



Unveiling the neural underpinnings of optimism: a systematic review

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Accepted: 6 July 2021 / Published online: 2 August 2021
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Abstract

Optimism is a personality trait strongly associated with physical and psychological well-being, with correlates in nonhuman species. Optimistic individuals hold positive expectancies for their future, have better physical and psychological health, recover faster after heart disease and other ailments, and cope more effectively with stress and anxiety. We performed a systematic review of neuroimaging studies focusing on neural correlates of optimism. A search identified 14 papers eligible for inclusion. Two key brain areas were linked to optimism: the anterior cingulate cortex (ACC), involved in imagining the future and processing of self-referential information; and the inferior frontal gyrus (IFG), involved in response inhibition and processing relevant cues. ACC activity was positively correlated with trait optimism and with the probability estimations of future positive events. Behavioral measures of optimistic tendencies investigated through the belief update task correlated positively with IFG activity. Elucidating the neural underpinnings of optimism may inform both the development of prevention and treatment strategies for several mental disorders negatively associated with optimism, such as depression, as well as help to foster new resilience promotion interventions targeting healthy, vulnerable, and mentally ill individuals.

Keywords Optimism · LOT-R · fMRI · VBM · Resting state · Systematic review

Introduction

Optimism is an important product of human evolution (Peterson, 2000). This personality trait, also referred to as “dispositional optimism,” was described by Scheier & Carver (1985) as a generalized tendency to expect positive outcomes even in the face of obstacles. Positive expectations for the future often are inaccurate or unrealistically optimistic (Weinstein, 1980; Weinstein & Klein, 1996). This “optimism bias” reflects the tendency of those optimistic individuals to underestimate their chance of experiencing negative life events and overestimate the probability that positive life events will happen to themselves rather than to others (Sharot, 2011).

Optimism is associated with better physical and psychological well-being; optimists live longer (Lee et al., 2019) and healthier lives (Rasmussen et al., 2009), recover more quickly from many ailments (Hevey et al., 2014; Kim et al., 2014, 2017; Scheier et al., 1989; Tindle et al., 2009), and have fewer undesirable psychological symptoms. While facing adversity, optimists tend to experience less distress and to engage in problem-focused coping when stressors can be overcome, or in emotion-focused coping when they need to be endured (Carver et al., 2010). In a broad sense, optimism serves an adaptive function by enhancing proactive behaviors and diminishing stress and anxiety related to possible negative outcomes (Scheier et al., 1989). Although the consequences of an optimistic illusion can be positive, extreme optimism can be harmful, leading to an underestimation of risk and failures (Crotty, 2009; Gibson & Sanbonmatsu, 2004; Hecht, 2013; Shepperd et al., 2017). For example, unrealistic optimism has been considered as a factor contributing to the global economic crisis that began in 2008 (Crotty, 2009) and a risk factor for problem gambling—highly optimists keep gambling and maintain positive expectations despite heavy losses (Gibson & Sanbonmatsu, 2004).

Some authors have reported different ways to measure this phenomenon. One way to assess trait optimism (i.e.,

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dispositional optimism) is to ask directly whether people expect positive or negative events in their lives through a validated scale (e.g., the Life Orientation Test (Scheier & Carver, 1985) or Life Orientation Test - Revised (Scheier et al., 1994)). A different approach is through observing the individual's change in expectation for the occurrence of events when they are presented with a challenge to their biased optimistic beliefs (Sharot, 2011; Sharot et al., 2011). When beliefs are adjusted to new information in an optimistic way (i.e., individuals update selectively their expectancies of future events, more for positive events and/or less for negative events), one can quantify the individual's optimism bias.

After decades of behavioral studies in both humans (Fotiadou et al., 2008; Haggström Westberg et al., 2017; Rasmussen et al., 2009; Scheier et al., 1989; Thomas et al., 2011) and nonhuman species (Douglas et al., 2012; Harding et al., 2004; Matheson et al., 2008; Salmeto et al., 2011), imaging the neural circuitry underlying optimism has only recently started to gain the attention it deserves. A putative candidate involved with the processing of optimism is the anterior cingulate cortex (ACC). This region is linked with imagining the future (Benoit & Schacter, 2015; Bertossi et al., 2016; Schacter et al., 2007), and have been implicated in self-referential processing (D'Argembeau, 2013; Northoff et al., 2006; Spreng et al., 2009; van der Meer et al., 2010). Additionally, given the human propensity toward optimism, when confronted with bad news, these information contrast with someone's expectations. It is reasonable to believe that regions like the adjacent medio-frontal and lateral prefrontal cortex, which are involved in error processing and conflict detection (Taylor et al., 2007), could be implicated in this scenario.

Although some authors have summarized part of the extant literature on the neurobiology of optimism and attempted to outline its hidden circuitry (Hecht, 2013; Kress & Aue, 2017; Sharot, 2011; Sharot & Garrett, 2016), no systematic review has focused on the neuroimaging of optimism. Efforts directed to describe its neurobiological basis contribute to the discovery of how optimism is built. Sharot (2011) provided a general overview of optimism bias, emphasizing their previous work on this topic. Furthermore, Sharot & Garrett (2016) conducted a narrative review focusing explicitly on optimism bias and its possible neural correlates. Hecht (2013) reviewed general concepts related to optimism and provided a qualitative synthesis of the neurophysiology of optimism, highlighting differences associated with the two cerebral hemispheres. The review by Kress & Aue (2017) also differs from the present review in that they conducted a nonsystematic review (i.e., there were no eligibility criteria) with focus on the common brain network between optimism bias and reward-related attention bias. To our knowledge, this is the first attempt to unveil the neurobiological underpinnings of optimism through a systematic review, designed to collate all empirical evidence meeting the prespecified eligibility criteria.

Methods

A systematic literature search was performed by two independent authors (F.S.E. and A.F.B.). Searches were conducted in the PubMed, ISI (Web of Knowledge - Thomson Reuters), and PsycInfo databases. The search strategy used the following keywords: "optimism"; "optimistic"; "positive illusion*" OR "positive bias" AND "fMRI"; "functional magnetic resonance imag*"; "neuroimag*"; "neurobiol*"; "functional neuroim*"; "functional anatomy"; "BOLD"; "blood oxygen level dependent"; "neural mechanisms"; "functional connect*" OR "resting state." Search terms had to appear in the title, abstract, or keywords. No time limits were set for any database. The last search was conducted on February 14, 2020.

The inclusion criteria were neuroimaging studies with magnetic resonance imaging (MRI), including functional MRI (fMRI), resting state fMRI, or anatomical MRI. All studies had to employ a measure of self-optimism (a validated scale or task) and to investigate the association between the optimism measure with a neuroimaging result. Specifically, only studies reporting correlations and/or regressions analyses between the optimism index and brain activity/structure/connectivity were included. Also, we only included original research studies with human adults. The upper limit of participants' age was not restricted.

Studies were not included if they: 1) assessed neurological patients (e.g., brain tumor, stroke); 2) employed diffusion tensor imaging, transcranial magnetic stimulation, electroencephalography, spectroscopy, or arterial spin labeling; 3) reported methodological or technical aspects of fMRI; 4) were reviews, meta analyses, opinions and/or editorials; 5) were not a peer-reviewed article; 6) did not measure optimism (dispositional optimism or optimism bias); and/or 7) did not associate an optimism measure with a neuroimaging result.

The initial analysis was based on titles and abstracts, followed by the evaluation of the full text if the previous step did not offer enough information to decide whether the text should be included. As stated above, the purpose of the present study was to systematically review the neural bases of optimism. Only the results associating the optimism measure with a neural correlate are described in detail.

Data Report

To summarize data from the selected studies, tables and figures are presented separately by optimism index and neuroimaging modality. An additional figure depicts all the coordinates associated with each optimism index.

To ensure coherence of the reported results, all tables and figures display the coordinates given by the authors. All labels were determined by means of the WFU Pickatlas, based on the coordinates given by the authors. When coordinates were reported in Talairach space, they were converted into MNI

space and then labeled according to the WFU PickAtlas (Maldjian et al., 2003, 2004).

Figures were created using Mango software (v. 4.1) (Lancaster & Martinez, 2019). Origin was set on anterior commissure and a reference image (a cube with 8mm of width or a sphere with 8mm of diameter) was created at each peak MNI coordinate. Cubes or spheres were chosen to represent results from different studies in the same figure. To depict the volume of each result proportionally to the size of the clusters reported, a normalization procedure was performed as follows. First, all results from the same brain area were identified among the studies; then, the biggest volume reported was selected; finally, the volumes from all studies that reported that same brain area were divided by the biggest volume identified. This procedure created a normalization index, which was multiplied by the cube or sphere created as previously described. The normalization procedure of the biggest volume resulted in a normalization index equal to “1”; the other indexes were less than “1.” The biggest volume reported among studies was plotted as a region of interest (ROI) with 8 mm of width (or 8 mm of diameter); smaller ROIs were depicted proportionally.

For example, ACC was reported in five different studies and the biggest volume reported was 1,171 mm³. So, all five volumes of ACC were divided by 1,171 (i.e., normalization). The biggest cluster reported was plotted as an 8-mm sphere, and the other four were displayed as smaller spheres.

When a study used an anatomical mask, a bigger cube (with 10 mm of width) or sphere (with 10 mm of diameter) was plotted close to the center of the reported region. When a study did not report the size of the brain area, an intermediate cube (with 4 mm of width) or sphere (with 4 mm of diameter) was plotted. Studies that did not report the peak coordinate of results were not depicted. Animated videos were provided as supplementary material to further facilitate viewing results.

