test of this hypothesis, future studies might examine whether changes in the magnitude of hippocampal–striatal functional coupling mediate the strength of the relationship between RE and positive affective states.

By harnessing data that objectively quantify defining features of locations, we found that exposure to diverse social and demographic features of visited locations was also associated with positive affect. This same approach could be leveraged to examine whether experiential diversity across other environmental feature dimensions (for example, developed versus natural environments[18]) relates to fluctuations in affective state. While our analysis focused on location-related diversity in daily experience, diverse experiences that occur independently of any change in physical location (for example, social interactions and professional or leisure activities) have also been related to positive affect[19]. Future studies seeking to link real-world daily activities to emotional well-being might assay such behaviors, as well as examine whether the relationship between experiential diversity and positive affect depends on the degree to which one's movements or activities are volitional or subject to external constraints[20].

Evidence from rodent models indicates that diversity of daily experience alters the function of neural circuits and increases behavioral indices of affective well-being. Here, we demonstrated that objectively measured increases in the daily diversity of one's physical location were associated with corresponding increases in positive affect, an effect that was related to greater functional coupling of a hippocampal–striatal circuit. Collectively, these findings translate a broad literature on the beneficial consequences of environmental enrichment across species, demonstrating a relationship between real-world exposure to novel and diverse experiences and increases in positive affect in humans and linking this bidirectional association to the engagement of hippocampal–striatal neural circuitry.

## Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41593-020-0636-4.

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## Methods

**Participants.** A total of 132 young adults (90 female; mean (s.d.) age = 23 (3.4) years, range 18–31 years) were recruited in three cohorts from the New York City and Miami areas via fliers and posted advertisements. Participants were required to have a smartphone that could receive text messages and that met system requirements to run the study application. A subset of participants recruited in New York City (first cohort) were not screened for MRI eligibility and only completed the geolocation and affect sampling assessments ($n = 31$). An additional group of MRI-eligible (right-handed, no MRI contraindications) participants were recruited both in New York City (second New York City cohort; $n = 60$) and Miami (third cohort; $n = 41$). All participants provided informed consent and were paid for their participation in the study. There was no randomization of participants to experimental conditions, and thus, data collection and analysis did not require blinding. This study was approved by the Weill Cornell Medicine and University of Miami Institutional Review Boards.

**Procedure.** During an initial in-laboratory session before the start of geolocation tracking, participants completed a series of baseline questionnaires including measures of depression (Beck Depression Inventory (BDI))[21] and trait anxiety (State–Trait Anxiety Inventory, Trait version (STAI-T))[22]. A geolocation application (Moves, ProtoGeo) was installed on each participant's phone to passively acquire geolocation data whenever the phone's accelerometer sensed motion. Geolocation data were synced to a participant-specific account on the application's online servers. Following the in-laboratory session, participants' geolocations were tracked continuously for 3–4 months (mean (s.d.) = 104.6 22.1) d) via the Moves application.

During this period, participants were prompted to provide assessments of their mood via a questionnaire sent by SMS to their mobile phones (MRI-eligible cohort) or via an app (first cohort only) installed on their phones. Participants rated their current mood in response to the following ten adjectives taken from the Positive and Negative Affect Scale (PANAS-X)[23]—PA: happy, excited, strong, relaxed, attentive; NA: nervous, jittery, upset, irritable, sluggish. Participants were also asked to rate their previous night's sleep on a scale of 'slept poorly' to 'slept well'. SMS assessments of mood and sleep were delivered at random times every other day during daytime hours. Due to technological limitations, the first cohort used a mood recording application (T2 Mood Tracker, DHA Connected Health) instead of SMS assessment and were queried to report their mood every other day at the same time. Positive affect and negative affect were operationalized as the mean of the adjectives for that assessment. Ten participants who responded to fewer than 20 SMS EMAs during the 3- to 4-month tracking period were excluded, leaving 122 participants who were included in the analyses (Supplementary Fig. 1; 84 female; mean (s.d.) age = 22.75 (3.36) years). For these, the number of completed affect assessments ranged from 22 to 78 (mean (s.d.) = 42.8 (9.4) years). Positive affect and negative affect exhibited an inverse relationship across participants ($B = -0.60$, $t(5{,}080) = -28.39$, $P < 0.001$), with a mean correlation of −0.54.

