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Associations between mental wellbeing and fMRI neural bases underlying responses to positive emotion in a twin sample

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Original Article

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Abstract

Background. Although mental wellbeing has been linked with positive health outcomes, including longevity and improved emotional and cognitive functioning, studies examining the underlying neural mechanisms of both subjective and psychological wellbeing have been sparse. We assessed whether both forms of wellbeing are associated with neural activity engaged during positive and negative emotion processing and the extent to which this association is driven by genetics or environment.

Methods. We assessed mental wellbeing in 230 healthy adult monozygotic and dizygotic twins using a previously validated questionnaire (COMPAS-W) and undertook functional magnetic resonance imaging during a facial emotion viewing task. We used linear mixed models to analyse the association between COMPAS-W scores and emotion-elicited neural activation. Univariate twin modelling was used to evaluate heritability of each brain region. Multivariate twin modelling was used to compare twin pairs to assess the contributions of genetic and environmental factors to this association.

Results. Higher levels of wellbeing were associated with greater neural activity in the dorsolateral prefrontal cortex, localised in the right inferior frontal gyrus (IFG), in response to positive emotional expressions of happiness. Univariate twin modelling showed activity in the IFG to have 20% heritability. Multivariate twin modelling suggested that the association between wellbeing and positive emotion-elicited neural activity was driven by common variance from unique environment ($r = 0.208$) rather than shared genetics.

Conclusions. Higher mental wellbeing may have a basis in greater engagement of prefrontal neural regions in response to positive emotion, and this association may be modifiable by unique life experiences.

Introduction

Although many psychological factors have been established as contributing to optimal mental health (including purpose in life, autonomy, positive affect; Keyes, 2007), we lack knowledge regarding the underlying neurobiological mechanisms by which such factors relate to wellbeing, which is comprised of two distinct, yet correlated, sub-constructs: subjective and psychological wellbeing. Subjective wellbeing relates to factors such as happiness, positive affect and life satisfaction, while psychological wellbeing refers to personal attributes such as autonomy, mastery, self-acceptance and finding a meaningful life purpose (Diener, Suh, Lucas, & Smith, 1999; Ryff & Singer, 2008). Although both sub-constructs have been extensively linked to positive outcomes such as decreased physical illness, greater work productivity and superior psychosocial functioning (e.g. Steptoe, Deaton, & Stone, 2015), they have often been examined independently of one another. However, it has been shown that they both contribute important and unique variance to total wellbeing (Henderson & Knight, 2012; Keyes & Annas, 2009), highlighting the importance of examining both aspects of wellbeing as one composite construct.

Reappraisal of emotional information is considered to be an important determinant of mental health outcomes including wellbeing (Davidson, 2004). Despite multiple behavioural studies showing an association between wellbeing and reaction time or accuracy to emotional stimuli, the corresponding evidence using neuroimaging methods is sparser and somewhat contradictory. In those neuroimaging studies available, wellbeing is usually only measured using subjective wellbeing or psychological wellbeing measures, but rarely both. Moreover, understanding whether the association between wellbeing and emotion processing is driven by genetics or environment (as can be evaluated using twin studies) would assist in

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understanding the underlying factors that drive this association. Our objective in this study was to address these gaps in knowledge assessing whether self-reported wellbeing (both subjective and psychological wellbeing) is associated with specific neural circuit regions probed by functional neuroimaging during the processing of salient emotional stimuli, and the extent to which such associations may be heritable and driven by shared genetics or environment.

Behavioural studies have shown a pattern of increased attentional bias to positive (i.e. happy) stimuli and reduced sensitivity to negative (i.e. fear) stimuli in individuals with higher levels of subjective wellbeing and life satisfaction (Sanchez & Vazquez, 2014; Vittersø, Oelmann, & Wang, 2009; Yu & Li, 2012). In our previous study with 1480 healthy twin participants from the TWIN-E cohort, we also observed an association between faster behavioural responses and the identification of happy faces in those with high wellbeing levels (Routledge et al., 2018). Prior functional magnetic resonance imaging (fMRI) studies have begun to address a complementary question, as to whether neural circuits in the human brain engaged by emotion processing are also associated with components of wellbeing – either subjective (defined as happiness and pleasure; Ryan & Deci, 2001) or psychological (defined as having a meaningful and purposeful life; Ryff & Singer, 2008). Higher levels of *subjective* wellbeing have been linked to greater amygdala activation in response to positive images (Cunningham & Kirkland, 2014), and also with stronger activations in parieto-temporal regions in response to negative facial emotion stimuli (Ren, Shi, Wei, & Qiu, 2019). Subjective wellbeing has also been associated with resting-state fMRI metrics (e.g. regional homogeneity; Kong et al., 2015; Kong, Wang, Song, & Liu, 2016; spontaneous low frequency fluctuations; Kong, Hu, Wang, Song, & Liu, 2015) and dynamic frontal connectivity between the default mode, salience and frontal-parietal networks (Shi et al., 2018).

