Cerebral Cortex, January 2020;30: 181–196

doi: 10.1093/cercor/bhz080
Advance Access Publication Date: 2 May 2019
Original Article

ORIGINAL ARTICLE

Functional and Structural Brain Correlates of Socioeconomic Status

Zachary A. Yaple[1] and Rongjun Yu[1,2,*]

[1]Department of Psychology, National University of Singapore, Singapore and [2]NUS Graduate School for Integrative Sciences and Engineering, National University of Singapore, Singapore

Address correspondence to Rongjun Yu, Department of Psychology, National University of Singapore, Block AS4, #02-17, 9 Arts Link, Singapore, 117570. Email: psyyr@nus.edu.sg

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

Abstract

Socioeconomic status (SES) is a multidimensional construct that includes not only measures of material wealth, but also education, social prestige, and neighborhood quality. Socioeconomic correlates between wealth and cognitive functions have been well established in behavioral studies. However, functional and structural brain correlates of SES remain unclear. Here, we sought to uncover the most likely neural regions to be affected by low SES, specifically associated with age. Using effect size–seed-based d Mapping, we compiled studies that examined individuals with low SES and performed functional magnetic resonance imaging and voxel-based morphometry meta-analyses. The results revealed that as from early to late age, individuals exposed to low SES are less likely to have sustained executive network activity yet a greater likelihood to enhanced activity within reward-related regions. A similar activity was shown for gray matter volume across early to older age. These findings provide the first quantitative integration of neuroimaging results pertaining to the neural basis of SES. Hypoactivation of the executive network and hyperactivation of the reward network in low SES individuals may support the scarcity hypothesis and animal models of the effects of early adversity.

Key words: Socioeconomic status, Seed-based d mapping, VBM, fMRI

Introduction

Wealth distinguishes individuals by their socioeconomic status (SES), a measure of an individual's sociological and economic status with respect to others within the social and economic hierarchy. SES is entrenched into one's political views, perhaps explained by economic self-interest and ideology (see Brown-Iannuzzi et al., 2017 for review). While SES has been shown to affect life satisfaction (Gerdtham and Johannesson, 2001; Kahnemann and Deaton, 2010; Haushofer and Fehr, 2014) and academic achievement (Duncan et al., 1994; Bradley and Corwyn, 2002), psychological studies have also revealed influences of SES on an individual's thought processes (see Lipina and Posner, 2012 for review). For instance, well-being, income, and SES have been shown to affect emotion regulation (Côté et al., 2010; Kim et al., 2013; Gianaros and Wager, 2015), cognitive functioning (Lupien et al., 2001; Mani et al., 2013; Hackman et al., 2015), and decision-making tendencies (Wood, 1998; Griskevicius et al., 2011; Spears, 2011; Brents et al., 2017), such as excessive borrowing (Shah et al., 2012) and choosing early as opposed to late rewards (Haushofer and Fehr, 2014).

Exposure to low SES also influences cognitive abilities in children (Norman and Breznitz, 1992; Brooks-Gunn and Duncan, 1997; McLoyd, 1998; Lupien et al., 2001; Raizada and Kishiyama, 2010; Hackman et al., 2015; Farah, 2017). For example, executive control functions have been shown to be influenced in children from families with low income compared to children from affluent families (Hsu et al., 2014; Hackman et al., 2015; He and Yin, 2016) that may be fundamental to the decrease in language and reading ability among children living in low SES environments

© The Author(s) 2019. Published by Oxford University Press. All rights reserved. For permissions, please e-mail: journals.permission@oup.com.

(Hoff, 2003; Novick et al., 2005, 2014; Noble et al., 2007; Raizada et al., 2008; Jednoróg, et al., 2012). Individuals developing in low SES environments may also develop a predisposition to reward sensitivity (Gonzalez et al., 2016) and an increase in risky decision-making (Furr-Holden et al., 2012; Carlson et al., 2014). Therefore, understanding developmental patterns associated with varied SES are important to consider for theoretical purposes, and in practice these differences may illuminate potential issues with regards to wealth.

Using functional magnetic resonance imaging (fMRI), attempts have been made to shed light on the functional and structural brain differences between high and low SES developing individuals, culminating into a recent review (Farah, 2017). For instance, socioeconomic disadvantages exert influences on functional brain network organization as well as brain volume and cortical thickness (Chan et al., 2018); most notably within the left hemisphere (see Holz et al., 2015a for review). Using small volume thresholding, several regions during development have been shown to be influenced by disadvantageous SES, namely the left inferior frontal cortex (Raizada et al., 2008; Noble et al., 2012), medial frontal cortex (Javanbakht et al., 2015), amygdala (Noble et al., 2012; Luby et al., 2013; Hanson et al., 2015; Javanbakht et al., 2015), bilateral hippocampi (Hanson et al., 2011, 2015; Jednoróg et al., 2012; Staff et al., 2012; Ellwood-Lowe et al., 2018) and the ventral striatum (Ly et al., 2011). The main drawback to using small volume corrections, however, is that it tends to bias one brain region over another and may therefore underestimate activity of other relevant regions for the socioeconomically disadvantaged. Whole-brain analysis has yet to reveal consistent patterns of brain functioning in individuals with high and low SES. For instance, while some studies report hyperactivity within the left frontal cortex for low SES (Sheridan et al., 2012; Kim et al., 2013; Gonzalez et al., 2015; Muscatell et al., 2016), others have shown hypoactivity for adjacent frontal regions (Gianaros et al., 2011; Sheridan et al., 2012), thereby questioning the homogeneity among these studies.

In addition to functional neural alterations, differences in structure among low SES individuals have been reported in studies using voxel-based morphometry (VBM). For instance, unlike children residing in high income families, among populations of children from lower income families, small increments in income were associated with relatively large differences in surface area (Noble et al., 2015). Specifically, while some report differences in gray matter volume within the perigenual anterior cingulate cortex and orbital frontal cortex in low SES individuals (Gianaros et al., 2007; Holz et al., 2015b; Yang et al., 2016), another study reported reduced gray matter volume within the bilateral hippocampi, insulae, and occipital-temporal gyri (Jednoróg et al., 2012). Consistent findings of gray matter volume using VBM among SES has yet to be determined. Thus, a quantitative analysis of VBM studies in low SES may provide additional information supporting the findings provided from fMRI studies.

Qualitative reviews call attention to inconsistent behavioral and neurobiological evidence (Holz et al., 2015a; Varnum, 2016; Farah, 2017). While lower SES individuals have stronger responses in mentalizing neural regions such as the dorsal-medial prefrontal cortex and posterior cingulate cortex (Muscatell et al., 2012), low compared to high SES individuals exhibit a stronger neural response within the amygdala when exposed to angry faces (Gianaros, et al., 2008), an area that is often associated with fear conditioning (Philips and LeDoux, 1992; Duvarci and Pare, 2014) and processing of dynamic faces (Zinchenko et al., 2018). Notably, the orbital frontal cortex, an area associated with choice evaluation (Diekhof et al., 2012) and reward processing (Holz et al., 2015a, 2015b) varies in neural response and gray matter volume density in adults exposed to urbanicity (Krämer et al., 2017) and early-life poverty (Holz et al., 2015a), respectively. Therefore, to discern which areas are most likely to be influenced by SES as a function of age we find it necessary to perform quantitative analyses on individuals with low SES.

The purpose of this study is to determine concordant patterns of brain activity and structural changes for low SES across age. The experience of SES affects the balance of these two competing systems. Interestingly, despite various research reports, much emphasis has been placed on decreased executive (Mani et al., 2013; Hsu et al., 2014; Hackman et al., 2015; He and Yin, 2016) and increased reward-related functioning (Furr-Holden et al., 2012; Carlson et al., 2014; Holz et al., 2015b; Gonzalez et al., 2016) with respect to developing children in low SES communities. Specifically, developing individuals with low SES lack efficient executive abilities (Hsu et al., 2014; Hackman et al., 2015) and are prone to reward sensitivity (Gonzalez et al., 2016). This premise concurs with the Scarcity Hypothesis, a behavioral model, which states that scarcity of resources affects how people allocate attention; individuals living in poverty tend to focus more on problems associated with money while neglecting non-monetary problems (Mullainathan and Shafir, 2013). These empirical findings also resonate with the competing neurobehavioral decision systems model that describes the decision-making process as two competing systems: an impulsive decision system that engenders individuals to choose immediate reinforcers and an executive decision system that support individuals to favor long-term outcomes and inhibit impulses (Bickel et al., 2012). The experience of SES may affect the balance of these two competing systems, making the executive decision system less effective than is required for adaptive decision-making.

We further examine whether low SES is associated with structural changes in brain regions that are engaged in reward processing and executive control. Corticolimbic brain areas continue to develop throughout childhood and adolescence (Casey et al., 2005; Blakemore, 2012), making them highly susceptible to environmental influence throughout development. It has been proposed that the neuroanatomical substrates linking socioeconomic position or perceived social standing to health-related risk factors likely involve frontal-striatal circuits that are associated with chronic stress in non-human animal models (McEwen, 2000). Animal research has shown that chronic and social stressors are associated with unique structural changes in the anterior cingulate cortex, orbital frontal cortex, hippocampus, amygdala, and striatum (Matthews and Robbins, 2003; Radley and Morrison, 2005). This corticolimbic circuitry coordinates behavior with neuroendocrine function in the service of adaptively coping with emotionally salient environmental and psychosocial challenges. For example, dopaminergic input from midbrain nuclei heavily innervate the ventral striatum, mediating striatal function in appetitive behaviors. Thus, according to a chronic social stress perspective (McEwen, 2000), low social status could plausibly covary with changes in the morphology of the striatum and prefrontal cortex. For this paper, we aim to explore the likelihood of concordance for functional brain activity and gray matter volume by performing several quantitative meta-analyses.

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

We hypothesize that subgroups classified as having a low compared to high SES may exhibit 1) greater concordance of functional brain activity/gray matter volume within reward-related areas (i.e. ventral striatum, putamen, caudate nucleus, and the orbital frontal cortex and; 2) less concordance of functional brain activity/gray matter volume within executive-related areas (frontal and medial frontal cortices). To test these hypotheses, we compiled fMRI studies that report foci (coordinates) from individuals classified as having a high or low SES depending on several socio- and/or economic measures such as occupation, income, and education. Consequently, to test which areas were most influenced by SES as a function of age we performed a meta-regression analysis.

Materials and Methods

Study selection

A search for fMRI articles on low SES was performed by entering keywords "Socioeconomic" AND "fMRI" into web of knowledge database (http://www.webofknowledge.com). This search includes articles up to 1 March 2018, which yielded a total of 73 articles and which were screened for eligibility. To identify eligible articles, we screened those that 1) did not report fMRI foci; 2) did not report foci in standard stereotactic coordinate space (either Talairach or Montreal Neurological Institute, MNI); 3) articles that did not use whole-brain analysis; 4) contrasts generated using fixed effects analyses; 5) contrasts isolated from unhealthy adults or non-humans; and 5) contrasts that did not include high or low socioeconomic groups. Six additional studies were discovered from several review articles bringing the total number of eligible studies to 17, which reported within group whole-brain results from healthy participants in MNI or Talairach space.

An independent search for VBM articles was performed using the key terms "Socioeconomic" and "voxel" and "morphometry" into web of knowledge. This search was performed on 18 April 2018 and which yielded a total of 34 studies. Because only five articles were eligible for the study, an additional search for articles was performed by browsing through PubMed and review articles and alternating key terms in web of knowledge. In total, we found 11 articles that performed VBM on healthy individuals with low SES. See Figure 1 for PRISMA flowchart of article selection for the functional and structural brain analysis.