Following the mobile tracking period, participants completed a second session in the laboratory. During this session, participants completed the BDI and STAI-T again. The depression and trait anxiety measures obtained before (mean (s.d.) BDI, 6.99 (6.38); STAI-T, 40.86 (11.25)) and after (mean (s.d.) BDI, 5.78 (5.31); STAI-T, 38.83 (11.06)) the 3- to 4-month sampling period did not differ (BDI: $B = 0.46$, $t(110) = 0.50$, $P = 0.62$; STAI-T: $B = -1.11$, $t(110) = -0.48$, $P = 0.63$; the model included cohort number to control for potential effects of seasonality), and mean RE (see equation below) was not correlated with self-reported depression ($r = -0.02$) or trait anxiety ($r = 0.01$).

At both sites, the subset of participants in the MRI-eligible cohort who were willing to undergo an fMRI scan completed a third session, which involved scanning no later than 4 weeks after the second laboratory session. During this session, a 15-min resting-state scan (TR = 2.0 s; flip angle = 75°; TE = 29 ms; $3.4 \times 3.4 \times 3.4\ mm^3$; 38 slices), as well as T1-weighted ($1\ mm^3$) and T2-weighted anatomical scans, was collected on each participant. A total of 38 participants were scanned at Weill Cornell on a 3T Siemens Trio, and 25 participants were scanned at the University of Miami on a 3T GE750. Two of the scanned participants were excluded from the analysis for failure to respond to a sufficient number of SMS EMAs (as described above), and three participants were excluded due to excessive motion (see 'fMRI data preprocessing'), leaving 58 participants included in our reported fMRI analyses.

**Geolocation data processing.** Before performing any analyses, we sought to determine the amount of geolocation data required on each day to extract a stable RE estimate. Missing data is unavoidable when collecting geolocation data from cellular phones (due to the device being shut off). Thus, we performed several analyses to identify an acceptable threshold for the amount of missing data that would enable reliable estimation of within-day RE while excluding the fewest number of days so that the day-to-day dynamics of RE could be examined.

The first analysis identified the robustness of RE estimates (see equation) to various levels of missing data by randomly removing a percentage of data from each day for which data were at least 99% complete. RE was recalculated from this subsample of data and compared to the full day's RE. A threshold of 90% complete geolocation data within a day closely approximated 99% complete data (Supplementary Fig. 2).

The second analysis examined how many days would be excluded as a function of the threshold of data required for inclusion. At the within-day thresholds of 30%, 20%, 10%, 1% and 0% allowable missing data, the mean percentage of days removed was 16.1%, 18.9%, 23.2%, 34.4% and 77.2%, respectively. Selecting a threshold of ≤10% missing data resulted in an average of 80.2 usable days per participant (Supplementary Fig. 3).

As a result of these analyses, we identified a maximum threshold of 10% of within-day missing data as being adequate to retain a sufficient number of days while ensuring that the calculation of a single day's RE would be accurate.

Geolocation data were preprocessed such that latitude and longitude coordinates were rounded to the fourth decimal (a spatial resolution of approximately 4–11 meters between each unique location). For each day, we converted continuous geolocation data, downsampled to 1-min temporal resolution, into a measure of daily RE that was previously used in studies quantifying rodent exploratory behavior[14,24], interpolating over time points when data were missing:

$$RE = \sum_{j=1}^{n} (p_{ij} \times (log_2 p_{ij}))/\log(n)$$

In this equation, $p_{ij}$ is the within-day historical probability that location $j$ was visited by participant $i$, quantified as the proportion of the day spent in each unique location (number of minutes in that location divided by the 1,440 min in a day), and $n$ is the total number of unique locations in the environment (calculated to be 648,000,000 unique locations on Earth at four-decimal degrees of GPS resolution).