Within the *psychological* wellbeing domain, individuals with greater psychological wellbeing levels have been shown to display longer (sustained) neural activity in the striatum and dorsolateral prefrontal cortex when viewing positive images (Heller et al., 2013), and increased activity in the ventral anterior cingulate cortex in response to negative information (van Reekum et al., 2007). Altogether, these findings suggest that neural circuits engaged during emotion processing are associated with wellbeing, although it is unclear to what extent heterogeneity in the results are due to differences in emotion tasks (such as the use of emotional scenes *v.* faces) and/or different ways of assessing subjective or psychological components of wellbeing. In this study, we used a well-standardised facial emotion task, an established measure of wellbeing that assesses both subjective and psychological components, and a well-powered sample to assess the association between wellbeing and whole-brain neural activation engaged by emotion stimuli.

By utilising a twin sample, it is also possible to quantify the amount of variance in a wellbeing–neural activation association that is due to genetic *v.* environmental factors. To the best of our knowledge, this has not yet been investigated despite previous studies reporting some heritability for emotion-related processes (unrelated to wellbeing). Behaviourally, the heritability of reaction times to emotional faces is small to moderate, ranging from 27% to 37% (Routledge et al., 2018). Studies utilising electroencephalography have also reported significant heritability for event-related potentials during emotional faces processing, ranging from 42% to 64%, suggesting that neural responses to such stimuli are influenced by genetic factors to some degree (Anokhin, Golosheykin, & Heath, 2010; Shannon, Patrick, Venables, & He, 2013). However for fMRI, Côté et al. (2007) reported no evidence of heritability for processing sadness (elicited via sad film excerpts) in 104 8-year-old twin pairs in two *a priori* defined regions of interest (medial and ventrolateral prefrontal cortex). The authors concluded that emotional experiences may instead be linked to the child's personal social relationships (i.e. unique environmental factors). Thus far, no other studies to date have examined the heritability of neural activity related to face emotion processing using fMRI. Furthermore, it is not yet known whether such regions may also be associated with wellbeing. An examination of a broader spectrum of emotions (both positive and negative) and their relationship with wellbeing levels is needed, as well as a focus on a broader age group given that emotion processing networks stabilise mostly in early adulthood (Vink, Derks, Hoogendam, Hillegers, & Kahn, 2014).

The goal of the current study was to examine the association between overall wellbeing, both subjective and psychological components, and neural circuits engaged during emotion processing in a subset of healthy adult twin participants from the TWIN-E cohort (for more detail about the cohort, see Gatt et al., 2012). We used fMRI in order to examine neural activity engaged by facial expressions of emotion using a well-standardised task (Korgaonkar, Grieve, Etkin, Koslow, & Williams, 2013). Our first working hypothesis was that higher levels of wellbeing would be associated specifically with neural activity elicited by positive emotional expressions of happiness, consistent with our previous behavioural findings (Routledge et al., 2018). Our second working hypothesis was that this association would also be driven more by genetic rather than environmental factors, also as identified by this previous study.

Material and methods

Participants

A total of 263 healthy same-sex monozygotic (MZ) and dizygotic (DZ) twins from the larger TWIN-E cohort study completed the MRI component (see Gatt et al., 2012). Inclusion criteria included being a same-sex, healthy adult twin, with English as their first language, European ancestry and an absence of past/current psychiatric illness or brain injury. Thirty-three participants were dropped due to missing data or being an incomplete twin pair. The final study sample for this study consisted of 230 participants (76 MZ and 39 DZ pairs; see Table 1). The study received approval from the Human Research Ethics Committee of the University of Sydney (03–2009/11430), and all participants gave their written informed consent to participate.

Psychometric measures

Self-report scales were used to measure wellbeing (the COMPAS-W scale of wellbeing; Gatt, Burton, Schofield, Bryant, & Williams, 2014) and negative mood symptoms (the DASS-42; Lovibond & Lovibond, 1995). More specifically, the COMPAS-W is a composite scale that measures both subjective and psychological wellbeing, while the DASS-42 measures depression, anxiety and stress symptoms (for more detail, see S1 in Supplemental Materials). *Z*-scores for the COMPAS-W and log-transformed scores for the DASS-42 were used in the current study to index the participant's levels of wellbeing and negative

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Table 1. Demographic characteristics for the final sample

Characteristic	MZ (n = 152)	DZ (n = 78)	Total (n = 230)
Sex (M/F)	58/94	28/50	86/144
Age (years ± s.d.)	39.7 (±11.8)	38.8 (±14.7)	39.4 (±12.8)
COMPAS-W (range: 26–130; ±s.d.)	99.0 (±10.8)	100.0 (±10.2)	99.3 (±10.6)
DASS-42 (range: 0–126; ±s.d.)	10.5 (±10.7)	11.8 (±11.1)	11.0 (±10.8)