Results

Studies' Characteristics

Figure 1 shows the flowchart for the included studies. Two hundred eighty-nine studies were selected from PubMed, 181 from ISI, and 176 from PsycINFO. After removal of duplicates, 475 studies were screened and 445 were excluded for not meeting the inclusion criteria, leaving a selection of 32 studies. From this sample, 18 studies were further excluded for different reasons, as depicted in Figure 1, leaving a final sample of 14 studies.

The studies included in the final sample correlated an index of optimism, measured through a task and/or a psychometric instrument, with neuroimaging parameters, such as brain volume, Blood Oxygen Level Dependent (BOLD) response

during a task, or functional connectivity indexes between the BOLD signal from different brain regions during a resting state period. See Table 1 for a general overview of the studies' characteristics.

Neuroimaging methods

From the final sample, nine fMRI studies used BOLD signal while participants performed a task (Aue et al., 2012; Bangen et al., 2014; Blair et al., 2013, 2017; Garrett et al., 2014; Kuzmanovic et al., 2016, 2018; Sharot et al., 2007, 2011), two resting state studies investigated brain functional connectivity indexes (Ran et al., 2017; Wu et al., 2015), and three studies measured grey matter volume (Chowdhury et al., 2014; Dolcos et al., 2016; Yang et al., 2013) (see Figure 2 for a depiction of results reported in fMRI and anatomical studies according to optimism index).

Participants

While most of the studies targeted brain response correlations with optimism in healthy adults (i.e., participants who had no known disease or health problem), two studies also investigated clinical samples: patients diagnosed with Generalized Anxiety Disorder/Social Anxiety Disorder (Blair et al., 2017) and Major Depressive Disorder (Garrett et al., 2014).

Most studies investigated optimism in adults except for Bangen et al. (2014) and Chowdhury et al. (2014), whose sample consisted of older adults. Both studies employed control analyses to address possible confounds, such as cortical thickness, cerebral blood flow, and neuropsychological tests.

Optimism indexes

Psychometry

All studies measuring optimism with a psychometric instrument employed the Life Orientation Test - Revised (LOT-R) (Scheier et al., 1994). LOT-R is a six-item, self-report scale (with 4 additional filler items) that assesses trait optimism (i.e., dispositional optimism) by asking whether people expect positive or negative outcomes for different daily situations. Subjects are asked to indicate their agreement with statements like "In uncertain times, I usually expect the best," and "I hardly ever expect things to go my way," through a 5-point scale that ranges from 0 (strongly disagree) to 4 (strongly agree). Scores are summed to yield an overall optimism score; high scores represent greater optimism.

Tasks

When optimism was measured through a task, the paradigms employed were "likelihood estimations of future life events"

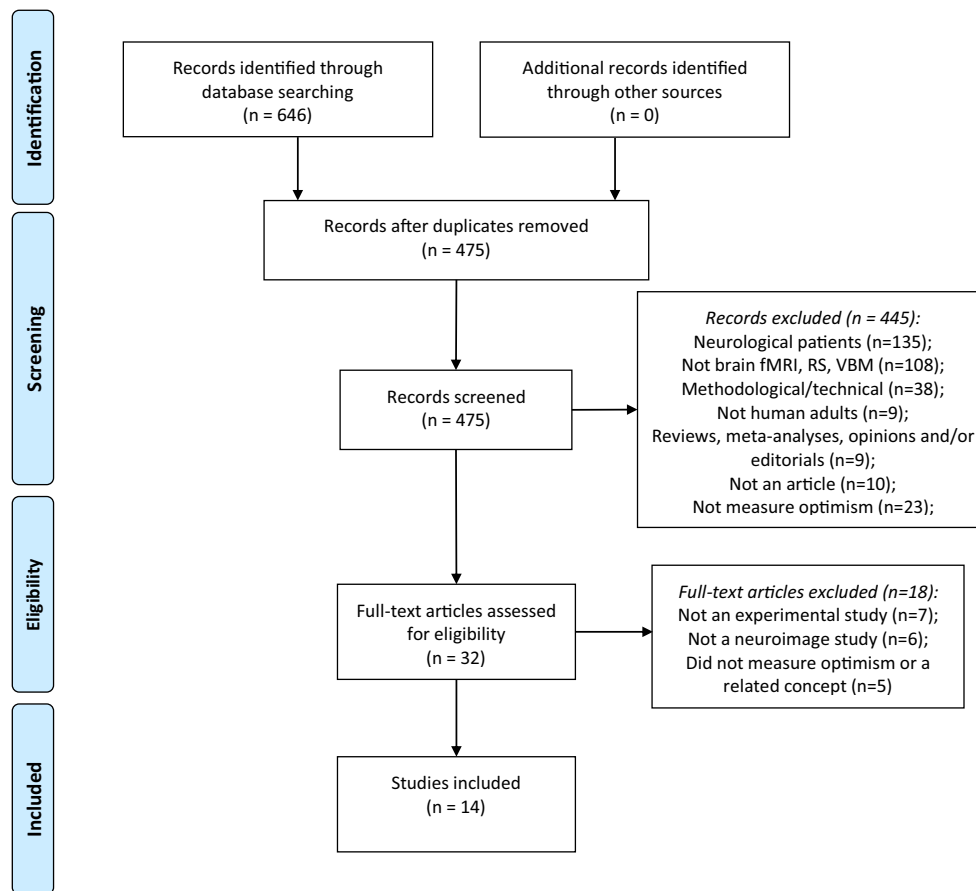


Fig. 1 Note: This data is mandatory. Please provide

or “belief update.” In all cases, the task involved some form of estimation of the probability of future events (“likelihood estimation of future life events”) or a challenge to the participants’ beliefs about the probability of future life events (“belief update”).

Because the studies included were quite diverse, in terms of the types of optimism index that were used (i.e., psychometry or tasks), from now on, the main neuroimaging results

associated with optimism indexes will be described separately by studies that assessed similar outcomes.

Neural correlates of optimism indexed by LOT-R

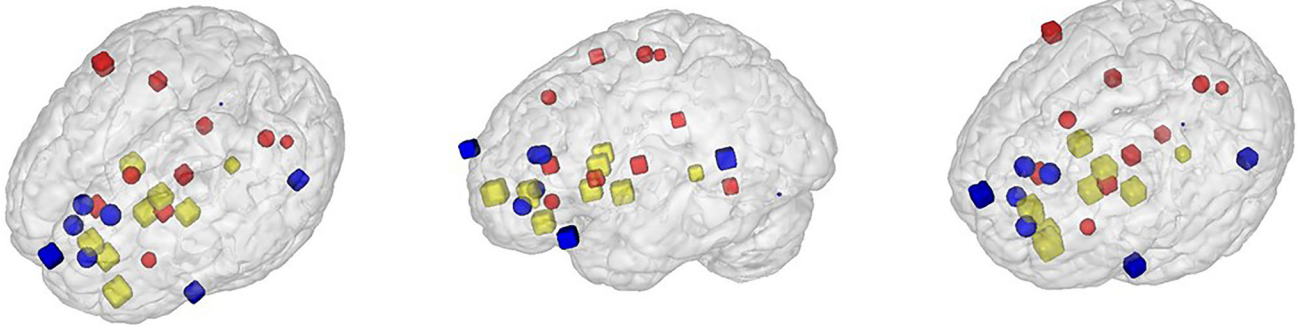
All of the results described in this and the following sections were labeled according to the WFU Pickatlas, based on the coordinates described in each study. When results were

Table 1 Studies’ characteristics

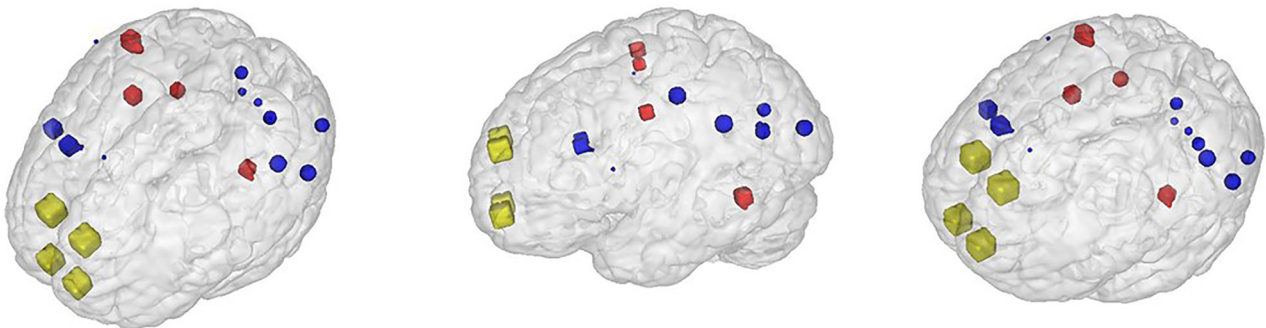
Neuroimaging methods	fMRI	Resting state connectivity	Anatomical MRI
Optimism indexes			
Psychometry			
- LOT-R	Sharot et al. (2007) Bangen et al. (2014) ^c	Ran et al. (2017) Wu et al. (2015)	Dolcos et al. (2016) Yang et al. (2013)
Tasks			
- Belief update	Kuzmanovic et al. (2016) ^a Kuzmanovic et al. (2018) Sharot et al. (2011) ^a Garrett et al. (2014) ^b		Chowdhury et al. (2014) ^c
- Likelihood estimations of future life events	Blair et al. (2013) Blair et al. (2017) ^b Aue et al. (2012)		