Several variables that might impact RE or affect were also acquired and used as covariates in analyses, including the time and day of the week that mood surveys were completed, the amount of precipitation and mean temperature for the modal location of the participant for that day, the total distance traveled for the day, and the cohort.

To extract weather information, weather data were collected using the API at http://weatherunderground.com. API requests for mean temperature and total precipitation data were made using participants' modal longitude and latitude for each day.

To calculate total distance traveled per day, the sum of distances between the successive points visited in a given day was calculated. Distance was calculated using the rdist.earth function in the R package 'fields', which uses the haversine formula:

$$d = 2r \arcsin\left(\sqrt{\sin^2\left(\frac{\phi_2 - \phi_1}{2}\right) + \cos(\phi_1)\cos(\phi_2)\sin^2\left(\frac{\lambda_2 - \lambda_1}{2}\right)}\right)$$

where $\Phi$ represents latitude, $\lambda$ is the longitude, $r$ is the radius of the Earth and $d$ *is* the distance between the two points.

**Location data analysis.** Multilevel models were run in R (3.5.0) using the nlme package[25] to examine whether RE predicted daily positive affect or negative affect. Participants and RE were treated as random factors. Using the lmerTest package, $t$ statistics and $P$ values were extracted from these models. We elected to run a model that included RE, as well as a number of additional factors that we hypothesized as being related to positive affect, including the time of day that mood assessment was completed, the amount of precipitation for modal location of that day, the mean temperature for the modal location of that day, the total distance traveled for that day, the day of the week and the cohort (both treated as a factor). Results reported in the manuscript are from models including this full set of covariates that we hypothesized, a priori, might account for the variance in positive affect. However, we also performed model fit comparisons using the 'dredge' function as part of the 'MUMIn' library in R, which ranks models via the Akaike information criterion (AIC)[26]. The best fitting model only included RE, cohort and day of the week. We repeated all analyses using this best fitting model, and the relationship between RE and positive affect held under this reduced model ($B = 0.63$, $t(3{,}993) = 2.07$, $P = 0.038$). Random-effect coefficients from the full model, reflecting the strength of the RE–positive affect association, were extracted for each participant and used as individual difference metrics to predict rs-fMRI connectivity.

**Determining whether analytic assumptions drive the observed RE–positve affect relationship.** In our geolocation analysis, we interpolated over gaps in location data caused by phones being off or by loss of GPS signal (for example, due to underground subway commutes). To test whether interpolation might artificially increase RE and account for effects, we recalculated RE assuming that the participant remained in the last observed location throughout the temporal window of the data gap, instead of interpolating, and reran our analyses testing for relationships between daily RE and positive affect. An identical linear mixed-effects model also demonstrated a significant association between non-interpolated RE and positive affect ($B = 0.78$, $t(3{,}834) = 2.457$, $P = 0.014$), suggesting that this result is robust to assumptions about behavior when the phone is off.

*Extraction of the number of novel locations visited.* For analyses examining whether the RE–positive affect effect could be accounted for by an estimate of the degree to which a participant encountered 'novel' locations on that day, we extracted the number of novel locations visited in a day (defined as the number of unique locations not previously visited during the observation period). An important caveat regarding this metric is that we were not able to determine in any absolute sense whether an individual had never previously visited a location and thus whether the location was truly novel for a participant. Instead, we could only make the more restricted inference of whether the participant had previously visited this location during the 3- to 4-month tracking period. To avoid inflation of this novelty estimate early in the observation period and to allow for adequate observation of visited locations before the designation of novel locations, we held out data from the first 10 d before estimating novelty.

*Estimation of entropy over sociodemographic features of the environment.* We suggest that a greater degree of daily 'experiential diversity' on high-RE days might contribute to the association between RE and positive affect. To test this hypothesis, we attempted to estimate the degree of diversity in the social and demographic features of the locations visited by participants on a given day.