Total number of the sample reflects the final sample of participants included in all analyses (fMRI, linear mixed model, univariate and multivariate twin models). COMPAS-W = total composite measure of wellbeing; DASS-42 = total measure of negative mood symptoms including depression, anxiety and stress.

mood symptoms, respectively. These measures were part of a larger WebQ online assessment, which was a test battery of self-report questionnaires on physical and emotional health, well-being, and environmental factors (for a more detailed list of the measures collected, please refer to Gatt et al., 2012).

fMRI paradigm

The MRI session was part of the TWIN-E study, which consisted of five fMRI tasks that were performed within a single session in the scanner to examine cognitive and emotional functioning. For the purposes of the current study, only the parameters from the conscious viewing of facial emotion of expression task are discussed here (Korgaonkar et al., 2013; Williams et al., 2015).

The emotion task consisted of 240 standardised faces that depicted fear, anger, disgust, sadness, happiness or neutral expressions. Each emotion was presented in a block of eight trials of different faces but all with the same emotion, and each emotion block was repeated five times, resulting in 30 blocks in total. Each trial consisted of the presentation of a single emotional face for 500 ms, followed by an interstimulus delay of 750 ms, with a block length of 10 s. No interblock interval was included in the current task. Both the faces within block and the emotion blocks were presented in a pseudorandomised order. No responses were required from the participants; however, instructions were given at the start of the task to pay close attention to the faces and that follow-up questions may be asked. After task completion, each participant was probed on the number of different emotions they observed during the task.

Image acquisition and preprocessing

MR images were acquired using a 3 T GE signa HDx scanner (GE Healthcare, Milwaukee, WI, USA) with an eight-channel head coil at the Westmead Hospital Medical Imaging Service, Sydney. 3D T1-weighted volumes were acquired using a spoiled gradient echo (SPGR) sequence (TR = 8.3 ms; TE = 3.2 ms; flip angle = 11 degrees; inversion time = 500 ms; FOV = 256 mm; 180 sagittal slices; matrix size = 256 × 256; voxel size = 1 × 1 × 1 mm; NEX = 1; ASSET = 1.5; scanning time = 7.12 min). The functional run consisted of 120 T2*-weighted echo-planar imaging (EPI) images (TR = 2500 ms; TE = 27.5 ms; FOV = 240 mm; flip angle = 90 degrees; 40 axial slices using an interleaved sequence; matrix size = 64 × 64; voxel size = 3.75 × 3.75 × 3.5 mm; scanning time = 5.13 min). Three dummy scans were acquired at the start of the EPI acquisition.

The fMRI images were preprocessed using SPM12 software (Wellcome Trust Centre for Neuroimaging, London, UK) running in MATLAB R2018b (MathWorks, Natick, MA, USA). This included coregistration of the structural and functional EPI images to the SPM template, segmentation and spatial normalisation of the structural image to the standard Montreal Neurological Institute (MNI) space, slice-time correction of the EPI images (using middle slice as the reference; interleaved acquisition), realignment and normalisation of the images, which were resliced to a voxel size of 1.5 × 1.5 × 2 mm, before being smoothed using an isotropic Gaussian filter of 6 × 6 × 6 mm at full-width half-maximum.

fMRI analyses

At the single-subject level, blood-oxygen level-dependant responses were modelled by using a boxcar stimulus function that was convolved with a canonical haemodynamic response function. This resulted in time courses that were then applied to the general linear model, which included the six experimental regressors (Happy, Angry, Sad, Fear, Disgust, and Neutral) as well as six movement regressors (of no interest; derived from the realignment step). A high-pass filter with a frequency cut-off of 128 s was applied to remove low frequency noise, and serial autocorrelations were estimated using an AR(1) model. Statistical parametric maps for each participant were then created by calculating simple linear contrasts that were applied to the parameter estimates. These included contrasting each affective emotion (Angry, Happy, Sad, Fear, Disgust) against Neutral, in order to identify the regions specific to each emotion (while controlling for lower-level visual and face-related processes).

At the group level, the single-subject contrast images for each of the five contrasts were taken to voxel-wise random-effects analyses regardless of zygosity. Age and sex were included as covariates-of-no-interest. One sample t tests were used to examine whole brain activity for each of the emotions to determine brain regions specific for each contrast (e.g. Happy>Neutral, Angry>Neutral, Sad>Neutral, Fear>Neutral and Disgust>Neutral). Significant activation threshold was set at $p < 0.05$ at the cluster level using family-wise error (FWE) correction with a voxel-wise threshold of $p = 0.001$. Masks for each significant cluster were created for each contrast separately. This was then used to extract t-contrast values from each voxel within the mask from the single-subject contrast images via the Volumes Toolbox (https://sourceforge.net/projects/volumes.spmtools.p/), and then averaged across the significant cluster for each participant.