OPTIMISM INDEXES (PSYCHOMETRY AND TASKS)

A- POSITIVE ASSOCIATIONS



B- NEGATIVE ASSOCIATIONS



LOT-R	LIKELIHOOD ESTIMATION	BELIEF UPDATE
■	■ Positive events ● Negative events	■ Estimation error ● Update bias

Fig. 2 Neural activity correlated with all optimism indexes . A- Brain areas that showed positive correlations and/or regressions with optimism indexes. B- Brain areas that showed negative correlations and/or regressions with optimism indexes. LOT-R (yellow cubes), likelihood estimate of future events (red spheres and red cubes) and belief update (blue

spheres and blue cubes). Each plot was centered on the coordinates reported in the studies. Talairach coordinates were converted into MNI space. Areas are displayed on a surface template brain provided by Mango software (v. 4.1)

described in the Talairach space, coordinates were converted to MNI before labeling.

fMRI

Two fMRI studies investigated the association between LOT-R scores and the BOLD signal. Sharot et al. (2007) employed a paradigm in which participants had to imagine the future or remember past autobiographical events, which could be positive or negative. Functional ROIs were selected based on the contrast of all trial types pooled together *versus* baseline. From this selection, only left ACC and right amygdala revealed a reduction of BOLD signal when imagining negative future events relative to positive future events and to all past events. More interestingly, the authors found a positive correlation between LOT-R and BOLD response at ACC when participants imagined future positive events in comparison with future negative events; the higher trait optimism, the higher the involvement of ACC during imagining future positive events (compared with negative ones).

Bangen et al. (2014) investigated the modulation of optimism over the neural network for the processing of emotional faces. Participants matched the affective expression (happy, angry, or fearful) of one of two faces to a target one. As control, participants matched geometric forms of one of two shapes to a target one. The sample comprised optimistic older adults, who reported average or higher levels of optimism on a modified version of LOT-R. Authors hypothesized that higher optimism would correlate with reduced processing of fearful faces. There was a negative correlation between the individual's score in LOT-R and BOLD contrast between matching fearful faces *versus* shapes in the right fusiform gyrus, the right inferior frontal gyrus (IFG), ventromedial prefrontal cortex (vmPFC), and the dorsomedial prefrontal cortex (dmPFC). Bangen et al. suggested that the negative correlation may be related to lower attentional salience of negative stimuli in optimistic older adults or to higher efficiency in the processing of those stimuli (which would lead to lower levels of activity due to higher efficiency). Table 2A summarizes the main findings of these studies.

Table 2 Description of the main results of included studies using LOT-R

A) fMRI Study	Sample N (M/F)	Mean age ± SD (or range)	Main results Contrast	Correction used	Functional ROI	Talairach coordinates (cluster size: n.r.)	MNI coordinates	Anatomical label	Association between contrast result and LOT-R
Sharot et al. (2007)	15 (7/8)	23.4 (18–36)	Imagine future positive events x imagine future negative events	$P < 0.00005$, uncorrected [†] more lenient threshold	Whole brain	[-9 39 -2] (cluster size: n.r.) [20 -9 -14] (cluster size: n.r.) [‡] [-4 -47 19] (cluster size: n.r.) [‡] [-8 12 52] (cluster size: n.r.) [‡]	[-9 40 0] [20 -9 -17] [-4 -49 18] [-8 10 57]	left ACC right amygdala left PCC left SMA	(+) ($r = 0.5$, $P < 0.05$) n.s. n.s. n.s.
Bangon et al. (2014)	16 (9/7)	72.3 ± 6.3	Matching fearful faces x shapes	$P < 0.01$ and minimum cluster size: 15 vx	Whole brain	(coordinates and cluster size: n.r.) (coordinates and cluster size: n.r.) Masks defined in AFNI by use of the Talairach Atlas: bilateral vmPFC ^a Bilateral dmPFC ^b	-- --	right fusiform gyrus ^a right IFG ^a	(-) ($r = -0.61$; $P = 0.01$) (- ($r = -0.54$; $P = 0.03$)) (- ($r = -0.54$; $P = 0.03$)) $r = -0.59$; $P = 0.02$) (- ($r = -0.56$; $P = 0.03$); right: $r = -0.55$; $P = 0.03$)
B) Resting state connectivity Study	Sample N (M/F)	Mean age ± SD (or range)	Main results Contrast	RS index	Talairach coordinates	MNI coordinates	Anatomical label	Association between functional connectivity and LOT-R	
Wu et al. (2015)	50 (4/46)	22.2 ± 1.7	$P < 0.00001$ (FDR corrected)	fALFF	--	[-9 39 48] 945 mm ³ [-21 -81 -33] 1,107 mm ³ [24 -75 -36] 1,512 mm ³ [-18 57 24] 1,107 mm ³ [-3 36 51] 4,077 mm ³	Left superior medial frontal gyrus Left cerebellum Crus 1 Right cerebellum Crus 1 Left superior frontal gyrus Left superior medial frontal gyrus	(+) ($r = 0.436$) (+) ($r = 0.523$) (+) ($r = 0.515$) (+) ($r = 0.506$) (+) ($r = 0.626$)	
Ran et al. (2017)	330 (144/186)	19.97 ± 1.27	$P < 0.05$ corrected for topological FDR	Functional connectivity with seed region at [-3 42 -21] sphere with a 6-mm radius	--	[57 -3 -21] 1,134 mm ³ [-30 -84 -39] 1,377 mm ³ [21 -83 -33] 1,971 mm ³ [51 2 -21] 107 vx	Right middle temporal gyrus Left cerebellum Crus 2 right cerebellum Crus 1 Right middle temporal gyrus	(+) ($r = 0.459$) (+) ($r = 0.477$) (+) ($r = 0.577$) (+) ($t = 5.52$)	
			Functional connectivity with seed region at [3 42 -21]	Functional connectivity with seed region at [3 42 -21]	--	[-54 27 27] 122 vx [60 12 33] 69 vx [51 3 -21] 57 vx	Left IFG triangularis Right precentral gyrus Right middle temporal gyrus ^b	(-) ($t = -4.36$) (-) ($t = -4.53$) (+) ($t = 4.55$)	

Table 2 (continued)

C) Anatomical MRI Study	Sample N (M/F)	Mean age ± SD (or range)	Main results Correction used	MRI index	Talairach coordinates	MNI coordinates	Anatomical label	Association between GMV and LOT-R
Yang et al. (2013)	361 (158/203)	19.96 ± 1.29	$P < 0.05$ (cluster-level) and non-stationary cluster correction with $P < 0.001$ (voxel-level)	GMV	--	[60 12 33] 97 vx	Right precentral gyrus	Left IFG ₊ triangularis (-) ($t = -4.25$) Left IFG ₋ triangularis (-) ($t = -4.15$)
Dolcos et al. (2016)	61 (24/37)	23.23 ± 4.00	<i>n.r.</i>	GMV	--	[-14 -39 -1] 748vx	Left lingual gyrus	(+) ($r = 0.21$; $P < 0.001$)
								(+) ($r = 0.301$; $P = 0.021$)
								(+) ($r = 0.310$; $P = 0.016$) (+) ($r = 0.262$; $P < 0.05$) (+) (left: $r = 0.261$; right: $r = 0.269$; $P < 0.05$) (+) ($r = 0.288$; $P < 0.05$) (+) ($r = 0.268$; $P < 0.05$)

Masks defined based on the Desikan-Killiany atlas:
 Left lateral OFC^a
 Left medial OFC^a
 Left accumbens^a
 Bilateral caudate^a
 Left pallidum^b
 Left rostral ACC^a

Resting state connectivity

Two studies investigated correlations between LOT-R and resting-state connectivity indexes. Wu et al. (2015) studied the neural correlates of optimism with two resting-state indexes (ReHo and fALFF) inside the Default Mode Network. The authors described positive correlations between LOT-R with these indexes in the medial frontal gyrus, the superior frontal gyri, middle temporal gyrus and with cerebellum. The activity in these regions is described as reflecting self-processing and valence. When thinking spontaneously, highly optimistic individuals present higher activity in these brain areas.

Ran et al. (2017) investigated whether differences in optimism trait were associated with resting state functional connectivity between rectus gyrus (defined as the seed region) and other brain regions. Results showed that more optimistic individuals had stronger connectivity between rectus gyrus and middle temporal gyrus. Authors point that this association in more optimistic individuals could be related to connections to emotion regulation functions. Also, more optimistic individuals had weaker connectivity between rectus gyrus and IFG, indicating that higher dispositional optimism might be related to self-referential processing and emotion regulation. The same patterns of correlations were observed with right and left rectus gyrus as seed regions (Table 2B).

Anatomical MRI

Two anatomical studies correlated brain volume with LOT-R. Yang et al. (2013) observed positive correlations with grey matter volume of left lingual gyrus. Dolcos et al. (2016), investigating the relationship between trait optimism, anxiety symptoms, and brain volume in healthy participants, found positive correlations with the left lateral and medial OFC, as well as with the basal ganglia nuclei (left accumbens, bilateral caudate, and left pallidum) and rostral ACC (Table 2C). A mediation analysis revealed that trait optimism mediated the relationship between left OFC volume and anxiety symptoms. See Figure 3 for the depiction of peak coordinates of fMRI and anatomical studies.