The first step in this analysis was to map each GPS coordinate that appeared in our dataset to its corresponding Federal Information Processing Standard (FIPS) code. A FIPS code uniquely identifies locations at the spatial resolution of a 'block group', the smallest geographic unit for which the US Census Bureau publishes data. The areas encompassed by block groups differ in size as they are determined by the approximate population size of 600 to 3,000 people each.

Block groups are used by US government agencies and other geographic information systems (GIS) to link geographic and demographic information to specific physical locations. We downloaded 53 variables capturing the demographic and socioeconomic features of a given block group (for example, population density, median age, total businesses, educational attainment, unemployment population, race and gender) from the US Census Bureau. See Supplementary Appendix 1 for a complete list of data sources.

We performed PCA to reduce the dimensionality of the 53 sociodemographic variables. PCA derives a smaller set of artificial variables ('components') that explain the maximum variance in all of the variables. All variables were mean centered and scaled by standard deviation. The 'principal' function from the R package psych (version 1.8.12)[27] was used to perform Varimax rotated PCA on the 53 sociodemographic variables. Varimax rotation was used to maximize orthogonality among the components. Examination of the scree plot and eigenvalues showed that the 53 census variables optimally clustered into 12 components that explained 80% of the variance in the data. Component weights indicate how strongly a sociodemographic variable is related to its component, with 1 reflecting the strongest positive associations and −1 indicating a strong inverse relationship (see Supplementary Table 3 for component weights for all variables). Individual component values for each block group were calculated using the regression method.

To better differentiate our measure of location in GPS coordinate space from a measure of location in sociodemographic feature space, we sought to define a sociodemographic feature space at a relatively lower level of spatial resolution. We took the first three principal components in our PCA analysis that explained the largest amount of variance in the sociodemographic data and discretized this three-dimensional (3D) space into 'high' and 'low' values for each component, based on a median split. This resulted in each block group being assigned one of eight possible positions in this 3D sociodemographic feature space (PC1 (2 levels) × PC2 (2 levels) × PC3 (2 levels)).

We converted the minute-by-minute GPS coordinate time series values for each participant into a time series consisting of minute-by-minute values in this 3D sociodemographic feature space for the corresponding block group. We then calculated daily entropy over this feature space. This entropy measure reflects day-to-day variability in exposure to sociodemographic features of the environment, with higher entropy achieved on days when an individual is exposed to greater sociodemographic diversity.

**fMRI data preprocessing.** Resting-state data were preprocessed using AFNI (version AFNI_17.2.17). rs-fMRI data were despiked, slice-time corrected, co-registered to the individual's T1 image, spatially registered using linear and nonlinear registration (3dQwarp) to the MNI152 template and smoothed with a 6 $mm^3$ isotropic kernel. Normalized T1 data were segmented into gray matter, white matter and the ventricles. We removed variance associated with motion, the derivative of motion, and the time series of blood oxygenation level-dependent (BOLD) activity in white matter and ventricles[28,29]. Times of repetition (TRs) with motion above 2 mm were censored, and the resulting data were bandpass filtered at 0.01–0.1 Hz. Participants with head motion above 3 mm in any direction were excluded from analyses ($n = 3$). The resulting residuals from the remaining 58 participants were used in the connectivity analyses.

Because of ongoing debate within the rs-fMRI literature on preprocessing best practices, in particular, the work indicating that the effects of motion on resting-state BOLD activity are nonlinear and spatially variable[30–32], we performed a second preprocessing approach similar to the one used by multiple groups[32]. Using this approach, we first identified frames that contained frame-wise displacement of >0.2 mm. These volumes were marked as outliers; however, we also marked one volume before and two volumes after any volumes with framewise displacement (FD) > 0.2. In addition, uncensored segments of data lasting fewer than five contiguous volumes were flagged as outliers. It has been suggested that this approach more completely removes volumes in which movement occurred, as well as the potential aftereffects of movement on the BOLD signal.