SES measures

The experiments included in the current meta-analysis include multiple measures of SES. For instance, the first measure of SES used was the Hollingshead's four-factor index of social status (Hollingshead, 1975), which assigns individuals to a social class using a 5-point scale calculated by the occupation and education level. Similarly, the MacArthur scale of subjective social status (Adler et al., 2000) uses a self-rating 10-point scale to assess income and occupational level. A more objective measure of SES is the income-to-needs ratio that assesses SES by dividing total family income by the poverty threshold specified in the US census (Noble et al., 2012; Sheridan et al., 2012). Other methods include individual scores of education, occupation and/or income level to categorize SES groups or self-report questionnaires that evaluate social interactions between parents and their children (Black et al., 2012; Takeuchi et al., 2015; Yang et al., 2018), and exposure to deprived neighborhoods (Gonzalez et al., 2015; Butler et al., 2018). Specifically for children and adolescents, parental education, occupation, and/or income level was assessed.

Functional brain activation and deactivation of SES was assigned depending on whether the original study using a continuous or discrete measure for assessing SES among individuals. For studies using continuous methods, we assigned activation and deactivation of SES based on the direction of the correlation with a measurement of SES (Noble et al., 2006; Kim et al., 2013; Gonzalez et al., 2015; Yang et al., 2016; Mattan et al., 2017). For these studies, positive (negative) correlations between neural activity and low (high) SES were assigned as activations, while the negative (positive) associations between brain activity and low (high) SES were assigned as deactivations. Continuous measures were also based on the results of a general linear model analysis (Gianaros et al., 2007; Takeuchi et al., 2015), revealed by a main/interaction effect associated with SES (Gianaros et al., 2011; Sheridan et al., 2012; Demir-Lira et al., 2016; Gonzalez et al., 2016; Kim et al., 2016, 2017; Conant et al., 2017). Other studies analyzed brain activity of SES by dividing into a high and low SES groups (Sheridan et al., 2012; Mackey et al., 2015; Finn et al., 2017; Wang et al., 2016). For these studies, SES groups were determined by using median-split (Sheridan et al., 2012; Wang et al., 2016), or by having an income below a specified percentage of the poverty level (Mackey et al., 2015; Finn et al., 2017). One article did not explicitly state the classification method (Silverman et al., 2009). We assigned low SES as activations and high SES groups as deactivations. See Table 1 for a list of all studies listing group type.

Software and analysis

Effect size–seed-based d mapping (ES-SDM) meta-analysis software from the seed-based d mapping project (http://www.sdmproject.com) was used to perform the main meta-analysis for adults (mean age >18 years old at the time of the scan). Based on activation likelihood estimation, this analysis combines statistical parametric t-maps and peak coordinates of clusters from multiple studies to increase statistical power (Radua et al. 2012). Effect-size brain maps and variances are derived from reported t-statistics. The full width at half maximum (FWHM) in SDM was set at the default (20 mm) to control for false positives (see Radua et al. 2012). To optimally balance sensitivity and specificity resulting statistical maps were thresholded at $P = 0.005$ to control for family-wise error rate (Radua et al., 2012).

To assess which brain areas are affected by age, linear models (meta-regression analysis) was performed on the mean age of each study at the time of the scan. Linear models are used for comparing two or more groups, controlling for potential confound variables, or assessing the heterogeneity of the findings by means of meta-regressions. For our purposes we used the map that reflects the differences between old aged individuals with low SES and young aged individuals with low SES (i.e. the "_1m0_z" map). The meta-regression included foci across all ages at the time of the scan. We report the statistical difference between individuals with low SES at maximum compared to minimum age thresholded at $P = 0.005$.

The meta-analyses will inevitably yield variation of activation across studies (study heterogeneity) depending on the modality of the task at hand, the measure of SES, or how the subjects were grouped into high and low SES. To account for study heterogeneity, heterogeneity Q statistic maps were

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

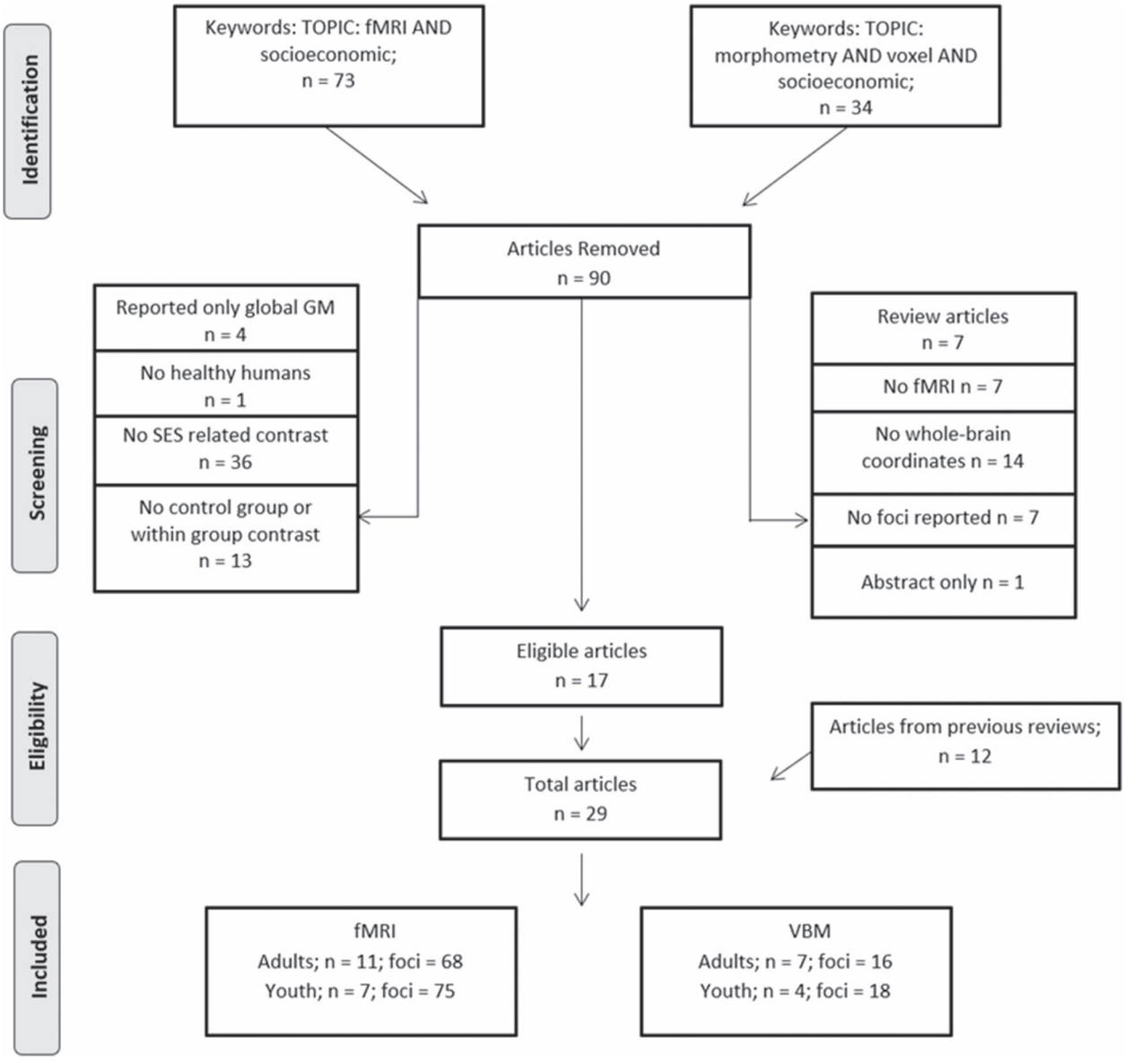

Figure 1. PRISMA flowchart for eligibility of articles for fMRI and VBM meta-analyses on SES.

calculated for each meta-analysis and thresholded at $P = 0.005$. The heterogeneity Q statistic determines which brain areas are likely to yield variation across studies. Heterogeneity Q statistic maps are calculated to determine the regions associated with high study heterogeneity that can then be compared with maps produced by the meta-analyses. This heterogeneity Q statistic is assessed in terms of a X^2 distribution automatically calculated with the main-meta-analysis and converted to standard z values in ES-SDM (Radua et al., 2012). Complementary analysis included jackknife sensitivity analysis; thresholded at $P = 0.005$ to assess the replicability of clusters. Jackknife sensitivity analysis is a linear bootstrapping sampling technique that repeats the meta-analysis as many times as the number of studies that have been included, removing each study per analysis. If an area remains significant in all or most (>75%) of the combinations of studies, it is considered highly replicable (Radua and Mataix-Cols, 2009).

Results

Whole-brain fMRI

Seventeen articles were eligible for inclusion in the meta-analyses. Studies reported varied contrasts (high SES > low SES; low SES > high SES; high SES > baseline; low SES > baseline, etc.). High SES was treated as control group and hence low SES > high SES contrasts represents activations, while the opposite contrast represents deactivations. Table 1a summaries participant demographics and contrast type. A total of 798 participants were included in the meta-analysis; 10 articles reported adults only (514 participants), 6 reported youth only (246 participants), and 1 reported both age groups (16 adults and 22 youth; Muscatell et al., 2012). Foci for each age group were separated for the main meta-analyses and compiled for the meta-regression. Mean age was 25.25 ± 6.68 for adults and 11.81 ± 2.79 for the youth group.

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

Table 1a Information on source datasets included in the meta-analysis for functional MRI

Article	n	Mean age (SD)	Age range	SES measure	Foci	Task type	Contrast type[a]	Age group	Analysis type[c]
Conant *et al.* (2017)	32	10.3 (1.54)	7–12	Paternal Edu.	4	Executive	–	Youth	Continuous
Demir-Lira *et al.* (2016)	33	13.4 (1.5)	11–16	Hollingshead	2	Executive	–	Youth	Continuous
Finn *et al.* (2016)	67	14.6	NA	Paternal Inc.	37	Executive	+/–	Youth	Discrete
Gianaros *et al.* (2011)	76	44.45	31–54	MacArthur	4	Reward	–	Adults	Continuous
Gonzalez *et al.* (2015)	85	25.5	25–26	NQ	5	Social	+	Adults	Continuous
Gonzalez *et al.* (2016)	83	24.41 (1.11)	NA	Hollingshead	10	Reward	+	Adults	Continuous
Kim *et al.* (2013)	49	23.61 (1.3)	20–27	I:N	12	Emotion	–	Adults	Continuous
Kim *et al.* (2016)	28	25.07 (5.64)	18–34	I:N	4	Emotion	–	Adults	Continuous
Kim *et al.* (2017)	38	24.41 (5.22)	18–36	I:N	3	Emotion	+/–	Adults	Continuous
Liberzon *et al.* (2015)	49	23.7	NA	I:N	1	Emotion	+	Adults	Continuous
Mackey *et al.* (2015)	58	14.41	NA	Paternal Inc.	6	Executive	–	Youth	Discrete
Mattan *et al.* (2018)	60	23.8 (4.59)	NA	MacArthur	13	Social	+	Adults	Continuous
Muscatell *et al.* (2012)[b]	16	19.81 (1.8)	18–24	MacArthur	3	Social	+	Adults	Continuous
Muscatell et al. (2012)[b]	22	13.02 (0.29)	12–13	MacArthur	2	Emotion	+	Youth	Continuous
Muscatell *et al.* (2016)	31	19	18–22	MacArthur	5	Social	+/–	Adults	Continuous
Noble *et al.* (2006)	38	7.11	6.9–9.7	I:N	8	Executive	+/–	Youth	Continuous
Sheridan *et al.* (2012)	18	9.86	8–12	I:N	16	Executive	+/–	Youth	Discrete
Silverman *et al.* (2009)	15	24	19–29	MacArthur	8	Emotion	–	Adults	Discrete

Note: *n* = sample size; SD = Standard deviation; NA = not available; [a] = low minus high SES subjects (+), high minus low SES subjects (–); [b] = study includes both groups; [c] = SES grouped by using a continuous or discrete measure; Edu. = education; Inc. = Income; NQ = Neighborhood Quality Questionnaire; I:N = Income-to-needs ratio