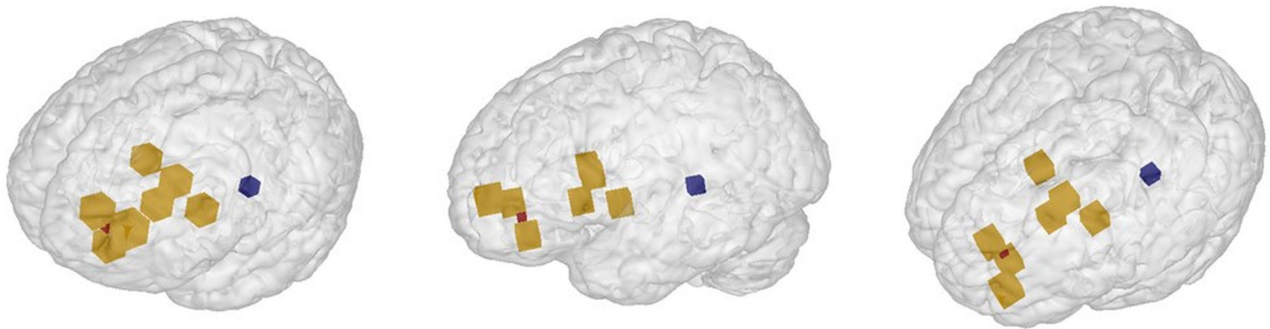
Neural correlates of optimism indexed by tasks

Task: estimation of the likelihood of possible future life events

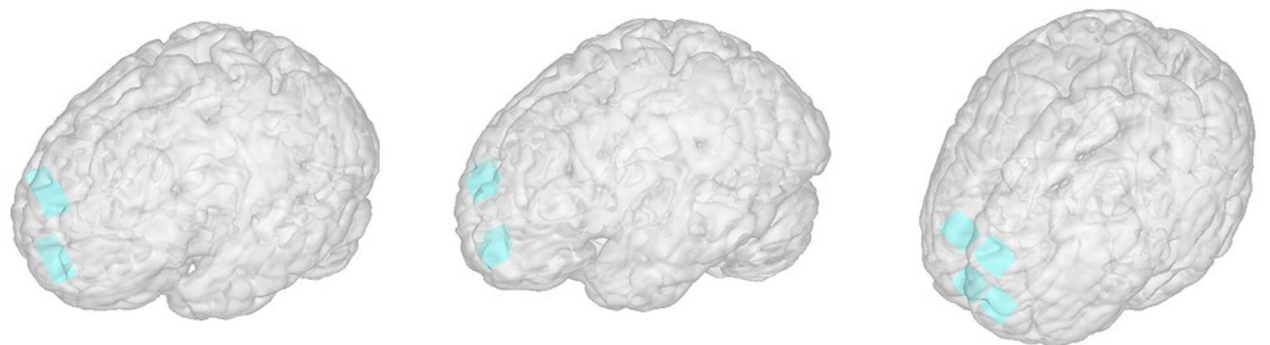
fMRI Three fMRI studies used the estimation of the likelihood of possible future life events as a score of optimism and investigated the association between this score and the BOLD signal. Aue et al. (2012) assessed the neural correlates of "wishful thinking," defined as the overestimation of the probability of desirable events. In their paradigm, participants had to estimate the likelihood of their favorite or least favorite

PSYCHOMETRY: LOT-R

A- POSITIVE ASSOCIATIONS



B- NEGATIVE ASSOCIATIONS



Sharot et al. (2007)	Yang et al. (2013)	Bangen et al. (2014) *	Dolcos et al. (2016)
■	■	■	■

Fig. 3 Neural activity correlated with LOT-R. A- Brain areas that showed positive correlations and/or regressions with LOT-R. B- Brain areas that showed negative correlations and/or regressions with LOT-R. Studies depicted are: Sharot et al. (2007) (dark red cube); Yang et al. (2013) (dark blue cube); Bangen et al. (2014) (light blue cube); and Dolcos et al. (2016) (dark yellow cube). Each plot was centered on the coordinates reported in the studies (see Table 2). Talairach coordinates were converted into MNI space. The size of cubes or spheres is proportional to the size

of the biggest cluster reported in the same brain area, applying a normalization procedure, as described in “2.1 Data report” section. Areas are displayed on a surface template brain provided by Mango software (v. 4.1). Asterisk indicates that the sample from the study (Bangen et al., 2014) was composed of older adults. Note: Sharot et al. (2007) did not report the cluster size; Dolcos et al. (2016) used only anatomical ROIs; Bangen et al. (2014) did not report peak coordinates of functional ROIs - so, only anatomical ROIs were depicted

football team winning in various situations. Clusters, where BOLD response to the favorite *versus* the least favorite teams differed significantly, were selected for correlation analysis with wishful thinking, measured as the subtraction of the winning odds for the favorite and least favorite teams. The authors observed that higher levels of wishful thinking were associated with increased connectivity between the occipital cortex and thalamus, and lingual gyrus. Results are discussed in terms of a higher attentional bias to the positive hedonic outcome (favorite team winning), revealed as higher connectivity between primary sensory areas (occipital) with the human reward system, that is absent for the negative outcome.

Blair et al. (2013) asked healthy participants to estimate the likelihood of possible future life events. They found a positive correlation between the estimation of future positive events and BOLD responses in the ACC, and a positive correlation

between the likelihood estimation of negative events with the left insula and the supplementary motor area (SMA) activity. The positive correlation between rostral ACC and optimistic evaluations of future positive events was interpreted as related to the involvement of rostral ACC in self-referential processing; thus, higher activity correlated with a higher likelihood estimation of positive events. For negative events, higher likelihood estimates led to increased activity in regions involved in the anticipatory response to negative events (insula and SMA); more optimistic participants had decreased activation of those regions when estimating the likelihood of future negative events.

In a more recent study, Blair et al. (2017) compared the results from a subsample (18 of 33 participants) of the 2013 study with patients diagnosed with Social Anxiety Disorder and Generalized Anxiety Disorder. A

main effect of group, modulated by the participants' estimations of positive events, was observed in the right mPFC (label reported by the authors), the bilateral caudate, right middle frontal gyrus, left thalamus, and right superior temporal gyrus. The main effect of group was driven by the Generalized Anxiety Disorder group. In all regions, Generalized Anxiety Disorder patients showed a significantly greater inverse modulation of activity by their probability estimates, whereas healthy participants and Social Anxiety Disorder patients showed no modulation. More specifically, for the Generalized Anxiety Disorder group, the lower their estimation of future positive events, the higher the BOLD activity in the right mPFC and all other regions. In fact, the authors consider results as difficult to interpret and that patients with Generalized Anxiety Disorder process positive events differently compared with controls. See Figure 4 for a depiction of peak coordinates reported by these two studies. Table 3 describes the main findings of the studies that used the "estimation likelihood of possible future life events" task.

Task: Belief update

In the belief update task, participants are asked to make a first estimation of the probability of experiencing adverse life events. After being exposed to the actual statistics of that event occurring to a person similar to themselves, participants make a new estimation, in which they can update their first estimation if they wish to. Two indexes are computed: "estimation error"—calculated as the difference between the participant's first estimation, and the actual statistics. When participants overestimate the probability of a negative event occurring to themselves (i.e., first estimation > actual statistics), the actual statistic signals good news, and the estimation error is classified as "desirable." When the participant underestimates the probability of a negative event occurring to themselves (i.e., actual statistics > first estimation), the actual statistic signals bad news and the estimation error is classified as "undesirable"; ii) "update bias"—calculated as the difference between the first and second estimations, separately for "desirable" and "undesirable." Optimism bias is assessed through a comparison between desirable updates and undesirable updates (Sharot et al., 2011).

In response to desirable and undesirable estimations, people usually update their estimations differently, suggesting an asymmetry in belief updating. On average, participants are more likely to update their beliefs to desirable estimations than to undesirable ones, indicating an optimistic bias (Kuzmanovic et al., 2016, 2018; Sharot et al., 2011).

fMRI Three studies investigated correlations between the indexes of the belief update task and the BOLD signal.

Sharot et al. (2011) investigated the neural correlates of estimation errors (i.e., first estimation *minus* actual statistics), separately for desirable and undesirable events. For this purpose, estimation errors were inserted as parametric regressors at the moment when participants were faced with the actual statistic for each event. The main findings from this study was a positive correlation between left IFG (label reported by the authors) activity and desirable estimation errors (i.e., when the actual statistic was lower than estimated by the participants) and a negative correlation between right IFG activity and undesirable estimation errors (i.e., when the actual statistic was higher than estimated by the participants). In other words, the BOLD signal in the left IFG was higher when participants' estimation was in a more desirable way; the BOLD signal was lower in the right IFG when participants' estimation was in a more undesirable way. Further analyses were performed in the clusters identified in this first analysis, inserting the update of estimations as parametric regressors instead of the estimation errors. Results showed that right IFG activity predicted update in response to undesirable information, while activity in superior frontal gyrus and right cerebellum predicted update in response to desirable information. Finally, highly optimistic participants (assessed through LOT-R) showed a weaker correlation of right IFG and undesirable errors, suggesting that optimism was associated with diminished coding of undesirable information in the IFG.