We then used the same nuisance regressors (six demeaned motion parameters, their derivative, their square and the square of the derivative; the averaged ventricular signal and its derivative and square; as well as the averaged white matter signal and its derivative and square) with a bandpass of 0.01 to 0.10 Hz. With the residual fMRI time series, we then implemented the Lomb–Scargle Periodogram censoring interpolation method[31] to perform signal recovery and interpolation. We extracted hippocampal–ventral striatal connectivity from these preprocessed data and tested whether we obtained the same result using this alternative preprocessing approach (Supplementary Note 2).

We conducted additional analyses to determine whether the seed region in the ventral striatum and the hippocampus cluster fell within traditional resting-state networks[33] (Supplementary Note 3).

**fMRI data analysis.** For each participant, the mean time series from voxels in the nucleus accumbens, anatomically defined using the Harvard–Oxford Atlas[34], was extracted from the preprocessed rs-fMRI data. This time series was correlated with the rest of the brain, and an $r$-to-$z$ transformation was performed to complete parametric statistical tests. The random effect coefficients from the multilevel model described above (along with average frame-wise displacement, scanner site (Miami or New York City), mean RE and mean positive affect as control variables) were then included as predictors in a robust regression model to predict nucleus accumbens–whole brain connectivity. These random-effects maps were corrected for multiple comparisons using FSL's FLAME with a threshold of $z > 2.7$, corrected at $P < 0.05$.

**Statistics.** Multilevel models were run in R (3.5.0) using the nlme package[25] to examine whether our geolocation-derived measures (RE, number of novel locations, entropy over sociodemographic (US Census-derived) space, number of unique locations) predicted daily positive affect or negative affect. Data were assumed to be normally distributed, but this was not formally tested. To view the distribution, scatterplots illustrating participant-level associations between RE ($z$-scored) and positive affect and negative affect are presented in Supplementary Figs. 4 and 5. Voxel-wise multiple regression imaging analyses were performed using FSL. No statistical methods were used to predetermine sample sizes, but our sample sizes were similar to those reported previously[18,35].

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

## Data availability

The raw geolocation datasets generated and/or analyzed during this study are not publicly available due to the inherently identifiable nature of geolocation data, but they are available from the corresponding authors on reasonable request. The processed data necessary to reproduce the central findings in the manuscript are available at http://github.com/manateelab/NatNeuro/.

## Code availability

Custom R scripts were used to analyze and plot all data. The main analysis code was used to calculate the mean and standard deviation for RE. Code is available online at http://github.com/manateelab/NatNeuro/.

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## Author contributions

A.S.H. and C.A.H. conceived and designed the study. T.C.S. and C.E.C.E. collected the data. A.S.H., T.C.S., T.R.R., L.M.B., C.J.G. and C.A.H. analyzed the data. A.S.H. and C.A.H. interpreted the data and wrote the manuscript with input from the other authors.

## Competing interests

The authors declare no competing interests.