Table 1b Information on source datasets included in the VBM meta-analysis

Article	n	Mean age (SD)	Age range	SES measure	Foci	Task type	Contrast type[a]	Group type	SES type[b]
Black *et al.* (2012)	51	5.59 (0.42)	5–7	Fam. R. Ind.	3	Executive	–	Youth	Continuous
Butler *et al.* (2018)	65	15.8 (1.1)	14–18	Parental Inc.^	2	No task	–	Youth	Continuous
Drakesmith *et al.* (2016)	125	20.11 (0.004)	NA	Maternal Edu.	3	No task	–	Adults	Continuous
Gianaros *et al.* (2007)	100	44.75	31–54	MacArthur	3	No task	–	Adults	Continuous
Jednoróg *et al.* (2012)	23	9.58 (0.5)	8–10	Hollingshead	11	Executive	–	Youth	Continuous
Kong *et al.* (2015a)	299	21.57 (1.01)	NA	Maternal Edu.	1	Executive	+	Adults	Continuous
Kong *et al.* (2015b)	294	21.57 (1.01)	NA	MacArthur	1	No task	+	Adults	Continuous
Takeuchi *et al.* (2015)	290	11.1	6–18	Parental Inc.^	2	No task	+	Youth	Continuous
Wang *et al.* (2016)	280	22.68 (1.07)	NA	MacArthur	5	No task	+/–	Adults	Discrete
Yang *et al.* (2016)	253	19.96 (1.35)	18–27	Parental Inc.	1	Executive	+	Adults	Continuous
Yang *et al.* (2018)	158	22.39 (1.54)	NA	Parental Inc.^	2	No task	+	Adults	Continuous

Note: *n* = sample size; SD = Standard deviation; NA = not available; [a] = increase in gray matter for low SES subjects (+), reduction in gray matter for low SES subjects (–); [b] = SES grouped by using a continuous or discrete measure; Fam. R. Ind. = Familial Risk Index; Edu. = education, Inc. = Income; NQ = Neighborhood Quality Questionnaire; ^ SES was based on both parental income and education

The main analysis for adults revealed five clusters for low compared to high SES (Fig. 2; Table 2a). All regions were present in at least 75% of the jackknife analyses. From largest to smallest in cluster size, these regions included a cluster within the left dorsolateral superior frontal gyrus [Brodmann area (BA) 9] (881 voxels), left lateral orbital frontal gyrus (BA 11; 263 voxels), left inferior temporal gyrus (BA 37; 159 voxels), left middle occipital gyrus (BA 18; 133 voxels), and right caudate nucleus, including anterior thalamic projections (42 voxels). The area with the highest z-score was the left lateral superior frontal gyrus. The opposite contrast (high compared to low SES, representing deactivations in low SES individuals) revealed three clusters within the left anterior cingulate/paracingulate gyrus (BA 32; 516 voxels), left angular gyrus (BA 39; 140 voxels, including superior longitudinal fasciculus II [29 voxels]), and a cluster including the left longitudinal fasciculus and inferior frontal gyrus, triangular part, (BA 48; 97 voxels). All three clusters were more than 75% replicable. With exception to the right caudate nucleus, all clusters were found within the left hemisphere. Hence, our results, in part, lend support to the notion that activation of the left hemisphere is affected by SES (Holz et al., 2015a).

Regarding the meta-regression, a peak within the right caudate nucleus with anterior thalamic projections (440 voxels) had increased in activation for low SES as a function of age (Fig. 2; Table 2b). This finding may suggest that as individuals with low SES age, the right caudate nucleus become more hyperactivate. Furthermore, the meta-regression revealed a linear trend of aging in low SES associated with hypoactivation of the left anterior cingulate/paracingulate gyrus and medial orbital gyrus (BA 32; 729 voxels), left angular gyrus (BA 39;

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

Table 2a Information on source datasets included in the VBM meta-analysis

Significant regions of activation for Low compared to High SES adults								
Region	BA[a]	x	y	z	SDM-Z	P	Voxels[b]	Jackknife
L Superior Frontal (lat.)	9(8)	−18	46	36	2.182	$1.549e^{-5}$	881	100*
L Orbital Frontal (lat.)	11	−30	46	−16	1.800	$2.632e^{-4}$	263	92.85*
L Inferior Temporal	37	−58	−56	−8	1.475	$1.207e^{-3}$	159	92.85*
L Middle Occipital	18(19)	−36	−94	8	1.471	$1.254e^{-3}$	133	100*
R Caudate Nucleus		14	24	−2	1.278	$3.075e^{-3}$	42	92.85*
Significant regions of deactivation for Low compared to High SES adults								
Region	BA[a]	x	y	z	SDM-Z	P	Voxels[b]	Jackknife
L Anterior Cingulate	32	−6	34	−4	−1.326	$8.257e^{-4}$	516	92.85*
L Angular	39	−44	−58	36	−1.365	$6.812e^{-4}$	140	92.85*
L Longitudinal fasciculus		−40	14	24	−1.622	$1.135e^{-4}$	97	85.71*

Note: BA = Brodmann area; [a] = peak coordinates with overlapping BA areas (in brackets); [b] = 2 mm × 2 mm × 2 mm; SDM-Z = signed differential mapping z-score; Jackknife replicability is represented as percentage; L = Left; R = Right; foci represented in MNI space; * regions greater than 75% replicability; lat. = lateral; thresholded at $P < 0.005$; FWHM 20 mm

Table 2b Meta-regression: changed in activation with Low SES as a function of age

Hyperactivity							
Region	BA[a]	x	y	z	SDM-Z	P	Voxels[b]
R Caudate Nucleus		18	20	8	1.066	$9.821e^{-4}$	440
Hypoactivity							
Region	BA[a]	x	y	z	SDM-Z	P	Voxels[b]
L Anterior Cingulate	32	−2	40	0	−3.249	$1.186e^{-4}$	729
L Angular	39	−44	−62	32	−3.490	$3.147e^{-5}$	262
L Superior Frontal (med.)	10	0	58	26	−2.691	$8.757e^{-4}$	135
L Longitudinal Fasciculus		−42	16	22	−2.778	$6.513e^{-4}$	70

Note: BA = Brodmann area; [a] = peak coordinates with overlapping BA areas (in brackets); [b] = 2 mm × 2 mm × 2 mm; SDM-Z = signed differential mapping z-score; L = Left; R = Right; foci represented in MNI space; med. = medial; thresholded at $P < 0.005$; FWHM 20 mm

262 voxels), left medial superior frontal gyrus (BA 10; 135 voxels), and left operculum (70 voxels). Interestingly, concurrent activation for these regions are identified as frontal-parietal and cinguloopercular executive networks (Dosenbach et al., 2007; Dosenbach et al., 2008; Gratton et al., 2018).

Whole-brain VBM

Eleven articles using 1938 participants (1509 > 18 years of age, 429 < 18 years of age) were eligible. The average age for adults was 24.71 ± 8.89 and 10.51 ± 4.21 for children. Table 1b summarizes participant demographics. The main analysis (for adults only) revealed increased volume size of the left medial superior/middle frontal cortex (BA 10; 970 voxels), which lies adjacent with the wall of the anterior cingulate, and another cluster within the left medial orbital frontal cortex (BA 11; 276 voxels), just above the orbital part of the frontal bone. Both regions were >75% replicable (see Fig. 3; Table 3a). Reductions in gray matter volume were found in left and right hippocampi and median network of the cingulum (383 and 274 voxels, respectively) and right precuneus/postcentral gyrus (182 voxels) in adults. This former finding corroborates both whole-brain (Jednoróg et al., 2012) and ROI studies (Hanson et al., 2011, 2015; Staff et al., 2012) that reveal reductions in hippocampi gray matter in individuals exposed to poor environments during childhood.

No main analysis on children could be performed due to the low sample size. To examine the influence of SES on age a meta-regression on gray matter volume was performed that included subjects from both adults and children with age as a regressor. This analysis revealed enlarged right and left angular/middle occipital gyri (BA 39; 282 and 183 voxels, respectively). A third cluster was found within the right orbital frontal cortex (BA 11; 148 voxels). In summary, both left and right orbital frontal cortex were affected by low SES, yet only right medial orbital frontal cortex increases linearly across development. Finally, the meta-regression analysis revealed gray matter reductions within the right anterior cingulate cortex/superior medial orbital frontal gyrus (BA 10; 228 voxels) and left superior temporal gyrus (BA 22; 106 voxels). See Figure 3 and Table 3b for visual representation and full list of statistical output for these clusters. Also see Figure 4 for histogram of increased and decreased activation and gray matter volume for reward and executive regions in low SES individuals. Note that while the frequency of activation of the caudate nucleus is relatively high in childhood and increases linearly during adulthood, the frequency of deactivation for the left superior frontal cortex increases linearly across age.

Heterogeneity Q statistic

To explore regions with higher heterogeneity, we performed heterogeneity Q statistic for each analysis. Clusters yielded

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

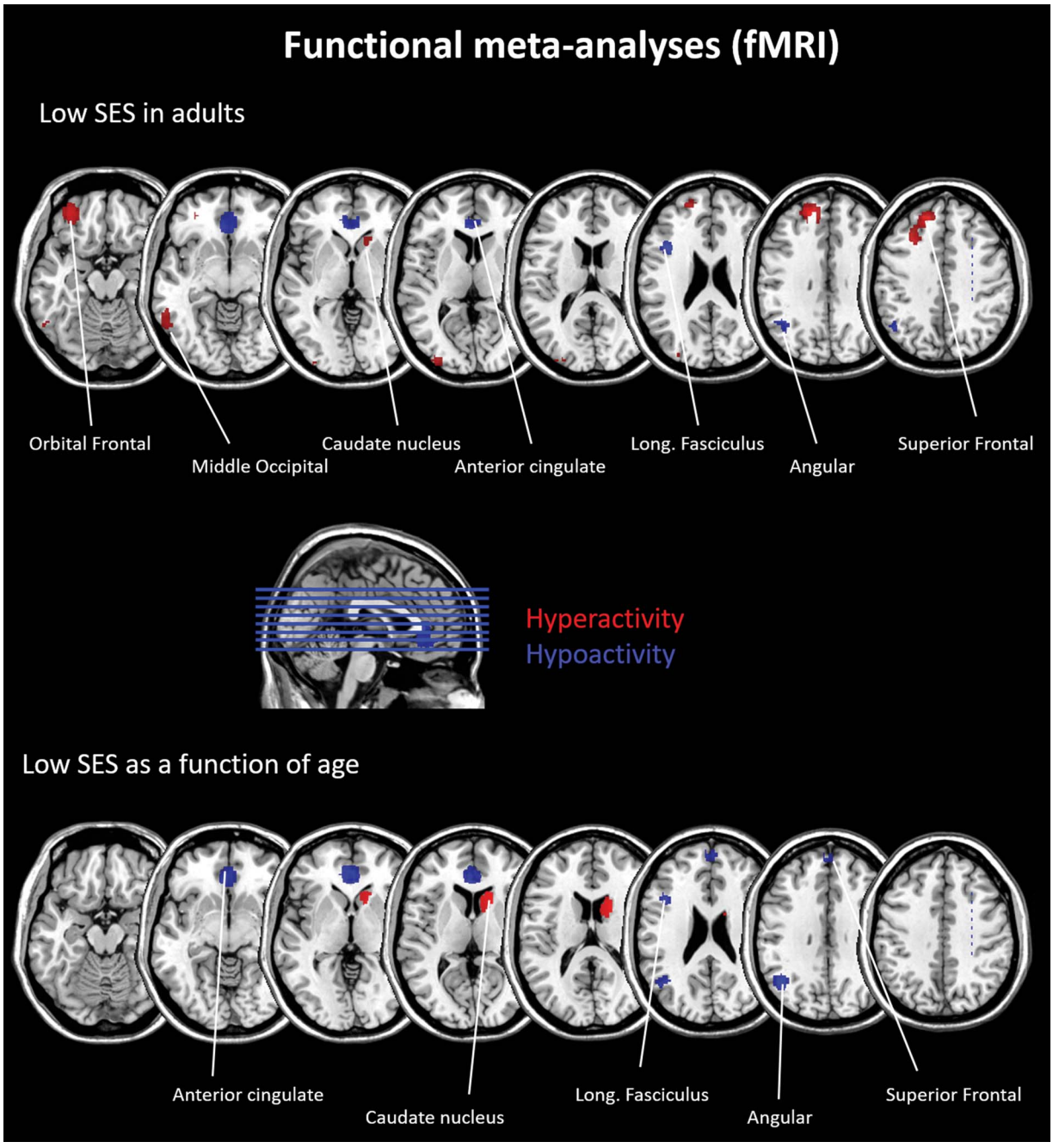

Figure 2. Histograms representing increases and decreases in activation/volume of four key regions of the reward and executive networks: caudate nucleus (CN), right orbitofrontal cortex (R OFC), left superior frontal gyrus (L SFG) and anterior cingulate cortex (ACC). Regions are both revealed by the functional (fMRI) and structural (VBM) meta-analyses.