Statistical analyses

Linear mixed-model analysis

In order to explore the potential associations between significant functional brain activity (indexed by t-contrast values extracted from the single-subject T maps, using the β estimate differences of the conditions), wellbeing and negative mood symptoms, linear mixed models were fit using the *lme4* package in *R*. Due to the exploratory nature of this analysis, no multiple corrections were made across the different contrasts for the number of statistical tests conducted. Age, sex, zygosity, COMPAS-W scores (measuring wellbeing) and DASS-42 scores (measuring negative mood symptoms) were included in the models as fixed-effects predictors. The DASS-42 scores were included to examine the unique associations between emotion processing and wellbeing, independent of negative mood symptoms, in light of the fact that both constructs contribute to mental health – albeit in opposing

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directions. In order to control for family relatedness between each twin pair, a family number was used as the random-effects predictor (e.g. the same family number was given to each twin pair, while different twin pairs all had different family numbers). Any significant associations between the brain region (indexed by the averaged *t*-contrast value across the cluster for each participant) and wellbeing scores from the linear mixed models were taken to univariate and multivariate twin modelling analyses. If there was no significant association between the cluster and wellbeing, no further analyses were conducted.

Univariate twin analysis

To assess the heritability of fMRI activity, wellbeing and negative mood symptoms, univariate twin analysis was conducted using the *OpenMx* package (version 2.13.2) in *R*. Using structural equation modelling, additive genetic (A), non-additive genetic (D), shared environmental (C) and non-shared environment (E) variance components for emotion-related brain activity were examined (for more detail, see S2 in Supplemental Materials). Age and sex were included as covariates. The full univariate ACE/ADE model was compared to its nested submodels (AE, CE, and E) by dropping one or two of the variance components. The significance of each component was determined by using a χ^2 goodness-of-fit test, which assessed whether dropping that component resulted in a significant decrease in the model fit. To confirm the parsimony of the model, Akaike Information Criterion (AIC) values were utilised for model comparisons.

Multivariate twin analysis

Lastly, multivariate genetic modelling was used to assess the shared and non-shared genetic and environmental variance between fMRI activity, wellbeing and negative mood symptoms. More specifically, a correlated factors model was run using *OpenMx* in *R* to examine the genetic and environmental contribution to the correlations (or the covariance) between the three variables. Age and sex were included as covariates. Genetic and environmental correlations between the variables were tested by systematically constraining each correlation to zero, then comparing the new model with the previous model. Again, this was conducted by using the χ^2 difference test, where a significant reduction of model fit indicated the significance of the tested correlation. This correlation was then included in the final model, which was chosen based on the AIC values.

Results

Demographics

Demographic characteristics for the final sample are shown in Table 1. From the initial 263 participants, 13 were dropped prior to any analyses due to missing twin data, resulting in 250 participants for fMRI analyses. Twenty participants were further dropped during statistical analyses due to missing functional activity or questionnaire data, and undetermined zygosity. In total, 152 MZ twin and 78 DZ twin participants were included in all analyses (fMRI, linear mixed modelling, univariate and multivariate twin modelling). There were no significant differences in the levels of wellbeing or negative mood symptoms between the MZ and DZ twin pairs.

Emotion-related fMRI results

The voxel-wise random-effects analyses showed significant activity for emotion in four out of the five emotion contrasts. This included inferior frontal gyri activations in Happy, Angry, Fear and Sad contrasts (all against Neutral), as well as additional cerebellar activity in the Angry condition, and insula activity in the Sad condition (see Table 2). No significant activations were observed for the Disgust>Neutral contrast.

Linear mixed modelling

Averaged *t*-contrast values for each cluster were used to examine associations between the functional activity, wellbeing (COMPAS-W) and negative mood symptoms (DASS-42). From the 250 participants that were included in the fMRI analysis, five MZ pairs and one DZ pair where one or both twins did not show any activity within this cluster, and two pairs of twins with undetermined zygosity were excluded from further analysis. Two additional MZ pairs were also dropped as one or both twin participants from each pair did not complete the COMPAS-W and/or the DASS-42 measures needed here. The results indicated a significant relationship between the right inferior frontal gyrus (IFG) cluster from the Happy>Neutral condition and wellbeing ($p = 0.026$; see Fig. 1 and Table 3). No other main or interaction effects were significant across the four contrasts. Therefore, only this cluster was used in the twin modelling.

Univariate twin modelling

The averaged *t*-contrast values from the right inferior frontal cluster for the Happy>Neutral condition were entered into a univariate twin modelling analysis to assess the heritability of functional activity within this region in response to positive emotion processing. Intra-class correlations between the MZ and DZ twins indicated that an ADE model would be the most appropriate. Nested models (AE and E) were then fitted to test whether dropping parameters (for the sake of model parsimony) would still be able to explain the variance in happy emotion processing. There was no significant change of fit when an AE model was compared against the ADE model ($p = 0.514$) suggesting the D component could be dropped from the model. When A was dropped from the model, the fit decreased marginally ($p = 0.053$), suggesting that genetic factors play a role in the heritability of functional activity in the right IFG (for positive emotions). The AIC value also decreased slightly, and despite the fact that an AIC difference of less than two may be considered trivial (Millar, 2011), the AE model was still chosen as the best fitting and parsimonious based on the marginal model fit difference. The heritability of functional activity within the right inferior cluster was found to be 20% (see Table 4).