## Additional information

**Extended data** is available for this paper at https://doi.org/10.1038/s41593-020-0636-4.

**Supplementary information** is available for this paper at https://doi.org/10.1038/s41593-020-0636-4.

**Correspondence and requests for materials** should be addressed to A.S.H. or C.A.H.

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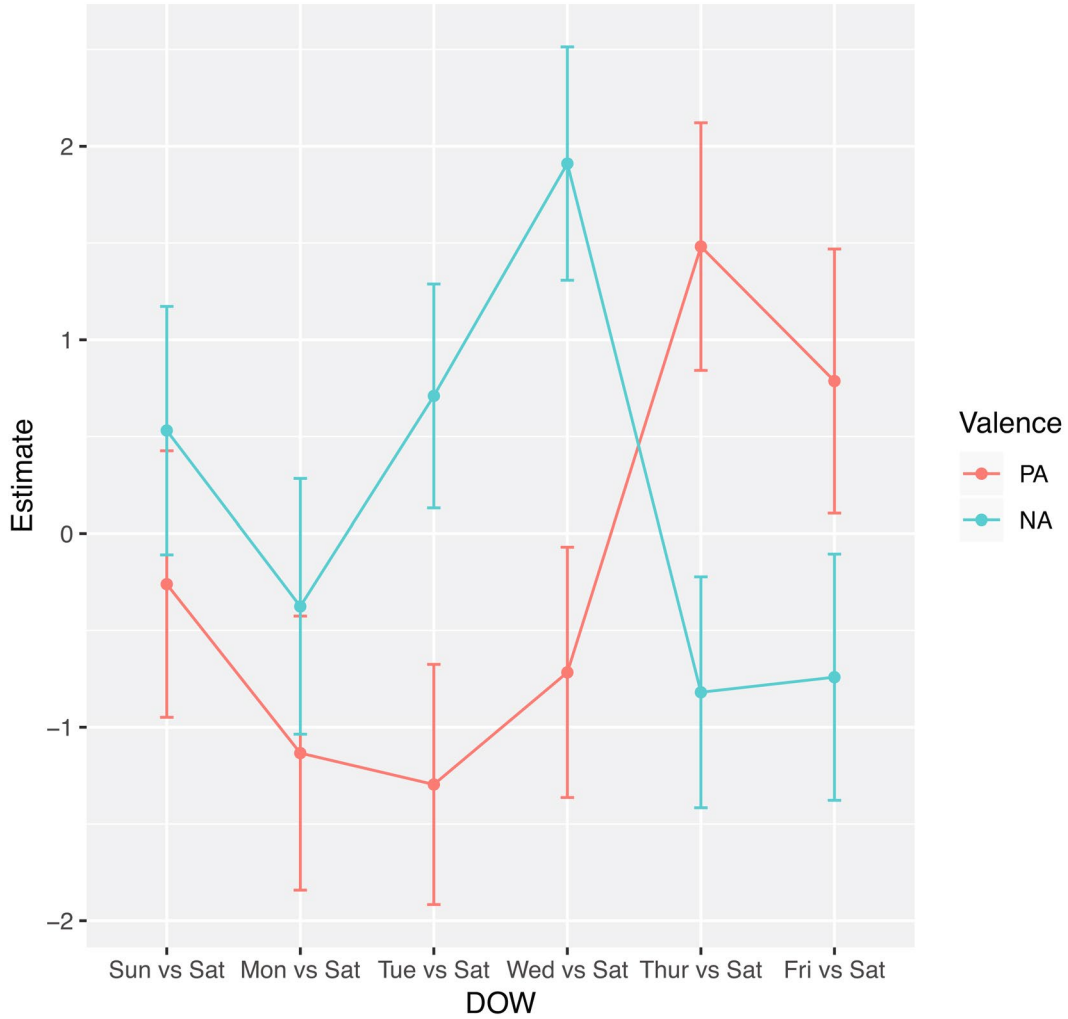


**Extended Data Fig. 1 | Positive and negative affect by day of week.** This figure depicts the parameter estimates of the effect of day of week (DOW) on positive and negative affect from linear mixed-effects models that included RE, time of day EMA was collected, distance travelled, mean temperature and precipitation (from the modal location of that day for that participant), and cohort as predictors (n = 122 independent human participants). Of the variables in models, only day of the week was also significantly associated with PA, with PA lower early to mid-week relative to the weekend ($F(3834) = 2.8$, $p = 0.011$). Both temperature ($B = 0.062$, $t(3835) = 2.585$, $p = 0.01$) and day of the week ($F(3835) = 3.0$, $p = 0.006$) were significantly associated with negative affect, which was greater on higher temperature days and in the early to mid-week relative to the weekend. Error bars represent standard error of parameter estimate.