by these maps would predict high heterogeneity, which could potentially confound the results of the main meta-analysis analysis and meta-regression. Multiple clusters were yielded by the heterogeneity Q statistic map, yet none of these clusters overlapped with the main meta-analysis in adults or the meta-regression across age for both functional and structure MRI data (see Supplementary Materials). Therefore, heterogeneity among studies (e.g. task design, task modality, type of SES measure, methods of analysis, etc.) do not account for the clusters reported in the main analysis and meta-regression. See Supplementary Material Figures 1–4 for funnel plots corresponding to activated and deactivated clusters across fMRI and VBM meta-analyses.

Discussion

Many have attempted to explore the differences between developing individuals with high and low SES, to which some

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

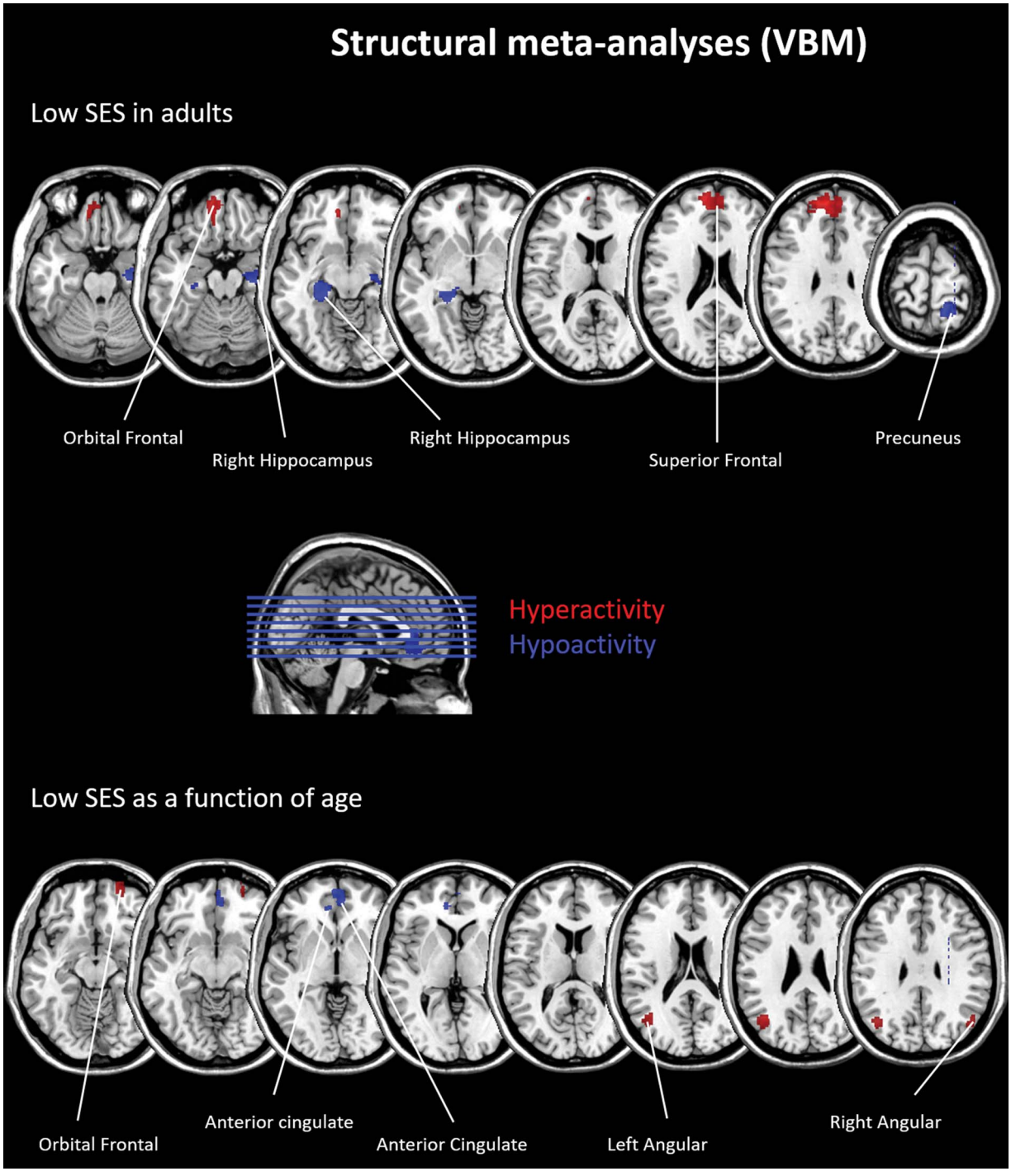

Figure 3. Results from functional MRI studies in low SES individuals compiled from fMRI studies. (*a*) Main analysis of adults compared low with high SES individuals; (*b*) meta-regression of hyper- and hypoactivity on SES as a function of age. Red represents activations; blue represents deactivations for low SES individuals.

have relied on region of interest analysis using small volume corrections (Ly et al., 2011; Noble et al., 2012; Luby et al., 2013; Hanson et al., 2015; Javanbakht et al., 2015), or have shown inconsistent patterns of activity between developing individuals with high and low SES (e.g. Gianaros et al., 2011; Sheridan et al., 2012; see Farah, 2017 for review). The aim for this study was to investigate the differences in functional brain activity and gray matter structure by performing quantitative meta-analyses. Our results reveal concordant hyper- and hypoactivity of the brain as well as structural differences in individuals with low SES. Throughout the following, we discuss the functional and structural brain differences in SES and how these findings are associated with prior empirical studies.

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

Table 3a Meta-regression: changed in activation with Low SES as a function of age

Increased gray matter in regions for Low compared to High SES adults								
Region	BA[a]	x	y	z	SDM-Z	P	Voxels[b]	Jackknife
L Superior Frontal (med.)	10	−8	56	28	2.020	$2.116e^{-5}$	970	100*
L Orbital Frontal (med.)	11	−12	46	−18	1.665	$3.065e^{-4}$	276	71.4*
Reduced gray matter in regions for Low compared to High SES adults								
Region	BA[a]	x	y	z	SDM-Z	P	Voxels[b]	Jackknife
L Hippocampus	37(20)	−24	−36	−2	−1.158	$2.167e^{-4}$	383	85.7*
R Hippocampus	20	24	−8	−18	−1.159	$1.976e^{-4}$	374	85.7*
R Precuneus	5	16	−48	68	−1.161	$1.873e^{-4}$	182	85.7*

Note: BA = Brodmann area; [a] = peak coordinates with overlapping BA areas (in brackets); [b] = 2 mm × 2 mm × 2 mm; SDM-Z = signed differential mapping z-score; Jackknife replicability is represented as percentage; L = Left; R = Right; foci represented in MNI space; *regions greater than 75% replicability; med. = medial; thresholded at $P < 0.005$; FWHM 20 mm

Table 3b Meta regression: changed in gray matter with Low SES as a function of age

Increases							
Region	BA[a]	x	y	z	SDM-Z	P	Voxels[b]
R Angular	39	48	−72	40	1.570	$7.998e^{-5}$	282
L Angular	39	−40	−66	24	1.208	$6.006e^{-4}$	183
R Orbital Frontal (med.)	11	22	60	−14	1.169	7.803^{-4}	148
Reductions							
Region	BA[a]	x	y	z	SDM-Z	P	Voxels[b]
R Anterior Cingulate	10(32)	0	58	0	−1.994	1.514^{-3}	228
L Superior Temporal	22	−62	−10	2	−2.053	1.203^{-3}	106

Note: BA = Brodmann area; [a] = peak coordinates with overlapping BA areas (in brackets); [b] = 2 mm × 2 mm × 2 mm; SDM-Z = signed differential mapping z-score; L = Left; R = Right; foci represented in MNI space; med. = medial; thresholded at $P < 0.005$; FWHM 20 mm

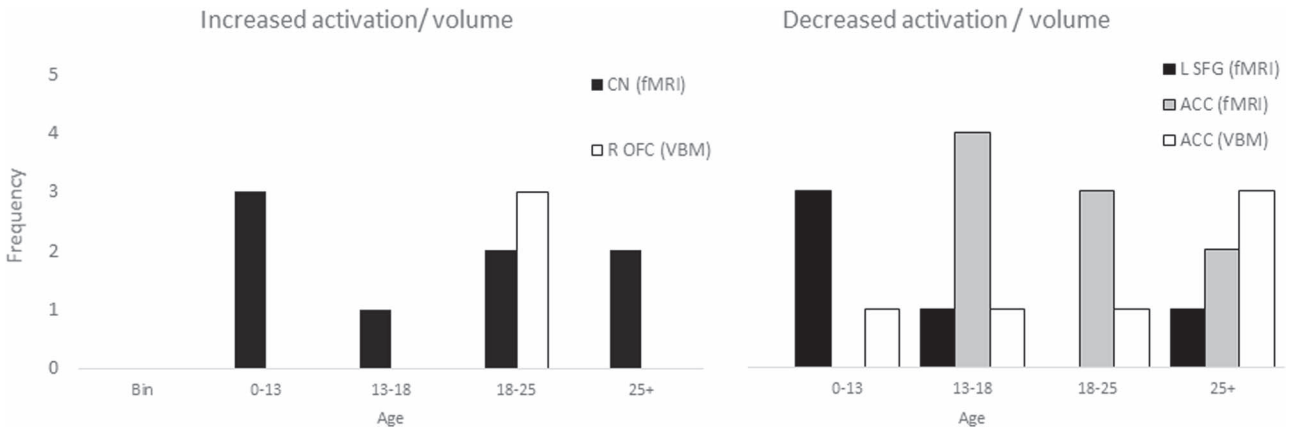

Figure 4. Results from structural MRI studies in low SES individuals compiled from studies using VBM analysis. (*a*) Main analysis of adults compared low with high SES individuals; (*b*) meta-regression of gray matter volume on SES as a function of age. Red represents extended gray matter volume across studies; blue represents reductions gray matter volume across studies for low SES individuals.

Functional brain correlates of SES

Based on previous literature, individuals with low SES exhibit differences in executive control functions (Hsu et al., 2014; He and Yin, 2016) and are more prone to seeking rewards (Furr-Holden et al., 2012; Carlson et al., 2014; Gonzalez et al., 2016). Therefore, we hypothesized that developing individuals with low SES would have hypoactivity within executive network regions and hyperactivity within reward-related regions. The results of the meta-analysis support these hypotheses by demonstrating hypoactivity of the fronto-parietal/cinguloopercular executive networks and hyperactivity of the right caudate nucleus both across age and as a function of age.