Kuzmanovic et al. (2016) used an updated version of the belief update task employed by Sharot et al. (2011). BOLD responses during the second estimation were parametrically modulated by the individual's updates and judgments were performed for the self and also for a similar other. Interestingly, they observed that the greater was the activity in ACC, the larger was the size of update for desirable estimations (i.e., when the actual statistic was lower than the first estimation and participants updated their estimation); the greater was the activity in ACC, the smaller was the size of update for undesirable estimations (i.e., when the actual statistic was higher than the first estimation). Further analysis revealed that the lower updates for undesirable information were driving the effect in ACC. This effect was observed only when judgments were related to the self and not when estimating the probability of negative events happening to a similar other. In supplementary analyses, these authors also investigated neural correlates of estimation errors and replicated Sharot's results—a positive correlation between left IFG and desirable estimation errors, and a negative correlation between right IFG and undesirable estimation errors.¹

In a more recent study, Kuzmanovic et al. (2018) employed a revised version of the belief update task and combined computational modeling of belief update parameters with fMRI

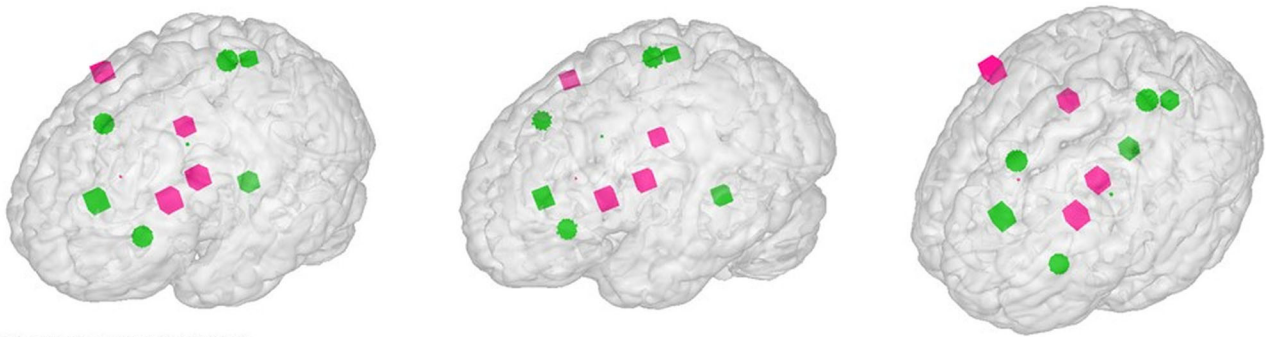
¹ These results were obtained with a more liberal threshold ($P < 0.001$ uncorrected).

Table 3 Description of the main results of included studies using the “likelihood estimate of future positive and negative events” task

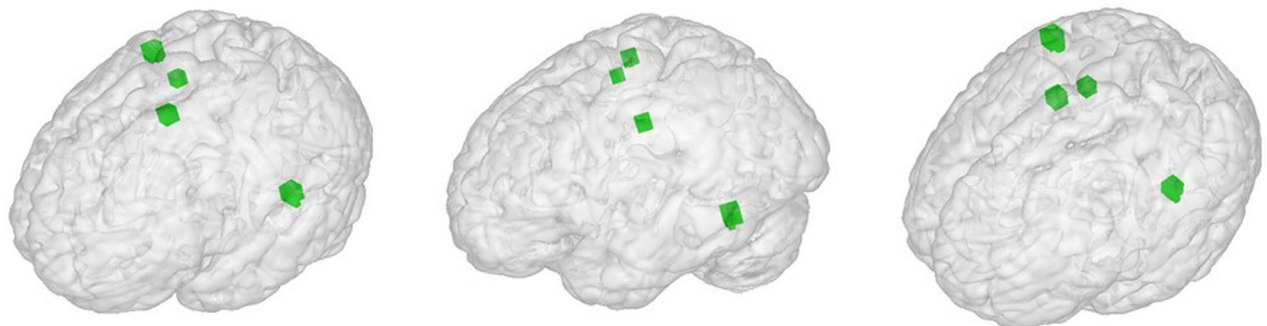
Study	Sample	Main results					
		Mean age ± SD (or range)	Correction used	Task index	Talairach coordinates		
	N (M/F)				MNI coordinates	Anatomical label	Association between <i>brain regions</i> and <i>task indexes</i>
Aue et al. (2012)	30 (28/2)	21.8 ± 3.82	$P < 0.01$ with minimum cluster size: 26 vox (720 μ - Monte Carlo simulation)	Estimation of future events	Seed region: [-34 -62 -6] 783 mm ³ Functional connectivity with: [18 -22 15] 4,779 mm ³ [-28 12 15] -28 12 15] 1,485 mm ³ [20 -53 4] 891 mm ³	Left fusiform gyrus	(+) connectivity between <i>seed region</i> (fusiform gyrus) with: r = 0.61; $P < 0.05$ r = 0.66; $P < 0.05$ r = 0.76; $P < 0.005$
Blair et al. (2013)	33 (18/15)	29.15 (22-48)	$P < 0.005$ (correction using AlphaSim)	Estimation of future positive events	[5 32 12] 1,171 mm ³ [-37 -31 55] 21,386 mm ³ [22 -52 -17] 4,570 mm ³ [6 -19 48] 2,103 mm ³ [41 -26 51] 33,617 mm ³ [-16 -52 -14] 3,870 mm ³ [40 -24 20] 5,277 mm ³ [-6 22 43] 2,789 mm ³ [-27 26 3] 1,143 mm ³ [-40 4 35; -31 -25 36] 1,119 mm ³ /12,195 mm ³ [36 -26 49] 21,759 mm ³	Right ACC Left postcentral gyrus Right cerebellum_6 Right SMA Right postcentral gyrus Left cerebellum_4_5 Right Rolandic opercular gyrus Left SMA Left insula Left precentral gyrus Right postcentral gyrus	(+) (t = 4.10) (+) (t = 10.76) (+) (t = 7.08) (-) (t = 5.42) (-) (t = 14.78) (-) (t = 6.96) (-) (t = 6.16) (+) (t = 5.25) (+) (t = 5.15) (+) (t = 4.11 / 6.88) (-) (t = 8.54)
Blair et al. (2017)*	HC: 18 (8/10) GAD: 18 (10/8) SAD: 18 (5/13)	HC: 31.9 ± 7.78 GAD: 31.0 ± 7.78 SAD: 32.4 ± 9.48	$P < 0.005$ (correction using ClustSim - minimum cluster size: 952 mm ³) †Small volume correction	Estimation of future positive events	[-20 -51 -18] 2,207 mm ³ [12 4 30] 1,103 mm ³ [-15 7 7] 1,673 mm ³ [17 14 12] 140 mm ³ † [38 2 53] 2,882 mm ³ [-6 -12 7] 6,805 mm ³ [41 -33 15] 3,313 mm ³	Left caudate Right caudate Right middle frontal gyrus Left thalamus Right STG	(-) (t = 5.89) Group main effect - modulated by individuals' estimation for positive events; F = 14.44 Post hoc GAD vs. HC: Inverse correlations (-) Group main effect - modulated by individuals' estimation for positive events; F = 18.08 Post hoc GAD vs. HC: Inverse correlations (-) Group main effect - modulated by individuals' estimation for positive events; F = 14.34 Post hoc GAD vs. HC: Inverse correlations (-) Group main effect - modulated by individuals' estimation for positive events; F = 22.44 Post hoc GAD vs. HC: Inverse correlations (-) Group main effect - modulated by individuals' estimation for positive events; F = 15.89 Post hoc GAD vs. HC: Inverse correlations (-) Group main effect - modulated by individuals' estimation for positive events; F = 19.99 Post hoc GAD vs. HC: Inverse correlations (-)

TASK: LIKELIHOOD ESTIMATION OF FUTURE EVENTS

A- POSITIVE ASSOCIATIONS



B- NEGATIVE ASSOCIATIONS



Blair et al. (2013)	Blair et al. (2017) *
■ Positive events	■ Positive events
● Negative events	

Fig. 4 Neural activity correlated with “likelihood estimate of future events” task. A- Brain areas that showed positive correlations and/or regressions with likelihood estimate of future events indexes. B- Brain areas that showed negative correlations and/or regressions with likelihood estimate of future events indexes. Studies depicted are: Blair et al. (2013) (light green spheres: “positive events”; light green cubes: “negative events”); Blair et al. (2017) (pink spheres: “positive events”). Each plot was centered on the coordinates reported in the studies (see Table 3).

Talairach coordinates were converted into MNI space. The size of cubes or spheres is proportional to the size of the biggest cluster reported in the same brain area, applying a normalization procedure, as described in “2.1 Data report” section. Areas are displayed on a surface template brain provided by Mango software (v. 4.1). Asterisk indicates that the sample from the study (Blair et al., 2017) was also composed of clinical patients (Social Anxiety Disorder and Generalized Anxiety Disorder)

and dynamic causal modeling. The computational modeling of belief update parameters considered the personal relevance of each item, the participants’ learning rate, and the estimation error, separately for good and bad news. The parametric modulation analysis showed that rectus gyrus was the only region in which BOLD responses to updates for good news (compared with bad news) correlated with optimism bias (positive correlation), measured as the subtraction of updates for bad news from updates for good news (updateGOOD-updateBAD). Analysis of connectivity by means of dynamic causal modeling was performed in a network comprising middle frontal gyrus, rectus gyrus, and superior frontal gyrus. In this model, middle frontal gyrus was considered as an “update processing node” tracking errors, rectus gyrus as a “valuation node” tracking valence, and superior frontal gyrus as a

“cognitive node” possibly associated with self-referential decision making. The comparison among ten different models of connectivity between nodes revealed that the model in which middle frontal gyrus modulates rectus gyrus (bidirectional connection) and superior frontal gyrus (through rectus gyrus) exhibited the highest significance above all others. Optimism bias correlated positively with the connectivity strength between rectus gyrus and superior frontal gyrus while participants updated their estimations. This supports the idea that rectus gyrus may influence superior frontal gyrus by filtering incoming signals in a valence-dependent manner.