Multivariate twin modelling

At the multivariate level, an AE model was fitted with the right inferior frontal activity, wellbeing and negative mood scores to examine possible genetic and environmental correlations between the three variables. Here, each phenotype (or variable) is decomposed into its genetic and non-shared environmental components, and the correlations across these variables are estimated. A significant genetic correlation (r_A) would indicate the extent to which the two variables share a common genetic influence, while a significant environmental correlation (r_E) suggests that

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Table 2. Significant brain regions associated with emotion-related activation

		Coordinates (MNI)				
Brain region	Side	*x*	*y*	*z*	*t*-value	*k*
1. Happy>Neutral						
Inferior frontal gyrus	R	42	28	30	4.09	664
2. Angry>Neutral						
Inferior frontal gyrus	R	48	32	20	4.69	2060
Extending to insula	R	42	5	48	4.31	
Precentral gyrus	L	−39	4	30	4.57	1629
Extending to IFG	L	−42	22	16	4.19	
Cerebellum (Crus 1)	R	33	−67	−30	5.00	645
Extending to fusiform gyrus	R	41	−55	−18	4.87	
3. Fear>Neutral						
Inferior frontal gyrus	L	−44	17	20	6.14	1776
Inferior frontal gyrus	R	35	11	26	4.41	1163
Extending to insula	R	42	23	18	4.10	
4. Sad>Neutral						
Inferior frontal gyrus	L	−45	22	14	5.80	2116
Extending to insula	L	−39	22	0	4.64	
Insula	R	44	20	16	4.76	1106
5. Disgust>Neutral						
N.S.						

L, left; R, right; IFG, inferior frontal gyrus; *k*, cluster size; N.S., not significant. Regions that survive FWE correction at the cluster level ($p < 0.05$) are listed in order of cluster size.

the relationship between the phenotypes is driven by unique environmental factors. The results showed a significant genetic correlation between wellbeing and negative mood symptoms ($r_A = -0.444$, $p = 0.037$), which accounted for 41% of the phenotypic correlation between the two variables [$r_{ph(A)} = -0.405$][†1]. There were no significant genetic correlations between the right inferior frontal activity and negative mood symptoms ($p = 0.626$) or wellbeing ($p = 0.591$). There was a significant environmental correlation between right inferior frontal activity and wellbeing ($r_E = 0.208$, $p = 0.047$) that was almost 100% accounted for by unique environmental factors. Finally, the environmental correlation between negative mood symptoms and wellbeing was also significant ($r_E = -0.383$, $p < 0.001$), which explained 59% of the phenotypic correlation (Fig. 2).

Discussion

Our findings highlight that neural responses elicited during the appraisal of positive emotion stimuli are associated with greater wellbeing. Neural responsivity to facial emotion stimuli expressing happiness was centred on activation of the dorsolateral prefrontal cortex, and more specifically within the right IFG. We also observed that functional activity within this region showed 20% heritability, with the remaining variance due to unique environmental factors. Lastly, multivariate modelling revealed no common genetic variance contributing to the association between IFG activity and wellbeing, or with negative mood symptoms. In contrast, we observed that unique environment accounted for the shared variance between IFG activity and wellbeing.

These results align with previous functional neuroimaging studies that have shown a relationship between neural bases of emotion processes and specific sub-components of wellbeing (i.e. subjective wellbeing: Cunningham & Kirkland, 2014; Ren et al., 2019; and psychological wellbeing: Heller et al., 2013; van Reekum et al., 2007). To this end, our finding of an association between right IFG activity and COMPAS-W adds to the evidence that there is an underlying mechanism that subserves the link between positive emotion appraisal and wellbeing. The IFG has been implicated in a range of emotion-related processes that include emotional face expressions (Jabbi & Keysers, 2008), social emotion reappraisals (Grecucci, Giorgetta, Bonini, & Sanfey, 2013) and emotional empathy (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009), as well as in resting-state and functional measures of wellbeing (Heller et al., 2013; Kong et al., 2016). Here, we further bridge the gap between the two fields of research and show that positive emotion-related activity within this region is associated with a measure of wellbeing that encapsulates both subjective and psychological wellbeing (but see Jo, Ou, & Kung, 2019).

No significant associations were found between neural activity related to negative emotions and levels of wellbeing, despite previous behavioural (Sanchez & Vazquez, 2014; Yu & Li, 2012) and neuroimaging (Chen et al., 2018; Ren et al., 2019) findings. This may be related to several factors, including recognition superiority

[†]The notes appear after the main text.