The organization of these executive networks across development has been suggested to shift from a local anatomical emphasis in children to a more "distributed" architecture in young adults (Fair et al., 2009). These local and distributed networks (i.e. frontoparietal and cinguloopercular) may account for multiple executive operations or may operate together

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

during a single cognitive process (Dosenbach et al., 2007; Dosenbach et al., 2008; Fair et al., 2011; Gratton et al., 2018). For example, the frontoparietal network may be relevant for rapid adaptive control, while the cinguloopercular network is thought to be more relevant for long-term stable set-maintenance (Fair et al., 2011). With regards to our findings, regions involving these networks were reduced in activity for low SES as a function of age, which may be associated with differences in executive control across development in individuals exposed to impoverished environments (Hsu et al., 2014; He and Yin, 2016).

The meta-analysis results also revealed that individuals exposed to low SES exhibited hyperactivation of the caudate nucleus as a function of age. The caudate nucleus is an area within the anterior striatum associated with stimulus–action–reward associative learning (Delgado et al., 2004; Haruno et al. 2004; Haruno and Kawato, 2006; Balleine et al., 2007). Specifically, when individuals learn to select behaviors to maximize profits, activity of the caudate nucleus correlates with the amount of behavioral differences associated with reward learning (Haruno et al. 2004) and which is associated with reward prediction errors (O'Doherty et al., 2004). Therefore, hyperactivity of the right caudate nucleus may indicate that individuals with low SES are prone to associate reward with actions.

Structural correlates of SES

Structural differences in individuals with low SES were complimentary to the functional brain analyses. Most notably, the anterior cingulate cortex was reduced in gray matter volume in individuals with low SES as a function of age, which has been reported in many empirical studies investigating the neural structures of individuals residing in impoverished conditions (Gianaros et al., 2007; Yang et al., 2016). Possible biological mechanisms have been suggested in a recent review on early life stress (Kelly et al., 2013; Teicher et al., 2016). For example, individuals exposed to early life stress as the result of residing in an impoverished environment may undergo gray matter differences in neural structures such as the anterior cingulate cortex (Cohen et al., 2006), orbirofrontal cortex (Chugani et al., 2001; Edmiston et al., 2011; Holz et al., 2015b), hippocampus (Andersen et al., 2008; Hanson et al., 2011, 2015; Jednoróg et al., 2012; Staff et al., 2012; Teicher et al., 2012; Opel et al., 2014), and white matter tracts such as the longitudinal fasciculus (Choi et al., 2012; Dufford and Kim, 2017). Overexposure to stressful stimuli may alter regions within the reward system adapted by regulation of the amygdala (LeDoux, 1996, 2002; Herman and Mueller, 2006; Maren et al., 2013; see Teicher et al., 2016 for review).

Others have shown that the anterior cingulate cortex is strongly linked with overexposure to stressful stimuli, particularly in those suffering from child abuse posttraumatic stress disorder (Thomaes et al., 2010, 2011, 2012). This in turn may shed light on the dysconnectivity of brain regions within the executive network for individuals exposed to child abuse (Hart et al., 2017; Hart et al., 2018). The anterior cingulate cortex is a thought-provoking region due to its functional diversity. The anterior cingulate cortex is often associated with many higher-order cognitive functions such as working memory (Owen et al., 2005; Yaple and Arsalidou, 2018), set-shifting (Bissonette et al. 2013), negative priming (Yaple and Arsalidou, 2016), and conflict resolution prior to responses when conflicting stimuli features are presented (Carter et al. 1998; Botvinick et al. 1999; van Veen and Carter 2002; Botvinick et al. 2004; Carter and Van Veen 2007; Kim et al. 2012). Overexposure to threatening and conflicting environments may result to desensitization of conflict and consequentially decreasing the plasticity of the anterior cingulate cortex, reflecting a cortical defense mechanism to threat.

Other regions that showed increased gray matter volume in low SES individuals were the orbital frontal cortex, dorsal lateral prefrontal cortex and hippocampus, key regions of the reward circuit (Teicher et al., 2016). These regions are targeted by midbrain dopamine neurons along mesolimbic and mesocortical pathways (Haber and Knutson, 2010). Specifically, the left orbital frontal cortex is often associated with the ability to assign value and pleasure to stimuli, facilitating decision-making (Grabenhorst and Rolls, 2011). Evidence for this claim derives from a series of studies demonstrating a sensitivity of orbital frontal neural firing rate in response to primary rewards (food, water) and secondary rewards (money; Louis and Zhao, 2002; Rolls and Grabenhorst, 2008). Similarly, we found an increase in activation and gray matter volume within the left dorsal prefrontal cortex, a region associated with volitional risky decision-making (Rao et al., 2008; Yaple et al., 2017). The increased gray matter within these regions for low SES individuals may provide support for the notion that individuals exposed to impoverished conditions are susceptible to oversensitivity to reward. The hippocampus is most often associated with memory functioning (Squire, 1992, Burgess et al., 2002); yet with regards to the reward system, the hippocampus is sensitive to approach-avoidance conflict processing when faced with uncertain decisions (O'Neil et al., 2015). This may suggest that developing individuals with low SES are prone to risky decision-making (Furr-Holden et al., 2012; Carlson et al., 2014) when faced with uncertain economic environments.

The left angular gyrus cluster was another area that overlapped across the meta-analyses. The meta-analysis revealed that studies on the individuals developing in low SES environments tend to have less active left angular gyrus yet extended gray matter volume. The angular gyrus projects to the ipsilateral inferior prefrontal cortex via the longitudinal fasciculus (Makris et al., 2004), all regions associated with functional and structural brain differences in SES in the current study. This pattern of results may offer a neurobiological trade-off between the structure and function of the left angular gyrus; however, without empirical testing it is not possible to draw conclusions on the causality of this mechanism. Therefore, further experimentation is necessary to assess the causality of these regions in individuals with low SES.

It is interesting to note that brain regions showing structural differences in individuals with low SES as a function of age overlap with brain regions identified in functional brain analysis. These concurrent changes characterize the multi-dimensionality of neuroplasticity as it enables adaptation to social environment. Overlapping in the structural and functional brain changes also raises the question whether and how changes in brain structure contribute to activity differences in those regions during experimental tasks. For future functional MRI research, researchers may consider controlling for changes in brain structures when interpreting SES related functional changes in the brain. Future studies may also further examine this issue by investigating the correspondence between functional and structural brain changes in the same project.

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

Behavioral models of SES

Our meta-analysis results may concomitantly support the scarcity hypothesis. The scarcity hypothesis states that individuals with low SES tend to focus more on monetary issues while neglecting other non-monetary issues (Mullainathan and Shafir, 2013). For example, financial resources at payday for a low-SES can affect the willingness to delay gratification (Carvalho et al., 2016). Hypoactivation of the executive network and hyperactivation of the reward network may correspond with the tendency for deprived individuals to focus attention on different sets of problems. Animal models also suggest a link between early adversity and significant reductions in executive control (Butts et al., 2011). In rats, acute stress led to cognitive impairments and blockade of glucocorticoid receptors in the prefrontal cortex attenuated stress-induced executive function impairment. Early-life stress also induces morphologic changes in primate brain. Compared with mother-reared monkeys, peer-reared monkeys showed an enlarged vermis, dorsomedial prefrontal cortex, and dorsal anterior cingulate cortex, possibly creating a sensitization to stress and vulnerability for compulsive/addictive behavior (Spinelli et al., 2009).

The competing neurobehavioral decision systems model proposes two systems that influence decision-making: the impulsive decision system which encodes immediate reinforcers and the executive decision system which favors long-term outcomes and inhibit impulses (Bickel et al., 2012). Our findings suggest that low SES may be associated with a less effective executive decision system, making the two systems unbalanced. The functional and structural brain changes in low SES support the idea of two competing decision-making systems.

Another relevant cognitive model that corresponds with the observed findings is the life-history evolutionary theory, which posits that organisms residing in impoverished environments tend to prefer behaviors motivated by immediate rewards since these behaviors are perceived as being highly adaptive for survival (Horn and Rubenstein, 1984; Griskevicius et al., 2011; Liu et al., 2012). The life-history evolutionary framework may explain the observed results. For example, individuals adapting to a low SES environment may be more prone to immediate gratification of rewards (as opposed to long-term rewards), which may in turn reflect adaptive cognitive processes as well as neural plasticity regarding structure and function (Demir-Lira et al., 2016). This explanation resonates with the allostatic load model and adaptive calibration model that state that the brain coordinates a distributed and dynamic set of neural circuits that regulate behavior to help the organism adapt to the demands of the environment (Del Giudice et al., 2011; McEwen and Gianaros, 2011). The allostatic load model posits that the organism respond to challenges in an attempt to restore its optimal state, often at the cost of long-term health (McEwen and Gianaros, 2011). The adaptive calibration model proposes that individual differences in stress reactivity are evolutionarily selected adaptations that enable the organism to match its behaviors to different environmental conditions (Del Giudice et al., 2011). It is premature to claim whether stress related changes in brain responses are adaptive or maladaptive (Hostinar and Gunnar, 2013).

Limitations

One of the main limitations to this study is that there were not enough studies within the youth group to perform an independent meta-analysis for each age group. Therefore, we encourage further investigations to discern the differences between individuals with varied SES, particularly on young individuals. Because of this disadvantage, we performed a meta-regression to illustrate the neural activity in low SES across the lifespan.

Another limitation is that the studies compiled for the meta-analyses associated different SES components (e.g. income, education, and occupation) with brain activity, of which may affect development processing in different ways (Duncan and Magnuson, 2012). While the Hollingshead's four-factor index of social status scale and the MacArthur scale of subjective social status may share similar self-report measures, they tend to differ on the items used to assess SES. The income-to-needs ratio is a more objective method to assess SES; however, the income to needs ratio is calculated on the poverty level of the US consensus and therefore cannot be attributed to other developed and underdeveloped countries. Despite these differences, all contrasts were based on one or more of the three items and therefore, there is some degree of consistency among the selected studies. To compensate for the heterogeneity among studies we performed heterogeneity Q statistic maps for each meta-analysis. Nevertheless, additional investigation is necessary to understand how income, education and occupation level each contribute to brain functioning and how they each influence neural tissue on a globe scale, i.e. how these findings may compare with individuals in underdeveloped countries.

More on this note, it is not clear from the meta-analysis technique whether and how executive and reward-related networks influence one another. The dual process theory (Kahneman, 2003; Kahneman and Frederick, 2007; Kahneman and Egan, 2011) states that decisions are governed by two completing systems: a slow executive-driven system and a fast, automatic system. Assuming that the automatic system may account for a reward-driven system, one may interpret that executive and reward related differences in neural activity/structure supports the dual process theory; however, no causal relationship between these neural networks can be assessed within the current report due to the nature of the meta-analysis technique. Hence, further work is necessary to explore this possibility.

Furthermore, individuals developing in urban environments have been shown to demonstrate *greater* activation in the perigenual anterior cingulate cortex while performing a paradigm that induces stress (Lederbogen et al., 2011; also see Gianaros and Wager, 2015). Together with the current results, the anterior cingulate cortex seems to alter in activation/gray matter volume depending on both SES and stress induced by urbanicity. However, it is important to emphasize that 1) the previous study on urbanicity did not control for SES when comparing urban, suburban and rural inhabitants; and 2) studies within the meta-analysis sampled data from both rural and urban environments. Therefore, greater anterior cingulate cortical activity in urban dwellers and results from the current meta-analysis may not be mutually exclusive. Individuals living in urban environments have an increased excitability of the anterior cingulate cortex only during stressful situations; which would correspond with the notion that the anterior cingulate cortex is down-regulated by the amygdala during the processing of threatening social cues (McEwen and Gianaros, 2010). To investigate this inconsistency, it is necessary to explore the neural sensitivity of the anterior cingulate cortex in low SES individuals residing in rural and urban areas under stressful and non-stressful situations.