Garrett et al. (2014) applied the belief update task to patients with Major Depression Disorder and healthy controls. Brain activity, parametrically modulated by estimation errors, was investigated during the confrontation with the actual

statistics, separately for desirable and undesirable information. For all participants, desirable estimation was positively correlated with left IFG and superior frontal gyrus. Undesirable information correlated negatively with right supramarginal gyrus and positively with middle temporal gyrus and superior medial frontal gyrus. The comparison between groups revealed that depressed participants updated their beliefs about future events in proportion to errors in the first estimation, in the same way for desirable and undesirable information. Healthy controls did so only for desirable estimates (when the first estimation was worse than the actual statistic). The authors investigated brain correlates for the differential estimation errors between groups in regions previously associated with the prediction of individuals' differences. Depressed participants tracked bad news errors (significant negative correlations) with greater fidelity than healthy controls at right IFG and supramarginal gyrus. It means that, for undesirable events, the lower the estimation error for bad news (i.e., the less optimistic the participant's estimation), the higher the BOLD response in the right IFG and right supramarginal gyrus. It signals better coding of errors that, when corrected, will represent a more negative (and accurate) view of the occurrence probability of undesirable events (Table 4A; Figure 5).

Anatomical MRI One study investigated correlations between the indexes of the belief update task and regional brain volume in healthy participants (Chowdhury et al., 2014). These authors correlated ROIs of the ventral and dorsal ACC with update bias (desirable *minus* undesirable update) and observed a positive correlation with dorsal and ventral ACC volumes only in older adults, who were also more optimistic than younger adults (Table 4B). The correlation coefficients differed between age groups only for the dorsal ACC. Results were observed even when confounding factors were considered as covariates (e.g., age, grey matter volume, or cognitive function). Results are discussed as evidence of more efficient emotion regulation and greater reappraisal in older age.

Discussion

Optimistic predispositions are an important attribute present not only in humans but also in other animals, such as chicks (Salmeto et al., 2011), starlings (Matheson et al., 2008), pigs (Douglas et al., 2012), and rodents (Harding et al., 2004). Besides being associated with numerous downsides potentially contributing to negative outcomes (Crotty, 2009; Gibson & Sanbonmatsu, 2004; Hecht, 2013; Shepperd et al., 2017), the greater majority of studies points that optimism serves an adaptive function by enhancing proactive behaviors and

diminishing stress and anxiety related to possible negative outcomes (Rasmussen et al., 2009; Scheier et al., 1989).

We systematically reviewed the neurobiological basis of optimism with a focus on neuroimaging studies. In terms of neuroimaging strategies, the majority of studies in healthy samples employed functional neuroimaging while participants performed a task (likelihood estimation of future life events or belief update); some studies investigated functional connectivity during a resting state period and others measured brain volume. We found two key brain regions involved in the neuroimaging of optimism: ACC and IFG.

Anterior Cingulate Cortex

The most consistent finding was a positive correlation between the BOLD signal or volume of the ACC and the different ways by which optimism was operationalized: 1) trait optimism—measured through LOT-R (Dolcos et al., 2016; Sharot et al., 2007); 2) likelihood estimations of positive future life events (Blair et al., 2013); and 3) belief update (Chowdhury et al., 2014; Kuzmanovic et al., 2016). These results indicate an association between increased activity in the ACC and optimism.

ACC also was implicated in the neurocircuitry of optimism in a clinical sample. Patients with Generalized Anxiety Disorder presented negative correlations between the BOLD signal in the ACC for the estimation of positive events and optimism compared with both healthy controls and Social Anxiety Disorder patients (Blair et al., 2017). Despite revealing the involvement of the ACC, the authors pointed out that results were unpredicted and difficult to interpret. Because most studies point to positive correlations between optimism indexes and activity in the ACC, data from their healthy controls are not in line with the current literature; in this sample, the correlation was close to zero.

Taken together, these results are in line with an extensive body of literature linking ACC with imagining the future (Benoit & Schacter, 2015; Bertossi et al., 2016; Schacter et al., 2007) and processing of self-referential information (D'Argembeau, 2013; Herold et al., 2016; Northoff et al., 2006; Spreng et al., 2009; van der Meer et al., 2010). We discuss each of these concepts below.

Studies on the neuroimaging of imagining the future converge over a core brain system encompassing the ACC (Benoit & Schacter, 2015; Bertossi et al., 2016; Schacter et al., 2007). Schacter et al. (2007) reviewed the evidence that a core system involved in remembering the past and envisioning the future comprised the Default Mode Network, which was further confirmed in a meta-analysis from Benoit & Schacter (2015). Matsunaga et al. (2016) showed correlation between activity at ACC and imagination of emotional life events and a correlation between gray matter density of the ACC and the score of

Table 4 Description of the main results of included studies using the “belief update” task

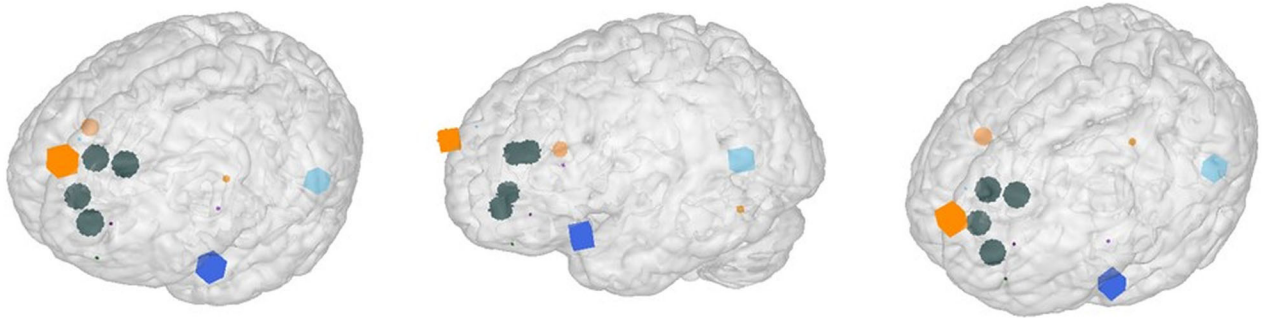
Study	Sample N (M/F)	Mean age ± SD (or range)	Main results Correction used	Task index	Talairach coordinates	MNI coordinates	Anatomical label	Association between brain regions and task indexes
Sharot et al. (2011)	19 (11/8)	(19–27)	$P < 0.05$, cluster level corrected; whole brain voxelwise threshold at $P < 0.001$, uncorrected	Whole brain Estimation errors	Desirable	[−58 21 −1] 274 vx [−10 62 28] 412 vx [33 −79 −28] 185 vx	NA Left superior frontal gyrus Right cerebellum Crus 2	(+) (n.r.) (+) (n.r.) (+) (n.r.)
Garrett et al. (2014)*	HC: 14 (9/5) MDD: 15 (9/6)	HC: 30.36 ± 8.35 MDD: 31.47 ± 9.16	$P < 0.05$, cluster level corrected (FWE); whole brain voxelwise threshold at $P < 0.001$, uncorrected	Functional ROI Whole brain Estimation errors	Desirable Undesirable	[−10 62 28] 412 vx [33 −79 −28] 185 vx [46 12 9; 60 10 9] 190 vx	Left superior frontal gyrus Right cerebellum Crus2 Right IFG_opercular	(+) ($z = 2.1$; $P < 0.05$) (+) ($t = 2.4$; $P < 0.05$) (+) ($t = 2.2$; $P < 0.05$)
Kuzmanovic et al. (2016)	24 (11/13)	25.13 ± 3.89 (19–38)	$P < 0.05$ (FWE), with an extent threshold of 10 vx †More liberal threshold	Anatomical ROI Whole-brain Estimation errors	Undesirable	[−44 −50 14] 1,174 vx [−2 50 31] 203 vx Mask obtained from WFU PickAtlas: right IFG	Left middle temporal gyrus Left superior medial frontal gyrus	(+) ($z = 4.92$) (+) ($z = 3.80$)

Table 4 (continued)