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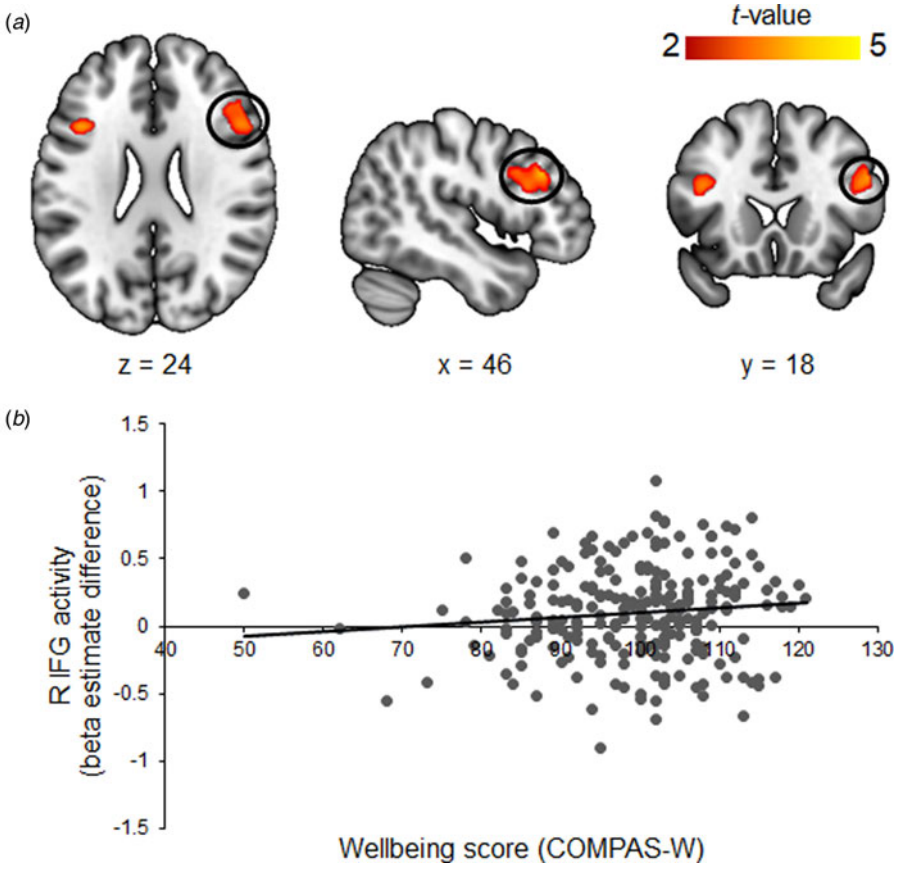

Fig. 1. Voxel-wise activation of the Happy>Neutral contrast in the right inferior frontal gyrus (denoted by black circles; A), which showed a significant association with levels of wellbeing (indexed by the total COMPAS-W scores; B).

Table 3. Linear mixed-model results of the significant association between the right inferior frontal gyrus cluster (from the Happy>Neutral condition) and wellbeing (COMPAS-W)

Effect	Estimate (β)	S.E.	*t*	*p* value
Happy>Neutral				
Inferior frontal gyrus (DLPFC)				
Intercept	0.096	0.108	0.892	0.374
Age	−0.001	0.002	−0.587	0.559
Sex	−0.038	0.050	−0.768	0.444
Zygosity	−0.051	0.051	−1.01	0.317
COMPAS-W	0.056	0.024	2.30	0.023*
DASS-42	0.100	0.058	1.72	0.087

L, left; R, right; *k*, cluster size; DLPFC, dorsolateral prefrontal cortex; S.E., standard error; COMPAS-W, composite measure of wellbeing; DASS-42, negative mood symptoms. *p* values were derived using Satterthwaite approximations for degrees of freedom, which produce acceptable Type 1 error rates (Luke, 2017).

and advantage conferred to happy emotion, where it has been shown that happy faces are identified more accurately and faster compared to the other basic emotions across different stimulus sets, modalities and exposure times (Calvo & Beltrán, 2013; Kirita & Endo, 1995). This is also in line with our previous finding of happy faces eliciting the fastest behavioural responses, which was associated with high levels of wellbeing (Routledge et al., 2018). However, the processing of negative emotions and their relationship with wellbeing may be mediated by other factors (e.g. emotion regulation and reappraisal), which are needed in order to process negative information in a rational and accurate manner (Schutte et al., 2010). Therefore, there may have been a qualitatively different type of processing inferred for the happy condition, which was also the *only* positive emotion (Becker & Srinivasan, 2014). Inclusion of a positive condition may also have affected the context of the experiment, compared to previous studies that did not include any positive stimuli in their paradigms (Chen et al., 2018; Ren et al., 2019). Therefore, the combination of a strong representation of happy faces in the brain and the well-established link between positive emotion and high levels of wellbeing is likely to have contributed to our result of an association between happy faces and wellbeing, but not with the negative emotions. Although causal inferences cannot be made here and the results need replication, we speculate that individuals who react strongly to happy faces may have a positivity bias that leads them to be more attentive to positive stimuli, which in turn contributes to their overall wellbeing and life satisfaction, or *vice versa* (Bastian, Kuppens, De Roover, & Diener, 2014; Lyubomirsky, 2001; Lyubomirsky, Dickerhoof, Boehm, & Sheldon, 2011).