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

Since our findings are based on a large population of individuals, another caveat is that our findings cannot account for individuals whom were exposed to low SES environments during childhood yet manage to maintain adequate physical and mental health during adulthood (Miller et al., 2011; D'Angiulli et al., 2012; Chen and Miller, 2013; Neville et al., 2013). It is important to clarify that our aim is not to discredit individuals previously exposed to low SES environments since developmental interventions have been shown to facilitate executive functions later in life which may allow the individual to live an adequate lifestyle (Jaeggi et al., 2011; Morrison and Chein, 2011; Hussey and Novick, 2012; Hsu et al., 2014).

Finally, our study cannot disentangle whether the functional/structural difference in low SES individuals is the cause or result of low SES. Exposure to adversity may produce changes in the brain as a result of stress from the social environment and limited access to social resources. However, it is also possible that individuals with certain brain activity patterns and thinking styles are more likely to make judgments and decisions that lead them to end up in low SES situations. Although our meta-analysis does not permit us to draw any definitive conclusions on the nature vs. nurture question regarding the relationship between the brain and SES, the brain changes as a function of age in low SES may provide some insights on this topic. We found that brain areas that exhibit functional and structural changes in low SES across age overlap with brain regions that show changes as a function of age in low SES. These findings indicate that chronic exposure to adversity in adulthood may continue to produce changes in the brain. The SES-related brain changes we identified are at least partially due to the result of low SES. Future studies may further examine the gene–brain–environment interactions in the context of SES.

Future directions

The main purpose of this study is to shed light on the brain regions most likely to be affected by SES as a function of age. Further work is necessary to discover how younger aged individuals in poverty may be affected in different contexts. For example, since only two studies included in the meta-analysis used reward-related tasks, it is worthwhile exploring how reward-related biases (e.g. delay discounting bias, framing bias) and the corresponding reward-related brain regions are affected by SES. We further argue that these differences may not be directly related to low SES as such but by additional mediators including early life stress, fear learning, neglect, urbanicity, environmental toxins such as lead, nutritional deficiencies, and exposure to other hostile environmental factors (DePrince et al., 2009; Haushofer and Fehr, 2014; McLaughlin et al., 2014; Lambert et al., 2015; Farah, 2017; Krämer et al., 2017). Therefore, we strongly encourage further experimentation to tend to these pending questions. Taken together, we hope our findings and interpretations inform current models on the importance of SES, poverty and wealth when designing future research projects. The impact of SES is likely to depend on the level of resilience or vulnerability of each person and should be considered when interpreting brain related data as detrimental (D'Angiulli et al., 2012; Ellwood-Lowe et al., 2016). While susceptible individuals poorly adapt to low SES, resilient individuals can shield themselves from the negative impacts of low SES and develop adaptive physiological and psychological responses. One interesting topic for future research is to investigate the neural mechanisms underlying such stark difference in individual resilience/vulnerability. Our findings shed light on how SES impacts our human brain and may also facilitate intervention or training programs designed to target brain regions and functions associated with SES in the hope of enhancing resilience to low SES.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

Funding

Singapore Ministry of Education (MOE) Tier 2 grant (MOE2016-T2-1-015), SSRC (MOE2017-SSRTG-026), Ministry of Health (MOH) Singapore National Medical Research Council (NMRC) (OFYIRG17may052 to [R.Y.]).

References

Adler NE, Epel ES, Castellazzo G, Ickovics JR. 2000. Relationship of subjective and objective social status with psychological and physiological functioning: preliminary data in healthy, white women. *Health Psychol*. 19(6):586.

Andersen SL, Tomada A, Vincow ES, Valente E, Polcari A, Teicher MH. 2008. Preliminary evidence for sensitive periods in the effect of childhood sexual abuse on regional brain development. *J Neuropsychiatry Clin Neurosci*. 20(3):292–301.

Balleine BW, Delgado MR, Hikosaka O. 2007. The role of the dorsal striatum in reward and decision-making. *J Neurosci*. 27(31):8161–8165.

Bickel WK, Jarmolowicz DP, Mueller ET, Gatchalian KM, McClure SM. 2012. Are executive function and impulsivity antipodes? A conceptual reconstruction with special reference to addiction. *Psychopharmacology*. 221(3):361–387.

Bissonette GB, Powell EM, Roesch MR. 2013. Neural structures underlying set-shifting: roles of medial prefrontal cortex and anterior cingulate cortex. *Behav Brain Res*. 250:91–101.

Black JM, Tanaka H, Stanley L, Nagamine M, Zakerani N, Thurston A. 2012. Maternal history of reading difficulty is associated with reduced language-related gray matter in beginning readers. *Neuroimage*. 59(3):3021–3032.

Blakemore SJ. 2012. Imaging brain development: the adolescent brain. *Neuroimage*. 61(2):397–406.

Botvinick M, Nystrom LE, Fissell K, Carter CS, Cohen JD. 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*. 402(6758):179.

Botvinick MM, Cohen JD, Carter CS. 2004. Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn Sci*. 8(12):539–546.

Bradley RH, Corwyn RF. 2002. Socioeconomic status and child development. *Ann Rev Psychol*. 53(1):371–399.

Brents LK, Young J, Knight B, Coker JL, Ray-Griffith SL, Stowe Z, Kilts C. 2017. Perceived social support and socioeconomic status predict maternal delay discounting behavior and neural function in healthy postpartum women. *Drug Alcohol Depend*. 171:e26.

Brooks-Gunn J, Duncan GJ. 1997. The effects of poverty on children. *Future Child*. 55–71.

Brown-Iannuzzi JL, Lundberg KB, McKee S. 2017. The politics of socioeconomic status: how socioeconomic status may influence political attitudes and engagement. *Curr Opin Psychol*. 18:11–14.

Burgess N, Maguire EA, O'Keefe J. 2002. The human hippocampus and spatial and episodic memory. *Neuron*. 35(4):625–641.

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

Butler O, Yang XF, Laube C, Kühn S, Immordino-Yang MH. 2018. Community violence exposure correlates with smaller gray matter volume and lower IQ in urban adolescents. *Hum Brain Mapp*. 39(5):2088–2097.

Butts KA, Weinberg J, Young AH, Phillips AG. 2011. Glucocorticoid receptors in the prefrontal cortex regulate stress-evoked dopamine efflux and aspects of executive function. *Proc Natl Acad Sci U S A*. 108(45):18459–18464.

Carlson DL, McNulty TL, Bellair PE, Watts S. 2014. Neighborhoods and racial/ethnic disparities in adolescent sexual risk behavior. *J Youth Adolesc*. 43(9):1536–1549.

Carter CS, Braver TS, Barch DM, Botvinick MM, Noll D, Cohen JD. 1998. Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*. 280(5364):747–749.

Carter CS, Van V. 2007. Anterior cingulate cortex and conflict detection: an update of theory and data. *Cogn Affect Behav Neurosci*. 7(4):367–379.

Carvalho LS, Meier S, Wang SW. 2016. Poverty and economic decision-making: evidence from changes in financial resources at payday. *Am Econ Rev*. 106(2):260–284.

Casey BJ, Tottenham N, Liston C, Durston S. 2005. Imaging the developing brain: what have we learned about cognitive development? *Trends Cogn Sci*. 9(3):104–110.

Chan MY, Na J, Agres PF, Savalia NK, Park D, Wig GS. 2018. Socioeconomic status moderates age-related differences in the brain's functional network organization and anatomy across the adult lifespan. *Proc Natl Acad Sci U S A*. 115(22): E5144–E5153.

Chen E, Miller GE. 2013. Socioeconomic status and health: mediating and moderating factors. *Annu Rev Psychol*. 9:723–749.

Choi J, Jeong B, Polcari A, Rohan ML, Teicher MH. 2012. Reduced fractional anisotropy in the visual limbic pathway of young adults witnessing domestic violence in childhood. *Neuroimage*. 59(2):1071–1079.

Chugani HT, Behen ME, Muzik O, Juhász C, Nagy F, Chugani DC. 2001. Local brain functional activity following early deprivation: a study of postinstitutionalized Romanian orphans. *Neuroimage*. 14(6):1290–1301.

Cohen RA, Grieve S, Hoth KF, Paul RH, Sweet L, Tate D. 2006. Early life stress and morphometry of the adult anterior cingulate cortex and caudate nuclei. *Biol Psychiatry*. 59(10):975–982.

Conant LL, Liebenthal E, Desai A, Binder JR. 2017. The relationship between maternal education and the neural substrates of phoneme perception in children: interactions between socioeconomic status and proficiency level. *Brain Lang*. 171:14–22.

Côté S, Gyurak A, Levenson RW. 2010. The ability to regulate emotion is associated with greater well-being, income, and socioeconomic status. *Emotion*. 10(6):923.

D'angiulli A, Lipina SJ, Olesinska A. 2012. Explicit and implicit issues in the developmental cognitive neuroscience of social inequality. *Front Hum Neurosci*. 6:254.

DePrince AP, Weinzierl KM, Combs MD. 2009. Executive function performance and trauma exposure in a community sample of children. *Child Abuse Negl*. 33(6):353–361.

Delgado MR, Stenger VA, Fiez JA. 2004. Motivation-dependent responses in the human caudate nucleus. *Cereb Cortex*. 14(9):1022–1030.

Del Giudice M, Ellis BJ, Shirtcliff EA. 2011. The adaptive calibration model of stress responsivity. *Neurosci Biobehav Rev*. 35(7):1562–1592.

Demir-Lira ÖE, Prado J, Booth JR. 2016. Neural correlates of math gains vary depending on parental socioeconomic status (SES). *Front Psychol*. 7:892.

Diekhof EK, Kaps L, Falkai P, Gruber O. 2012. The role of the human ventral striatum and the medial orbital frontal cortex in the representation of reward magnitude–an activation likelihood estimation meta-analysis of neuroimaging studies of passive reward expectancy and outcome processing. *Neuropsychologia*. 50(7):1252–1266.

Dosenbach NU, Fair DA, Cohen AL, Schlaggar BL, Petersen SE. 2008. A dual-networks architecture of top-down control. *Trends Cogn Sci*. 12(3):99–105.

Dosenbach NU, Fair DA, Miezin FM, Cohen AL, Wenger KK, Dosenbach RA. 2007. Distinct brain networks for adaptive and stable task control in humans. *Proc Natl Acad Sci U S A*. 104(26):11073–11078.

Drakesmith M, Dutt A, Fonville L, Zammit S, Reichenberg A, Evans CJ, David AS. 2016. Volumetric, relaxometric and diffusometric correlates of psychotic experiences in a non-clinical sample of young adults. *Neuroimage Clin*. 12:550–558.

Dufford AJ, Kim P. 2017. Family income, cumulative risk exposure, and white matter structure in middle childhood. *Front Hum Neurosci*. 11:547.

Duncan GJ, Brooks-Gunn J, Klebanov PK. 1994. Economic deprivation and early childhood development. *Child Dev*. 65(2):296–318.

Duncan GJ, Magnuson K. 2012. Socioeconomic status and cognitive functioning: moving from correlation to causation. *Wiley Interdiscip Rev Cogn Sci*. 3(3):377–386.

Duvarci S, Pare D. 2014. Amygdala microcircuits controlling learned fear. *Neuron*. 82(5):966–980.

Edmiston EE, Wang F, Mazure CM, Guiney J, Sinha R, Mayes LC, Blumberg HP. 2011. Corticostriatal-limbic gray matter morphology in adolescents with self-reported exposure to childhood maltreatment. *Arch Pediatr Adolesc Med*. 165(12):1069–1077.

Ellwood-Lowe ME, Humphreys KL, Ordaz SJ, Camacho MC, Sacchet MD, Gotlib IH. 2018. Time-varying effects of income on hippocampal volume trajectories in adolescent girls. *Dev Cogn Neurosci*. 30:41–50.