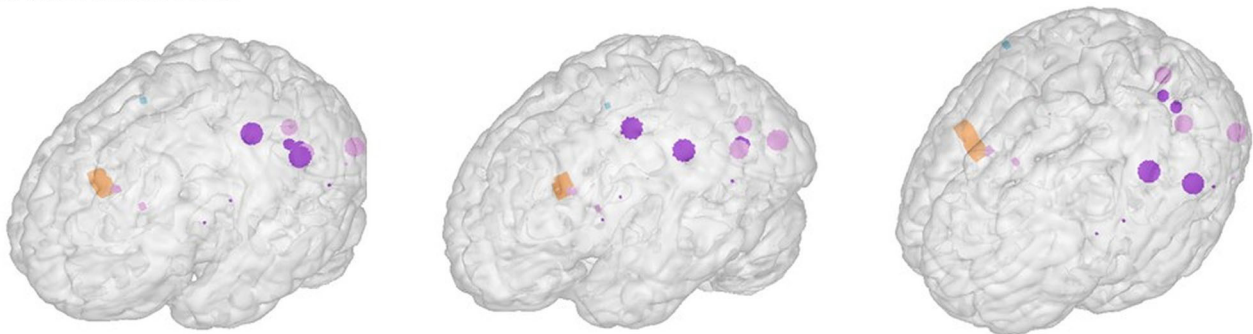
Study	Sample N (M/F)	Mean age ± SD (or range)	Main results Correction used	Task index	Talairach coordinates	MNI coordinates	Anatomical label	Findings	
Kuzmanovic et al. (2018)	24 (10/14)	27.38 ± 5.15	<i>P</i> < 0.05 (FWE), with an extent threshold of 10 vx	<i>Whole-brain</i>	Optimism bias	--	23 vx	Left middle temporal gyrus	(-) (<i>t</i> = 5.13; <i>P</i> = 0.014)
							[-48 -26 42]	Left IPL	
							17 vx		
							[14 -84 10]	Right calcarine gyrus	(-) (<i>t</i> = 7.93; <i>P</i> = 0.000)
							[-16 -70 8]	Left calcarine gyrus	(-) (<i>t</i> = 7.38; <i>P</i> = 0.000)
							5,240 vx		
							[52 -34 -6]	Right middle temporal gyrus	(-) (<i>t</i> = 5.45; <i>P</i> = 0.003)
							16vx		
							[-40 -80 12]	Left middle occipital gyrus	(-) (<i>t</i> = 5.34; <i>P</i> = 0.006)
							13 vx		
							[-60 -58 18]	Left middle temporal gyrus	(-) (<i>t</i> = 5.03; <i>P</i> = 0.021)
							10 vx		
							[-50 20 24]	Left IFG <i>triangularis</i>	(+) (<i>t</i> = 3.47; <i>P</i> = 0.001 uncor.)
							18 vx†		
[38 -2 -6; 44 6 6]	Right insula	(-) (<i>t</i> = 5.14; <i>P</i> = 0.014 / <i>t</i> = 4.29; <i>P</i> = 0.336)							
[42 8 8]†	Right IFG <i>opercular</i>	(-) (<i>t</i> = 4.01)							
234 vx†									
[-12 44 -16]	Left rectus gyrus	(+) (<i>t</i> = 5.63; <i>P</i> < 0.001)							
49 vx									
[-2 46 -22]	Left rectus gyrus	(+) Connectivity between superior frontal gyrus and middle frontal gyrus during updates							
27 vx									
[-16 44 40]	Left superior frontal gyrus	estimation (<i>r</i> = 0.47; <i>P</i> = 0.020)							
30 vx									
[44 42 26]	Left middle frontal gyrus	(+) Differential modulation of superior frontal gyrus- middle frontal gyrus connection by favorable vs. unfavorable updates (<i>r</i> = 0.52; <i>P</i> = 0.009)							
1,414									
B) Anatomical MRI									
Study	Sample N (M/F)	Mean age ± SD (or range)	Main results Correction used	Task index	Talairach coordinates	MNI coordinates	Anatomical label	Findings	
	Young adults: 18 (8/10)	Young adults: 22 ± 2.29	ROI analysis	Optimism bias	<i>Mask obtained from the Automated Anatomical Labeling atlas:</i>				
Chowdhury et al. (2014)	Old adults: 18 (7/11)	Old adults: 66 ± 5.62			Bilateral dorsal IACC			(+) (<i>r</i> = 0.649; <i>P</i> = 0.004) ACC in older adults; greater for older compared with younger adults (<i>z</i> = -1.78; <i>P</i> = 0.036)	

TASK: BELIEF UPDATE

A- POSITIVE ASSOCIATIONS



B- NEGATIVE ASSOCIATIONS



	Sharot et al. (2011)	Garret et al. (2014) *	Chowdhury et al. (2014) **	Kuzmanovic et al. (2016)	Kuzmanovic et al. (2018)
□ <i>estimation error</i>	<ul style="list-style-type: none"> ■ desirable ■ undesirable 	<ul style="list-style-type: none"> ■ desirable ■ undesirable 	-	<ul style="list-style-type: none"> ■ desirable ■ undesirable 	-
○ <i>update bias</i>	<ul style="list-style-type: none"> ● desirable ● undesirable 	<ul style="list-style-type: none"> ● desirable ● undesirable 	<ul style="list-style-type: none"> ● optimism bias 	<ul style="list-style-type: none"> ● optimism bias ● desirable ● undesirable 	<ul style="list-style-type: none"> ● optimism bias

Fig. 5 Neural activity correlated with “belief update” task. A- Brain areas that showed positive correlations and/or regressions with belief update indexes. B- Brain areas that showed negative correlations and/or regressions with belief update indexes. Studies depicted are: Sharot et al. (2011) (orange cubes: “desirable estimation error”; light orange cubes: “undesirable estimation error”; orange spheres: “desirable update”; light orange spheres: “undesirable update”); Garrett et al. (2014) (blue cubes: “desirable estimation error”; light blue cubes: “undesirable estimation error”; blue spheres: “desirable update”; light blue spheres: “undesirable update”); Chowdhury et al. (2014) (dark gray sphere: optimism bias); Kuzmanovic et al. (2016) (purple cubes: “desirable estimation error”; light purple cubes: “undesirable estimation error”; purple spheres: “desirable update”; light purple spheres: “undesirable update”); dark purple

sphere: optimism bias); Kuzmanovic et al. (2018) (dark green sphere: optimism bias). Each plot was centered on the coordinates reported in the studies (see Table 4). Talairach coordinates were converted into MNI space. The size of cubes or spheres is proportional to the size of the biggest cluster reported in the same brain area, applying a normalization procedure, as described in “2.1 Data report” section. Areas are displayed on a surface template brain provided by Mango software (v. 4.1). Asterisk indicates that the sample from the study (Garrett et al., 2014) was also composed of clinical patients (Major Depressive Disorder). † indicates that the sample from the study (Chowdhury et al., 2014) was composed of younger and older adults. Note: Chowdhury et al. (2014) used only anatomical ROIs

Subjective Happiness Scale. Corroborating these results, Bertossi et al. (2016) observed that lesions of the vmPFC, extending to ACC, lead to impairments in the construction of past and future events.

Besides imagining future events, meta-analyses from different groups pointed to the involvement of the ACC in the processing of self-relevant information (Northoff et al., 2006; Spreng et al., 2009; van der Meer et al., 2010). Northoff et al.

(2006) described the correspondence between self-referential processing and the Cortical Midline Structures, a functional and anatomical unit that spans vmPFC, ACC, and posterior cingulate cortex (PCC), among other regions. Other studies show that ACC also is involved in autobiographical memory, prospection (i.e., imagining ourselves in the future), and theory of mind (Spreng et al., 2009). In a review of fMRI and PET studies using autobiographical recall to induce emotions,

Suardi et al. (2016) observed that remembering happy and negative events were primarily associated with the activation in the ACC, PFC, and insula—reinforcing the involvement of these areas with the processing of self-relevant information.

A possible involvement of ACC with positive emotional states also has been proposed. Reviewing a series of studies, some authors suggest that happiness, pleasure, and reward processing are localized rostrally and dorsally in the pregenual ACC (Vogt, 2005, 2014; Vytal & Hamann, 2010). It is noteworthy that in the studies reviewed by Vogt, subjects were frequently instructed to recall or imagine an emotionally laden personal event. Interestingly, Moran et al. (2006) observed that ventral ACC conveys self-relevant information in a valence-dependent manner: ventral ACC activation increases as a function of self-relevance and positive valence, reducing activity for unfavorable information, even when it is self-relevant.

Inferior frontal gyri

The second brain region where activity was closely associated with optimism was the IFG. This region was implicated in the optimistic asymmetrical coding of errors during the belief update task. BOLD responses in the IFG were positively correlated with estimation errors for desirable information and negatively correlated for undesirable ones (Sharot et al., 2011). Moreover, activity in the IFG predicted updates for undesirable information. For depressed individuals (Garrett et al., 2014), more accurate estimations for undesirable events were associated with higher activity in the IFG.

The IFG has been consistently implicated in response inhibition (Aron, Monsell, Sahakian, & Robbins, 2004a; Chikazoe et al., 2007; Swick et al., 2008), defined as the "cognitive process required to cancel an intended movement" (Aron, Robbins, & Poldrack, 2004b, p. 170). In fact, IFG lesions both in humans (Aron et al., 2004a) or in its homolog in primates (Iversen & Mishkin, 1970) result in deficient response inhibition, which is proportional to the damage in the case of humans. The seminal work by Hampshire et al. (2010) proposed that the actual role of the IFG was to process relevant cues during a task, irrespective of the activation or inhibition of a motor response or even when no motor response at all was required. Greening et al. (2011) also pointed to the involvement of the IFG not only in response inhibition but also in the modulation of stimulus-response maps.

Notably, the characteristic optimistic asymmetry in updates favoring desirable information can be disrupted when transcranial magnetic stimulation is used to inhibit left IFG activity (Sharot et al., 2012). Sharot & Garrett (2016) proposed that the pattern of activity of the IFG could be attributed to the coding of errors in an asymmetrical pattern, influenced by the valence of the information being processed. When an update signals good news (e.g., when the participant is given the

information that he/she overestimated his/her chance to have cancer), error coding could be more precise and with higher IFG engagement. When the update brings bad news (e.g., when the participant underestimates his/her chance of being robbed), error coding could be less precise and with lower engagement of the IFG. Following this line of reasoning, the involvement of the IFG could be attributed to the processing of salient cues compared with less-important information (Hampshire et al., 2010). According to this hypothesis, IFG recruitment could be explained based on the relevance of good news for optimistic individuals compared with bad news.