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| ☐ | ☒ | The statistical test(s) used AND whether they are one- or two-sided<br>*Only common tests should be described solely by name; describe more complex techniques in the Methods section.* |
| ☐ | ☒ | A description of all covariates tested |
| ☐ | ☒ | A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons |
| ☐ | ☒ | A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals) |
| ☐ | ☒ | For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted<br>*Give P values as exact values whenever suitable.* |
| ☒ | ☐ | For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings |
| ☐ | ☒ | For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes |
| ☐ | ☒ | Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated |

*Our web collection on statistics for biologists contains articles on many of the points above.*

## Software and code

Policy information about availability of computer code

| | |
|---|---|
| Data collection | A geolocation application (Moves; ProtoGeo, Helsinki, Finland) was installed on each participant's phone to passively acquire geolocation data. For the first NYC cohort, EMA data were collected with T2 Mood Tracker (DHA Connected Health, Joint Base Lewis-McChord, WA, USA). For the second NYC cohort and the Miami cohort, EMA data were collected using Qualtrics (Provo, UT). Scheduling of SMS messages were managed by a custom built system using FileMaker (Apple, Inc). |
| Data analysis | FMRI data preprocessing was done using AFNI (AFNI_17.2.17). For additional fMRI preprocessing using the lomb-scargle periodogram censoring interpolation method, we used the CBIG_preproc pipeline by Yeo and colleagues (https://github.com/ThomasYeoLab/CBIG/; Date: Jun.3, 2016).<br><br>nlme was used to perform multilevel model analyses (Package nlme version 3.1-139) using R (version 3.5.0). We calculated distance traveled using the rdist (v 0.0.3) R-package.<br><br>Custom R scripts were used to analyze and plot all data. The main analysis code (written in R) was used for calculation of roaming entropy and deviation in roaming entropy. Code are available online at https://github.com/manateelab/NatNeuro |

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## 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 list of figures that have associated raw data
- A description of any restrictions on data availability

The datasets generated during and/or analyzed during the current study are not publicly available due to inherently identifiable nature of geolocation data, but are available from the corresponding author on reasonable request.

# 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

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# Behavioural & social sciences study design

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

| | |
|---|---|
| Study description | This is a quantitative study employing neuroimaging and mobile Health (mHealth) methods to investigate associations between real-world behavior and individual differences in neurocircuitry |
| Research sample | Sample includes 132 young adults, aged 18-31 (mean age: 23, sd: 3.4; 90 female) from the New York City (n = 91; Cohort 1: n=31; Cohort 2: n=60) and Miami (Cohort 3: n = 41) metropolitan areas. Participants were required to have smart phones and a subset were required to be MRI compatible. This is a representative sample from the University of Miami and Weill-Cornell University areas. |
| Sampling strategy | The participant sample was a convenience sample recruited via fliers and posted advertisements in the community. No predetermined statistical method was used to determine sample size. Within each of the three cohorts, we recruited as many individuals as possible within a one month period, so that participants within each cohort would share the maximal number of tracking dates in common. |
| Data collection | During an initial session in the lab prior to the start of geolocation tracking, participants completed a series of baseline questionnaires including measures of depression (Beck Depression Inventory [BDI]) and trait anxiety (State-Trait Anxiety Instrument [STAI-T]). A geolocation application (Moves; ProtoGeo, Helsinki, Finland) was installed on each participant's phone to passively acquire geolocation data whenever the phone's accelerometer sensed motion. Geolocation data was synced to a participant-specific account on the application's online servers. Following the initial in-lab session, participants' geolocations were tracked continuously for 3-4 months (mean 104.6 days, sd = 22.1) via the Moves application.<br><br>During this period, participants were prompted to provide assessments of their mood via a questionnaire sent by SMS to their mobile phones (MRI-eligible cohort) or via an app (first cohort only) installed on their phones. Participants rated their current mood in response to the following 10 adjectives, taken from the Positive and Negative Affect Scale (PANAS-X): Positive Affect (PA): happy, excited, strong, relaxed, attentive; Negative Affect (NA): nervous, jittery, upset, irritable, sluggish. Participants were also asked to rate their previous night's sleep on a scale of "slept poorly" to "slept well." SMS assessments of mood and sleep were delivered at random times every other day during daytime hours. Due to technological limitations, the first cohort used a mood recording application (T2 Mood Tracker; DHA Connected Health, Joint Base Lewis-McChord, WA, USA) instead of SMS assessment, and were queried to report their mood every other day at the same time of day. |
| Timing | mHealth: Cohort 1 (New York City): March 11, 2015 - June 29, 2015; Cohort 2 (New York City): October 5, 2015 - February 16, 2016; Cohort 3 (Miami): October 28, 2015 - April 13, 2016<br><br>fMRI: Februrary 7, 2016 - February 27 2016 (NYC); March 18, 2016 - April 28, 2016 (Miami) |
| Data exclusions | mHealth: For inclusion of mHealth analysis, participants were required to have completed at least 20 SMS EMA assessments. Ten participants responded to fewer than 20 SMS EMA assessments during the 3-4 month tracking period were excluded from analyses, leaving 122 participants.<br><br>fMRI: Participants with >3mm head motion in any direction were excluded from analyses (n = 3). |
| Non-participation | No participants dropped out or declined to participate |
| Randomization | Participants were not allocated to experimental groups. |