We also examined whether the neural correlates elicited during facial emotion processing have a genetic basis. By expanding this to an adult sample and testing both positive and negative emotions using fMRI, we found a small but marginally significant heritability estimate of 20% for the activity in the right IFG elicited for the happy faces, with the remainder being due to unique environmental influences. To our knowledge, this is the first time that the magnitude of neural activity within a specific brain region has been found to be heritable for emotion appraisal, and adds to the evidence that genetic factors have a role in influencing positive

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Table 4. Univariate heritability estimates for the right inferior frontal gyrus cluster from the Happy>Neutral condition

	ICC		Model fit						Parameter estimates		
Model	MZ	DZ	Comparison	−2LL	AIC	df	$\Delta\chi^2$	*p*	A [CI]	D [CI]	E [CI]
ADE	0.242	−0.031	*v.* saturated	156.82	−299.18	228	0.26	1.00	0	0.223 [0, 0.41]	0.777 [0.59, 0.99]
AE			***v.* ADE**	**157.25**	**−300.75**	**229**	**0.43**	**0.51**	**0.204 [0, 0.39]**	**0**	**0.796 [0.61, 1]**
E			*v.* AE	161.00	−299.00	230	3.75	0.05			1

ICC, intra-class correlation; MZ, monozygotic twins; DZ, dizygotic twins; −2LL, minus twice the log likelihood; df, degrees of freedom; AIC, Akaike's information criterion; CI, 95% confidence intervals. The variance was decomposed into additive (A), non-additive (D) and unique environmental (E) factors. The AE model (in bold) was selected as the best-fitting model based on parsimony and lowest AIC value.

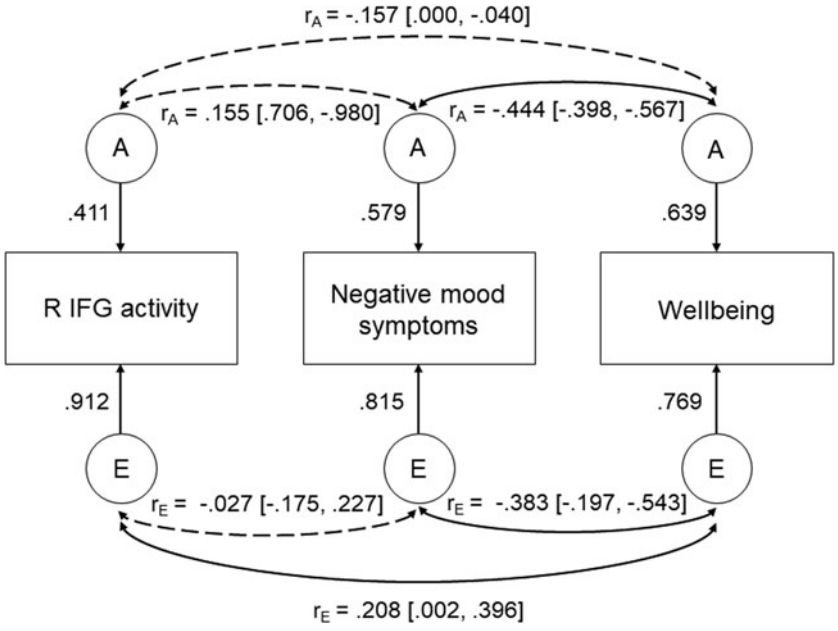

Fig. 2. AE correlated factors model for the three observed variables. Right IFG activity from the Happy>Neutral contrast was indexed by the extracted *t*-contrast values from the region. Negative mood symptoms and wellbeing were measured using the DASS-42 and COMPAS-W scales, respectively. The circles indicate latent factors, where A indicates the additive genetic effect, and E indicates the unique environmental effect of each component. Values on single-headed arrows indicate standardised path coefficients. Double-headed arrows indicate either genetic (r_A) or environmental (r_E) correlations between the latent factors with 95% confidence intervals (in square brackets). Solid and dotted lines indicate significant and non-significant correlations, respectively. R, right; IFG, inferior frontal gyrus.

emotion processing, as observed in genetic (e.g. Wingo et al., 2017) and behavioural studies (e.g. Routledge et al., 2018).