Ellwood-Lowe ME, Sacchet MD, Gotlib IH. 2016. The application of neuroimaging to social inequity and language disparity: a cautionary examination. *Dev Cogn Neurosci*. 22:1–8.

Fair DA, Cohen AL, Power JD, Dosenbach NU, Church JA, Miezin FM. 2009. Functional brain networks develop from a "local to distributed" organization. *PLoS Comput Biol*. 5(5): e1000381.

Fair DA, Dosenbach NU, Petersen SE, Schlaggar BL. 2011. Resting state studies on the development of control systems. *Cognitive Neuroscience of Attention*. 2:291–311.

Farah MJ. 2017. The neuroscience of socioeconomic status: correlates, causes, and consequences. *Neuron*. 96(1):56–71.

Finn AS, Minas JE, Leonard JA, Mackey AP, Salvatore J, Goetz C. 2017. Functional brain organization of working memory in adolescents varies in relation to family income and academic achievement. *Dev Sci*. 20(5).

Furr-Holden CDM, Milam AJ, Reynolds EK, MacPherson L, Lejuez CW. 2012. Disordered neighborhood environments and risk-taking propensity in late childhood through adolescence. *J Adolesc Health*. 50(1):100–102.

Gerdtham UG, Johannesson M. 2001. The relationship between happiness, health, and socio-economic factors: results based on Swedish microdata. *J Socio-Econ*. 30(6):553–557.

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

Gianaros PJ, Horenstein JA, Cohen S, Matthews KA, Brown SM, Flory JD. 2007. Perigenual anterior cingulate morphology covaries with perceived social standing. *Soc Cogn Affect Neurosci*. 2(3):161–173.

Gianaros PJ, Horenstein JA, Hariri AR, Sheu LK, Manuck SB, Matthews KA, Cohen S. 2008. Potential neural embedding of parental social standing. *Soc Cogn Affect Neurosci*. 3(2):91–96.

Gianaros PJ, Manuck SB, Sheu LK, Kuan DC, Votruba-Drzal E, Craig AE, Hariri AR. 2011. Parental education predicts corticostriatal functionality in adulthood. *Cereb Cortex*. 21(4):896–910.

Gianaros PJ, Wager TD. 2015. Brain-body pathways linking psychological stress and physical health. *Curr Dir Psychol Sci*. 24(4):313–321.

Gonzalez MZ, Allen JP, Coan JA. 2016. Lower neighborhood quality in adolescence predicts higher mesolimbic sensitivity to reward anticipation in adulthood. *Dev Cogn Neurosc*. 22:48–57.

Gonzalez MZ, Beckes L, Chango J, Allen JP, Coan JA. 2015. Adolescent neighborhood quality predicts adult dACC response to social exclusion. *Soc Cogn Affect Neurosci*. 10(7):921–928.

Grabenhorst F, Rolls ET. 2011. Value, pleasure and choice in the ventral prefrontal cortex. *Trends Cogn Sci*. 15(2):56–67.

Gratton C, Sun H, Petersen SE. 2018. Control networks and hubs. *Psychophysiology*. 55(3).

Griskevicius V, Tybur JM, Delton AW, Robertson TE. 2011. The influence of mortality and socioeconomic status on risk and delayed rewards: a life history theory approach. *J Pers Soc Psychol*. 100(6):1015.

Haber SN, Knutson B. 2010. The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology*. 35(1):4.

Hackman DA, Gallop R, Evans GW, Farah MJ. 2015. Socioeconomic status and executive function: developmental trajectories and mediation. *Dev Science*. 18(5):686–702.

Hanson JL, Chandra A, Wolfe BL, Pollak SD. 2011. Association between income and the hippocampus. *PloS one*. 6(5): e18712.

Hanson JL, Nacewicz BM, Sutterer MJ, Cayo AA, Schaefer SM, Rudolph KD. 2015. Behavioral problems after early life stress: contributions of the hippocampus and amygdala. *Biol Psychiatry*. 77(4):314–323.

Hart H, Lim L, Mehta MA, Chatzieffraimidou A, Curtis C, Xu X. 2017. Reduced functional connectivity of fronto-parietal sustained attention networks in severe childhood abuse. *PLoS one*. 12(11):e0188744.

Hart HC, Lim L, Mehta MA, Curtis C, Xu X, Breen G *et al*. 2018. Altered functional connectivity of fronto-cingulo-striatal circuits during error monitoring in adolescents with a history of childhood abuse. *Front Hum Neurosci*. 12:7.

Haruno M, Kawato M. 2006. Different neural correlates of reward expectation and reward expectation error in the putamen and caudate nucleus during stimulus-action-reward association learning. *J Neurophysiol*. 95(2):948–959.

Haruno M, Kuroda T, Doya K, Toyama K, Kimura M, Samejima K. 2004. A neural correlate of reward-based behavioral learning in caudate nucleus: a functional magnetic resonance imaging study of a stochastic decision task. *J Neurosci*. 24(7):1660–1665.

Haushofer J, Fehr E. 2014. On the psychology of poverty. *Science*. 344(6186):862–867.

He ZH, Yin WG. 2016. Family environments and children's executive function: the mediating role of children's affective state and stress. *J Genet Psychol*. 177(5):143–155.

Herman JP, Mueller NK. 2006. Role of the ventral subiculum in stress integration. *Behav Brain Res*. 174(2):215–224.

Hoff E. 2003. The specificity of environmental influence: socioeconomic status affects early vocabulary development via maternal speech. *Child Dev*. 74(5):1368–1378.

Hollingshead AA. 1975. Four-factor index of social status (unpublished data). New Haven, CT: Yale University

Holz NE, Laucht M, Meyer-Lindenberg A. 2015a. Recent advances in understanding the neurobiology of childhood socioeconomic disadvantage. *Curr Opin Psychiatry*. 28(5):365–370.

Holz NE, Boecker R, Hohm E, Zohsel K, Buchmann AF, Blomeyer D. 2015b. The long-term impact of early life poverty on orbital frontal cortex volume in adulthood: results from a prospective study over 25 years. *Neuropsychopharmacology*. 40(4):996.

Horn HS, Rubenstein DI. 1984. Behavioral adaptations and life history. In: Krebs JR, Davies NB, editors. *Behavioural ecology: an evolutionary approach*. 2nd ed. Oxford, England: Blackwell, pp. 279–300

Hostinar CE, Gunnar MR. 2013. The developmental effects of early life stress: an overview of current theoretical frameworks. *Curr Dir Psychol Sci*. 22(5):400–406.

Hsu NS, Novick JM, Jaeggi SM. 2014. The development and malleability of executive control abilities. *Front Behav Neurosci*. 8:221.

Hussey EK, Novick JM. 2012. The benefits of executive control training and the implications for language processing. *Front Psychol*. 3:158.

Jaeggi SM, Buschkuehl M, Jonides J, Shah P. 2011. Short-and long-term benefits of cognitive training. *Proc Natl Acad Sci U.S.A*. 108(25):10081–10086.

Javanbakht A, King AP, Evans GW, Swain JE, Angstadt M, Phan KL, Liberzon I. 2015. Childhood poverty predicts adult amygdala and frontal activity and connectivity in response to emotional faces. *Front Behav Neurosci*. 9:154.

Jednoróg K, Altarelli I, Monzalvo K, Fluss J, Dubois J, Billard C. 2012. The influence of socioeconomic status on children's brain structure. *PloS one*. 7(8):e42486.

Kahneman D. 2003. A perspective on judgment and choice: mapping bounded rationality. *Am Psychol*. 58(9):697.

Kahneman D, Deaton A. 2010. High income improves evaluation of life but not emotional well-being. *Proc Natl Acad Sci U.S.A*. 107(38):16489–16493.

Kahneman D, Egan P. 2011. *Thinking, fast and slow*. Vol 1. New York: Farrar, Straus and Giroux

Kahneman D, Frederick S. 2007. Frames and brains: elicitation and control of response tendencies. *Trends Cogn Sci*. 11(2):45–46.

Kelly PA, Viding E, Wallace GL, Schaer M, De Brito SA, Robustelli B, McCrory EJ. 2013. Cortical thickness, surface area, and gyrification abnormalities in children exposed to maltreatment: neural markers of vulnerability? *Biol Psychiatry*. 74(11):845–852.

Kim C, Chung C, Kim J. 2012. Conflict adjustment through domain-specific multiple cognitive control mechanisms. *Brain Res*. 1444:55–64.

Kim P, Capistrano C, Congleton C. 2016. Socioeconomic disadvantages and neural sensitivity to infant cry: role of maternal distress. *Soc Cogn Affect Neurosci*. 11(10):1597–1607.

Kim P, Capistrano CG, Erhart A, Gray-Schiff R, Xu N. 2017. Socioeconomic disadvantage, neural responses to infant emotions,

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

and emotional availability among first-time new mothers. *Behav Brain Res*. 325:188–196.

Kim P, Evans GW, Angstadt M, Ho SS, Sripada CS, Swain JE. 2013. Effects of childhood poverty and chronic stress on emotion regulatory brain function in adulthood. *Proc Natl Acad Sci U S A*. 110(46):18442–18447.

Kong F, Chen Z, Xue S, Wang X, Liu J. 2015a. Mother's but not father's education predicts general fluid intelligence in emerging adulthood: Behavioral and neuroanatomical evidence. *Hum Brain Mapp*. 36(11):4582–4591.

Kong F, Hu S, Xue S, Song Y, Liu J. 2015b. Extraversion mediates the relationship between structural variations in the dorsolateral prefrontal cortex and social well-being. *Neuroimage*. 105:269–275.

Krämer B, Diekhof EK, Gruber O. 2017. Effects of city living on the mesolimbic reward system—an fmri study. *Hum Brain Mapp*. 38(7):3444–3453.

Lambert KG, Nelson RJ, Jovanovic T, Cerdá M. 2015. Brains in the city: neurobiological effects of urbanization. *Neurosci Biobehav Rev*. 58:107–122.

Lederbogen F, Kirsch P, Haddad L, Streit F, Tost H, Schuch P. 2011. City living and urban upbringing affect neural social stress processing in humans. *Nature*. 474(7352):498.

LeDoux J. 1996. Emotional networks and motor control: a fearful view. In Progress in brain research. *Prog Brain Res*. 107:437–446.

LeDoux J. 2002. *Synaptic self: How our brains become who we are*. London: Viking, Penguin.

Liberzon I, Ma ST, Okada G, Shaun Ho S, Swain JE, Evans GW. 2015. Childhood poverty and recruitment of adult emotion regulatory neurocircuitry. *Soc Cogn Affect Neurosci*. 10(11):1596–1606.

Lipina SJ, Posner MI. 2012. The impact of poverty on the development of brain networks. *Front Hum Neurosci*. 6:238.

Liu L, Feng T, Suo T, Lee K, Li H. 2012. Adapting to the destitute situations: poverty cues lead to short-term choice. *PloS one*. 7(4):e33950.

Louis VV, Zhao S. 2002. Effects of family structure, family SES, and adulthood experiences on life satisfaction. *J Fam Issues*. 23(8):986–1005.

Luby J, Belden A, Botteron K, Marrus N, Harms MP, Babb C. 2013. The effects of poverty on childhood brain development: the mediating effect of caregiving and stressful life events. *JAMA Pediatr*. 167(12):1135–1142.

Lupien SJ, King S, Meaney MJ, McEwen BS. 2001. Can poverty get under your skin? Basal cortisol levels and cognitive function in children from low and high socioeconomic status. *Dev Psychopathol*. 13(3):653–676.

Ly M, Haynes MR, Barter JW, Weinberger DR, Zink CF. 2011. Subjective socioeconomic status predicts human ventral striatal responses to social status information. *Curr Biol*. 21(9):794–797.