# 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 |
| ☒ | ☐ Animals and other organisms |
| ☐ | ☒ Human research participants |
| ☒ | ☐ Clinical data |

## Methods

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

# Human research participants

Policy information about studies involving human research participants

| | |
|---|---|
| Population characteristics | See above. |
| Recruitment | Participants were recruited in three cohorts from the New York City and Miami areas via fliers and posted advertisements. Participants were required to have a smartphone (either Android or iOS) that could receive text messages and that met system requirements to run the study application. Due to the requirement of smart phones, our sample may have had slightly higher SES than a completely representative sample. |
| Ethics oversight | Weill Cornell Medical College IRB (1406015178), and University of Miami IRB (20150678) approved of the study protocol |

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

# Magnetic resonance imaging

## Experimental design

| | |
|---|---|
| Design type | resting-state |
| Design specifications | 15 minute resting-state scan |
| Behavioral performance measures | N/A |

## Acquisition

| | |
|---|---|
| Imaging type(s) | Functional |
| Field strength | 3T |
| Sequence & imaging parameters | Gradient echo, EPI scan (FOV 220mm, 2.0s TR, Flip Angle = 75, TE: 29 ms, 3.4 x 3.4 x 3.4 mm) |
| Area of acquisition | whole brain scan |

Diffusion MRI ☐ Used ☒ Not used

## Preprocessing

| | |
|---|---|
| Preprocessing software | Resting state data were preprocessed using AFNI (version AFNI_17.2.17). Resting state functional MRI (rsFMRI) data were despiked, slice-time corrected, coregistered to the subject's T1 image. |
| Normalization | Data were spatially registered using linear and nonlinear registration (3dQwarp) to the MNI152 template, and smoothed with a 6mm isotropic kernel. |
| Normalization template | MNI152 template |
| Noise and artifact removal | Normalized T1 data were segmented into grey matter, white matter, and the ventricles. We removed variance associated with motion, the derivative of motion, and the timeseries of BOLD activity in white matter and ventricles. TRs with motion above 2mm were censored and the resulting data were bandpass filtered at 0.01 - 0.1 Hz. Participants with >3mm head motion in any direction were excluded from analyses (n = 3). |
| Volume censoring | Motion correction was performed using AFNI. TRs with > 2mm motion were censored |

## Statistical modeling & inference

| | |
|---|---|
| Model type and settings | For each participant, the mean timeseries from voxels in the nucleus accumbens (NAcc), anatomically defined using the Harvard-Oxford Atlas, was extracted from the preprocessed rsFMRI data. This timeseries was correlated with the rest of the brain, and an r-z transformation was performed to complete parametric statistical tests. The random effect coefficients from the best-fitting multilevel model described above (along with average framewise displacement, scanner site (Miami or New York City), mean positive affect, and mean roaming entropy) were then included as predictors in a robust regression model to predict NAcc-whole brain connectivity. |
| Effect(s) tested | See above. |

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

| | |
|---|---|
| Statistic type for inference (See Eklund et al. 2016) | Cluster-wise. |
| Correction | These random effects maps were corrected for multiple comparisons using FSL's FLAME (Family Wise-Error with a threshold of $z > 2.7$, corrected at $p < .05$. |

## 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 | Pearson Correlation |