Finally, we conducted a multivariate twin analysis to examine whether there are any shared genetic or environmental bases between IFG activation and wellbeing (and negative mood symptoms), which contribute to the overall phenotypic expression. We did not find any evidence of a shared genetic covariance between any of the three variables. This indicates that despite the heritability of positive emotion-related neural activity (and its associations with wellbeing), there is no evidence of a *shared* genetic component for this phenotype and wellbeing (or negative mood) levels in our sample. This is possible even if each phenotype is highly heritable (independently of one another)[2] due to a lack of overlap of genetic effects on both, leading to a non-significant genetic *correlation* between the phenotypes (Røysamb & Tambs, 2016). In contrast, a novel finding we identified in the multivariate model was a significant unique environmental correlation between wellbeing and the IFG activity to happy faces ($r_E = 0.21$). Interestingly, the environmental covariance between these two variables accounted for almost 100% of the phenotypic correlation observed, which suggests that this association mainly depends on experiences that are unique to each twin (regardless of the same family environment) and some measurement error (Plomin, 2011). Such unique environmental sources can include life experiences such as major illnesses or peer groups that are not shared between siblings, and tend to become much more frequent in adulthood (to the extent that most adult twins will lead separate, non-shared lives). Therefore, the presence of external events specific to each twin may have played an essential role in the expression of IFG activity and sense of wellbeing, especially considering that our participants were all adults with a mean age of 39.4 years. Again, although our study design does not allow for causal inferences, a possible explanation for this may be that individuals who are frequently exposed to positive environments (especially in adulthood, where such event occurrences may differ between twins) are biased towards the processing of positive emotions, which then has cascading effects on higher wellbeing (in line with the broaden-and-build theory of positive emotions; Fredrickson, 2004). Alternatively, it may be possible that given a particular (i.e. positive) environment, a person with higher levels of wellbeing show a disposition towards greater neural activation in response to positive emotional stimuli.

There are several limitations to the current study that need to be acknowledged. Specifically, we conducted multiple linear mixed-model analyses in an exploratory manner as this was one of the first studies examining the link between fMRI brain activity to emotion and wellbeing. Therefore, our results will need replication in an independent sample. Furthermore, our heritability estimate for the right IFG activity was only marginally significant, and therefore also requires replication. This may be related to

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our sample size, which despite being large for MRI studies, is relatively modest for biometric twin analyses. Additionally, it has been noted that contrasting between two conditions (e.g. happy faces>neutral faces), rather than using a baseline may weaken the effects of heritability as the composition of a difference score can remove some of the genetic variance (Li et al., 2019). Therefore, it is unclear whether this smaller heritability estimate is due to the effect itself or simply because we examined a contrast between conditions. Lastly, our emotion task only required passive viewing of faces, rather than active responses, which may elicit stronger emotion-related neural activity. On a more general note, there are limitations regarding assumptions of the twin model that need to be mentioned, including the main assumption that MZ and DZ twins share equal environmental influences (Derks, Dolan, & Boomsma, 2006; but see Felson, 2014). In future studies, it would be worth considering gene-by-environment interactions or gene-environment correlations that may contribute to the model effects reported here (Rathouz, Van Hulle, Lee Rodgers, Waldman, & Lahey, 2008).

In conclusion, we sought to examine the associations between neural bases of emotion processing and wellbeing, as well as the potential heritability of the emotion-wellbeing link. We found that positive emotion was associated with wellbeing, where individuals with highest levels of wellbeing displayed the largest neural activity for happy faces in the right IFG. This activation was further found to be heritable, but there was no evidence for shared genetic correlations between the neural activity and wellbeing, or with negative mood symptoms. In contrast, a significant unique environmental correlation was observed between neural activity and wellbeing. Altogether, these results support the idea of a mutual relationship between emotion and wellbeing, and suggest that positive emotion processing may play an important role in optimal psychological functioning. Moreover, it seems that unique life events are able to influence both the neural responses to positive emotion as well as levels of wellbeing, further supporting the notion of a positive emotion-wellbeing link.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0033291721002695.

Author contributions. HRPP conceptualised the aims of the paper, ran formal data analyses, and drafted and revised the paper. MRC aided in the statistical modelling of the twin data. JMG, LMW and PRS designed the study and oversaw the running of the larger project. JMG also conceptualised the aims of the paper, supervised analyses, and helped edit the original draft and revised versions. All authors reviewed the results, and revised and edited the final version of the paper.

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Conflict of interest. LMW has received advisory board fees from One Mind Psyberguide and the Laureate Institute for Brain Research unrelated to this study. JMG is a stockholder in MAP Biotech Pty Ltd. All other authors declare that they have no conflicts of interest.

Notes

1 $r_{ph(A)} = \left(\sqrt{a_1} \times r_A \times \sqrt{a_2}\right)/r_{ph}$ where $r_{ph(A)}$ denotes the proportion of the contribution of genetic correlation (r_A) between two variables to the phenotypic correlation (r_{ph}). a_1 and a_2 denote the standardised variance components for each latent variable.

2 On this note, we also calculated the heritability estimates of wellbeing scores in our sample and found a moderate level of heritability (40%; please see online Supplementary Table S2), in line with what has been reported in a large meta-analysis of nearly 56 000 individuals (36%; Bartels, 2015).

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