Mackey AP, Finn AS, Leonard JA, Jacoby-Senghor DS, West MR, Gabrieli CF, Gabrieli JD. 2015. Neuroanatomical correlates of the income-achievement gap. *Psychol Sci*. 26(6):925–933.

Makris N, Kennedy DN, McInerney S, Sorensen AG, Wang R, Caviness VS Jr, Pandya DN. 2004. Segmentation of subcomponents within the superior longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. *Cereb Cortex*. 15(6):854–869.

Mani A, Mullainathan S, Shafir E, Zhao J. 2013. Poverty impedes cognitive function. *Science*. 341(6149):976–980.

Maren S, Phan KL, Liberzon I. 2013. The contextual brain: implications for fear conditioning, extinction and psychopathology. *Nat Rev Neurosci*. 14(6):417.

Mattan BD, Kubota JT, Dang TP, Cloutier J. 2017. External motivation to avoid prejudice alters neural responses to targets varying in race and status. *Soc Cogn Affect Neurosci*. 13(1):22–31.

Matthews K, Robbins TW. 2003. Early experience as a determinant of adult behavioural responses to reward: the effects of repeated maternal separation in the rat. *Neurosci Biobehav Rev*. 27(1–2):45–55.

McEwen BS. 2000. Effects of adverse experiences for brain structure and function. *Biol Psychiatry*. 48(8):721–731.

McEwen BS, Gianaros PJ. 2010. Central role of the brain in stress and adaptation: links to socioeconomic status, health, and disease. *Ann NY Acad Sci*. 1186(1):190–222.

McEwen BS, Gianaros PJ. 2011. Stress-and allostasis-induced brain plasticity. *Annu Rev Med*. 62:431–445.

McLaughlin KA, Sheridan MA, Lambert HK. 2014. Childhood adversity and neural development: deprivation and threat as distinct dimensions of early experience. *Neurosci Biobehav Rev*. 47:578–591.

McLoyd VC. 1998. Socioeconomic disadvantage and child development. *Am Psychol*. 53(2):185.

Miller GE, Chen E, Parker KJ. 2011. Psychological stress in childhood and susceptibility to the chronic diseases of aging: moving toward a model of behavioral and biological mechanisms. *Psychol Bull*. 137(6):959.

Morrison AB, Chein JM. 2011. Does working memory training work? The promise and challenges of enhancing cognition by training working memory. *Psychon Bull Rev*. 18(1):46–60.

Mullainathan S, Shafir E. 2013. *Scarcity: why having too little means so much*. New York: Macmillan.

Muscatell KA, Dedovic K, Slavich GM, Jarcho MR, Breen EC, Bower JE. 2016. Neural mechanisms linking social status and inflammatory responses to social stress. *Soc Cogn Affect Neurosci*. 11(6):915–922.

Muscatell KA, Morelli SA, Falk EB, Way BM, Pfeifer JH, Galinsky AD. 2012. Social status modulates neural activity in the mentalizing network. *Neuroimage*. 60(3):1771–1777.

Neville HJ, Stevens C, Pakulak E, Bell TA, Fanning J, Klein S, Isbell E. 2013. Family-based training program improves brain function, cognition, and behavior in lower socioeconomic status preschoolers. *Proc Natl Acad Sci U S A*. 110(29):12138–12143.

Noble KG, Houston SM, Brito NH, Bartsch H, Kan E, Kuperman JM. 2015. Family income, parental education and brain structure in children and adolescents. *Nat Neurosci*. 18(5):773.

Noble KG, Houston SM, Kan E, Sowell ER. 2012. Neural correlates of socioeconomic status in the developing human brain. *Dev Sci*. 15(4):516–527.

Noble KG, McCandliss BD, Farah MJ. 2007. Socioeconomic gradients predict individual differences in neurocognitive abilities. *Dev Sci*. 10(4):464–480.

Noble KG, Wolmetz ME, Ochs LG, Farah MJ, McCandliss BD. 2006. Brain–behavior relationships in reading acquisition are modulated by socioeconomic factors. *Dev Sci*. 9(6):642–654.

Norman G, Breznitz Z. 1992. Differences in the ability to concentrate in first-grade Israeli pupils of low and high socioeconomic status. *J Genet Psychol*. 153(1):5–17.

Novick JM, Hussey E, Teubner-Rhodes S, Harbison JI, Bunting MF. 2014. Clearing the garden-path: improving sentence processing through cognitive control training. *Lang Cogn Neurosci*. 29(2):186–217.

Novick JM, Trueswell JC, Thompson-Schill SL. 2005. Cognitive control and parsing: Reexamining the role of Broca's

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020

area in sentence comprehension. *Cogn Affect Behav Neurosci*. 5(3):263–281.
O'Doherty J, Dayan P, Schultz J, Deichmann R, Friston K, Dolan RJ. 2004. Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science*. 304(5669):452–454.
O'Neil EB, Newsome RN, Li IH, Thavabalasingam S, Ito R, Lee AC. 2015. Examining the role of the human hippocampus in approach–avoidance decision making using a novel conflict paradigm and multivariate functional magnetic resonance imaging. *J Neurosci*. 35(45):15039–15049.
Opel N, Redlich R, Zwanzger P, Grotegerd D, Arolt V, Heindel W. 2014. Hippocampal atrophy in major depression: a function of childhood maltreatment rather than diagnosis? *Neuropsychopharmacology*. 39(12):2723.
Owen AM, McMillan KM, Laird AR, Bullmore E. 2005. N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. *Hum Brain Mapp*. 25(1):46–59.
Phillips RG, LeDoux JE. 1992. Differential contribution of amygdala and hippocampus to cued and contextual fear conditioning. *Behav Neurosci*. 106(2):274.
Radley JJ, Morrison JH. 2005. Repeated stress and structural plasticity in the brain. *Ageing Res Rev*. 4(2):271–287.
Radua J, Mataix-Cols D. 2009. Voxel-wise meta-analysis of grey matter changes in obsessive–compulsive disorder. *Br J Psychiatry*. 195(5):393–402.
Radua J, Mataix-Cols D, Phillips ML, El-Hage W, Kronhaus DM, Cardoner N, Surguladze S. 2012. A new meta-analytic method for neuroimaging studies that combines reported peak coordinates and statistical parametric maps. *Eur Psychiatry*. 27(8):605–611.
Raizada RD, Kishiyama MM. 2010. Effects of socioeconomic status on brain development, and how cognitive neuroscience may contribute to leveling the playing field. *Front Human Neurosci*. 4:3.
Raizada RD, Richards TL, Meltzoff A, Kuhl PK. 2008. Socioeconomic status predicts hemispheric specialisation of the left inferior frontal gyrus in young children. *Neuroimage*. 40(3):1392–1401.
Rao H, Korczykowski M, Pluta J, Hoang A, Detre JA. 2008. Neural correlates of voluntary and involuntary risk taking in the human brain: an fMRI study of the balloon analog risk task (BART). *Neuroimage*. 42(2):902–910.
Rolls ET, Grabenhorst F. 2008. The orbitofrontal cortex and beyond: from affect to decision-making. *Prog Neurobiol*. 86(3):216–244.
Shah AK, Mullainathan S, Shafir E. 2012. Some consequences of having too little. *Science*. 338(6107):682–685.
Sheridan MA, Sarsour K, Jutte D, D'Esposito M, Boyce WT. 2012. The impact of social disparity on prefrontal function in childhood. *PloS one*. 7(4):e35744.
Silverman ME, Muennig P, Liu X, Rosen Z, Goldstein MA. 2009. The impact of socioeconomic status on the neural substrates associated with pleasure. *Open Neuroimag J*. 3:58.
Spears D. 2011. Economic decision-making in poverty depletes behavioral control. *BE J Econ Anal Poli*. 11(1).
Spinelli S, Chefer S, Suomi SJ, Higley JD, Barr CS, Stein E. 2009. Early-life stress induces long-term morphologic changes in primate brain. *Arch Gen Psychiatry*. 66(6):658–665.
Squire LR. 1992. Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychol Rev*. 99(2):195.
Staff RT, Murray AD, Ahearn TS, Mustafa N, Fox HC, Whalley LJ. 2012. Childhood socioeconomic status and adult brain size: childhood socioeconomic status influences adult hippocampal size. *Ann Neurol*. 71(5):653–660.
Takeuchi H, Taki Y, Hashizume H, Asano K, Asano M, Sassa Y. 2015. The impact of parent–child interaction on brain structures: cross-sectional and longitudinal analyses. *J Neurosci*. 35(5):2233–2245.
Teicher MH, Anderson CM, Polcari A. 2012. Childhood maltreatment is associated with reduced volume in the hippocampal subfields CA3, dentate gyrus, and subiculum. *Proc Natl Acad Sci U S A*. 109(9):E563–E572.
Teicher MH, Samson JA, Anderson CM, Ohashi K. 2016. The effects of childhood maltreatment on brain structure, function and connectivity. *Nat Rev Neurosci*. 17(10):652.
Thomaes K, Dorrepaal E, Draijer N, de Ruiter MB, van Balkom AJ, Smit JH, Veltman DJ. 2010. Reduced anterior cingulate and orbitofrontal volumes in child abuse-related complex PTSD. *J Clin Psychiatry*. 71(12):1636.
Thomaes K, Dorrepaal E, Draijer N, de Ruiter MB, Elzinga BM, Sjoerds Z. 2011. Increased anterior cingulate cortex and hippocampus activation in complex PTSD during encoding of negative words. *Soc Cogn Affect Neurosci*. 8(2):190–200.
Thomaes K, Dorrepaal E, Draijer ND, De Ruiter MB, Elzinga B. 2012. Treatment effects on insular and anterior cingulate cortex activation during classic and emotional Stroop interference in child abuse-related complex post-traumatic stress disorder. *Psychol Med*. 42(11):2337–2349.
van Veen VV, Carter CS. 2002. The timing of action-monitoring processes in the anterior cingulate cortex. *J Cogn Neurosci*. 14(4):593–602.
Varnum. 2016. The emerging (social) neuroscience of SES. *Soc Personal Psychol Compass*. 10(8):423–430.
Wang Y, Zhang L, Kong X, Hong Y, Cheon B, Liu J. 2016. Pathway to neural resilience: self-esteem buffers against deleterious effects of poverty on the hippocampus. *Hum Brain Mapp*. 37(11):3757–3766.
Wood M. 1998. Socio-economic status, delay of gratification, and impulse buying. *J Econ Psychol*. 19(3):295–320.
Yang J, Liu H, Wei D, Liu W, Meng J, Wang K. 2016. Regional gray matter volume mediates the relationship between family socioeconomic status and depression-related trait in a young healthy sample. *Cogn Affect Behav Neurosci*. 16(1):51–62.
Yang J, Wei D, Wang K, Yi Z, Qiu J. 2018. Regional gray matter volume mediates the relationship between maternal emotional warmth and gratitude. *Neuropsychologia*. 109:165–172.
Yaple Z, Arsalidou M. 2016. Negative priming: a meta-analysis of fMRI studies. *Exp Brain Res*. 235(11):3367–3374.
Yaple Z, Arsalidou M. 2018. N-back working memory task: meta-analysis of normative fMRI studies with children. *Child Dev*. https://doi.org/10.1111/cdev.13080.
Yaple Z, Martinez-Saito M, Feurra M, Shestakova A, Awasthi B, Klucharev V. 2017. Transcranial alternating current stimulation modulates risky decision making in a frequency-controlled experiment. *eNeuro*. 4(6):ENEURO.0136-17.2017.
Zinchenko O, Yaple ZA, Arsalidou M. 2018. Brain responses to dynamic facial expressions: a normative meta-analysis. *Front Hum Neurosci*. 12:227.

Downloaded from https://academic.oup.com/cercor/article-abstract/30/1/181/5482262 by guest on 25 February 2020