Brain regions and optimism tasks

Despite the reduced number of studies found in this systematic review, a pattern of brain activity emerged depending on which kind of measurement of optimism was employed. When optimism was measured through the "estimation of the likelihood of possible future life events" task, participants made a deliberate estimation regarding specific future events, both positive and negative. In this paradigm, actual statistics of that event occurring to a person similar to themselves are not presented to participants—different from the belief update task. An optimistic bias for positive future events (i.e., the overestimation of positive events happening to themselves) was correlated with increased activity at ACC.

As described in section 3.4.2, in the belief update task, participants are asked to (1) make a first estimation of the probability of experiencing adverse life events, and then (2) they are exposed to the actual statistic (related to this event). Finally, (3) participants make a new estimation, in which they can update their first estimation if they wish to. We believe that the belief update task measures a different aspect of optimism, which could be considered as a "challenge" to the participant's optimistic estimation of events. Using this paradigm, different results can be expected if different task phases are evaluated. Indeed, studies measuring brain activity during the presentation of the actual statistics (the second phase as described above, considered as the estimation error) report results in the IFG, while those investigating the second estimation (the last phase, considered as the update of the estimation) report results in the ACC. In this sense, both approaches may be investigating different aspects of the same phenomena—optimism.

Other brain regions

Although ACC and IFG represented by far the main regions involved in the processing of optimism, increased activation in other brain regions also were seen (Supplementary Table S1), because optimism can be investigated in so many ways.

A frequently reported brain region is the middle temporal gyrus. Through resting state functional connectivity, Ran et al. (2017) showed that more optimistic individuals had stronger connectivity between rectus gyrus (seed region) and the middle temporal gyrus. Wu et al. (2015) reported positive correlation between a functional connectivity index (including middle temporal gyrus) and optimism. Using the belief update task, Kuzmanovic et al. (2016) assessed brain activity when participants updated their estimation and found a negative correlation between activity in the middle temporal gyrus and the update for desirable estimations (i.e., when the actual statistic was lower than the first estimation)—the greater was the activity in the middle temporal gyrus, the smaller was the size of update for desirable estimations. Garrett et al. (2014) assessed brain activity during the confrontation with the actual statistics (estimation error) and found a positive correlation between activity in the middle temporal gyrus and undesirable estimation. These results are in line with the evidence of the anterior portion of middle temporal gyrus as a critical part of the Default Mode Network (Xu et al., 2016, 2019). Additionally, as shown by Stawarczyk & D’Argembeau (2015), the middle temporal gyrus is involved in tasks involving episodic future thinking—a concept embedded in optimism.

Another often reported brain region is the superior frontal gyrus (SFG). Sharot et al. (2011) reported positive correlation between SFG activity and desirable estimation. Kuzmanovic et al. (2018) found a positive correlation with the connectivity strength between rectus gyrus and SFG while participants updated their estimations. According to Li et al. (2013), part of the SFG is connected anatomically with ACC, and functionally correlated with the Default Mode Network, which suggests that SFG is embedded in a network involved with self-referential processing. Indeed, the results from Wu et al. (2015) corroborate this idea, in which they showed that highly optimistic individuals present higher activity in brain areas, including the SFG when thinking spontaneously.

Optimism and positive health outcomes

The elucidation of the neural substrates of optimism may enlighten our understanding of the link between optimism and the positive impact it has on the lives of human beings. Optimism has been associated with numerous positive outcomes—increased longevity and physical health being the most important ones (Boehm et al., 2018; Giltay et al., 2004; Ho et al., 2010; Rasmussen et al., 2009). Optimism was shown to promote mental and physical health and well-being (Scheier et al., 1989; Scheier & Carver, 2018), and greater meaning in life (Ho et al., 2010). It also is associated with improved mood and better immune responses to stress (Nes & Segerstrom, 2006; Segerstrom et al., 1998).

An optimistic view of life and one’s ability to cope under stress may lead to overall positive coping, such as implementing appraisal strategies, reframing, and reasoning to alter perception. In fact, trait optimism was strongly correlated with positive coping styles (Hatchett & Park, 2004). Importantly, Holz et al. (2016) reported a correlation between positive coping styles and the volume of ACC. The strongest brain-behavior correlation was for positive self-instructions, followed by denial of guilt. As pointed by the authors, the direction of this relationship cannot be assertive, which means that it is not possible to infer causality. One possibility is that thinking about positive events and not thinking about negative ones are incentives in themselves, thus maintaining these processes (Krizan & Windschitl, 2007). The occurrence of habitual positive coping styles/optimistic views could lead, in time, to a higher ACC volume.

Additionally, optimism was positively correlated with heart rate variability (Oveis et al., 2009)—considered as an index of cardiac vagal tone, which reflects the parasympathetic modulation over the heart (Laborde et al., 2017; Task Force of The European Society of Cardiology and The North American Society of Pacing and Electrophysiology, 1996). It is well-established that reduced HRV is associated with higher psychosocial stress and an increase in a range of risk factors for cardiovascular diseases and mortality (Kemp & Quintana, 2013; Thayer et al., 2010), leading some authors to propose HRV as a biomarker for healthy adaptations to environmental challenges (Carnevali et al., 2018; Perna et al., 2020; Thayer et al., 2012). Also important, converging neuroimaging, neuropsychological, physiological, and clinical findings has highlighted positive correlations between HRV and activity in the ACC (Matthews et al., 2004; Thayer et al., 2012). However, more studies are needed to investigate the link between optimism - ACC - HRV more directly.

The link between positive emotional states and physical, psychological, intellectual, and social resources was described in detail in a series of studies by Barbara Fredrickson, including the buffering (“undoing”) effect of positive emotions against the negative consequences of stress (Fredrickson, 2001, 2003; Fredrickson et al., 2003; Fredrickson & Joiner, 2002). This better adaptation to stress could reduce the allostatic load, diminishing the negative impact of chronic stress on peripheral organ systems (McEwen, 2016), and potentially account for the positive impact of optimism on physical health and longevity.

Clinical implications

Recent evidence reveals a strong association between optimism and positive physical (Carver et al., 2010; Kim et al., 2017; Kress & Aue, 2017; Rasmussen et al., 2009; Rozanski et al., 2019; Scheier & Carver, 2018) and mental health

outcomes (Gallagher et al., 2020; Prati & Pietrantonio, 2009). Despite some evidence of a trait-like personality feature, psychological interventions can in fact increase optimism (Kress & Aue, 2019; Malouff & Schutte, 2016), with measurable positive effects. For example, the induction of a transient experimental increase in optimism significantly eliminated the negative influence of pain over the performance of an executive functioning task (Boselie et al., 2014). For trauma-exposed individuals, optimism has a protective role; higher levels of optimism are associated with reduced expression of numbing, avoidance arousal, and dysphoric arousal symptoms over time (Birkeland et al., 2017).

Therapeutic modalities designed to increase optimism, such as the “Best Possible Self Intervention” (Meevissen, 2011), should be considered as target interventions for both treatment of physical and mental health disorders and prevention of maladaptive responses to stress especially in individuals (e.g., health or police workers), who are at increased risk to develop mental disorders. This approach, combined with neuroimaging, could provide robust evidence about its effectiveness based on its neurobiological substrates. Neurofeedback targeting brain regions involved in the processing of optimism also could help to clarify the link between optimism and brain functioning, despite the utility of this technique in therapeutic scenarios are still in the early stages.

Limitations

There are some limitations to consider. Different measures of optimism were pooled together, which could contribute to many “disparate” regions. Additionally, in the present systematic review, we did not include studies that explored other-related optimistic estimates (Dricu et al. (2020) and Moser et al. (2020)). Because the number of studies is small, the inclusion of those studies would add even more variability to the results.

Most of the fMRI studies included in the present review assessed samples with less than 30 participants, which could increase variability and reduce statistical power (Szucs & Ioannidis, 2020). Most of the results reported here are correlational in nature and thus do not support conclusions about causality. Finally, the limited number of studies in this field precludes a meta-analytic approach, which means that conclusions should be drawn with caution.

Conclusions

The present systematic review reveals neural correlates of optimism based on 14 neuroimaging studies. The results indicate that two key brain areas are linked to optimism:

The ACC, involved in imagining the future (Benoit & Schacter, 2015; Bertossi et al., 2016; Schacter et al., 2007) and processing of self-referential information (D’Argembeau, 2013; Herold et al., 2016; Northoff et al., 2006; Spreng et al., 2009; van der Meer et al., 2010); and the IFG, involved in response inhibition (Aron, Robbins, et al., 2004; Chikazoe et al., 2007; Swick et al., 2008) and processing relevant cues (Hampshire et al., 2010). To the best of our knowledge, this is the first review to systematically summarize the current literature on the neuroimaging of optimism.

One goal of the present review is to encourage research on the interplay of optimism and neuroimaging, giving substrates for the development of reliable biomarkers. More studies in this field will allow meta-analytic approaches, providing more accurate mapping of the dynamics of brain networks associated with optimism and its positive health outcomes.

In summary, monitoring of ACC activation during psychological, pharmacological, and neurofeedback interventions directed to enhance optimism could be a useful biomarker to evaluate treatment responses and to open new pathways of treatment for many psychiatric conditions.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.3758/s13415-021-00931-8>.

Funding This work was supported by the National Council for Scientific and Technological Development (CNPq), the Carlos Chagas Filho Foundation of Research Support in Rio de Janeiro (FAPERJ), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES - Finance Code 001), and Financiadora de Estudos e Projetos (FINEP - Apoio Institucional 03/2016 - Ref 0354/16).

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