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Review article

Alterations in EEG functional connectivity in individuals with depression: A systematic review

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ABSTRACT

The brain works as an organised, network-like structure of functionally interconnected regions. Disruptions to interconnectivity in certain networks have been linked to symptoms of depression and impairments in cognition. Electroencephalography (EEG) is a low-burden tool by which differences in functional connectivity (FC) can be assessed. This systematic review aims to provide a synthesis of evidence relating to EEG FC in depression. A comprehensive electronic literature search for terms relating to depression, EEG, and FC was conducted on studies published before the end of November 2021, according to PRISMA guidelines. Studies comparing EEG measures of FC of individuals with depression to that of healthy control groups were included. Data was extracted by two independent reviewers, and the quality of EEG FC methods was assessed. Fifty-two studies assessing EEG FC in depression were identified: 36 assessed resting-state FC, and 16 assessed task-related or other (i.e., sleep) FC. Somewhat consistent findings in resting-state studies suggest for no differences between depression and control groups in EEG FC in the delta and gamma frequencies. However, while most resting-state studies noted a difference in alpha, theta, and beta, no clear conclusions could be drawn about the direction of the difference, due to considerable inconsistencies between study design and methodology. This was also true for task-related and other EEG FC. More robust research is needed to understand the true differences in EEG FC in depression. Given that the FC between brain regions drives behaviour, cognition, and emotion, characterising how FC differs in depression is essential for understanding the aetiology of depression.

1. Introduction

The brain is a network of functionally interconnected regions. Connections between regions can be quantified based on the relationships between patterns of activity (haemodynamic or electromagnetic) generated by separate brain regions, which vary across time. The synchronised activity of certain brain regions is believed to form "networks" of activity, and the activity of these networks is believed to underpin distinct behaviours, cognitions, and mood states (Anderson et al., 2016). There are three ways in which these connections are defined: structural connectivity, effective connectivity, and functional connectivity (FC). FC is defined as statistical dependencies or associations between one signal, in relation to another signal, recorded concurrently (Sakkalis, 2011; H.E. Wang et al., 2014; L. Wang et al., 2014). While structural connectivity examines anatomical connections, FC is based on patterns of activity between brain regions. Effective connectivity on the other hand, can be based on patterns of activity or anatomical connections between brain regions; however, it is directional, and can thus assess the causal relationships between regions (Sakkalis, 2011).

Commonly, connectivity/FC is measured via functional Magnetic Resonance Imaging (fMRI) which assesses brain activity with the timescale precision of seconds (Hall et al., 2016). Human cognitions and emotions are produced on the scale of hundreds of milliseconds (~10th of a second; Hari and Parkkonen, 2015; da Silva, 2013); therefore, techniques with higher temporal resolution are likely to provide useful information not available with fMRI measures. Electroencephalography

Abbreviations: EEG, Electroencephalography; FC, Functional connectivity; MDD, Major depressive disorder; HC, Health controls.

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(EEG) on the other hand, is a technique that can measure ongoing electrical activity with millisecond precision (Jackson and Bolger, 2014; Michel, 2009). EEG FC measures aim to identify statistically significant synchronisation between the signals obtained from two (or more) EEG scalp electrodes. Recent evidence has suggested that EEG and fMRI measure different aspects of FC and therefore any comparisons between the two techniques may not be accurate (Nentwich et al., 2020). As such, this paper will focus solely on EEG and the conclusions around cognition and depressive neurophysiology that come about from EEG.

Physiologically, EEG is believed to arise from post-synaptic potentials (Hall et al., 2014), and EEG FC is believed to be greatly influenced by white matter myelinated cortico-cortical axons (Katznelson, 1981; Nunez and Srinivasan, 2014; Nunez et al., 2015; Braitenberg and Schüz, 2013). Myelin is believed to control the speed of action potentials (and thus, the release of neurotransmitters at synapses), as well as the synchronous communication between proximal and distant cortical regions, which is crucial for optimal mental performance (Nunez et al., 2015). As a result, the brain is believed to have varying "myelin" strengths, in addition to a broad range of distances for brain signals to travel, with varying axon speeds between pairs of cortical locations (to ensure all signals – proximal or distal – reach the same target site at the same point), the interactions between these factors are suggested to be what produces the broad range of brain frequencies (Nunez et al., 2015). Indeed, the global oscillation frequencies, which are a product mainly of axon delays, can exert a top-down modulatory influence on local networks (Nunez, 1989; Nunez et al., 2015; Nunez and Srinivasan, 2010; Nunez and Srinivasan, 2014), thus providing a global binding mechanism in addition to local/regional binding.

EEG FC studies have further demonstrated that source EEG estimates across all frequency bands can partially predict both direct and indirect white matter connectivity (Chu et al., 2015). Further, studies have noted that when structural (white matter) support is absent (i.e., in the form of a lesion), FC is significantly reduced for high frequency bands compared to low frequency bands (Nunez et al., 2015). This dependence of FC on structural support for the coupling of higher frequency brain activity makes clear how the brain's underlying anatomy directly shapes emergent brain dynamics at fast time scales and across distances.

Indeed, EEG FC measures like narrow band alpha and theta coherence have been proposed to be linked to cortico-cortical axon propagation (i.e., propagation time which appears to be critical in ensuring synaptic signals arrive simultaneously at a target brain region; Nunez et al., 2015). Overall, propagation times have been suggested to have important implications for diagnosis and treatment of brain disorders (Fields, 2008; Fields, 2015). Indeed, a broad range of psychiatric disorders, including schizophrenia, chronic depression, bipolar disorder, have been associated with white matter defects (Bracht et al., 2015; Kanaan et al., 2017; Sussmann et al., 2009). If, as research suggests, white matter connections are one of the key drivers of EEG FC, then changes to EEG FC in individuals with brain disorders or psychiatric conditions that affect white matter connectivity could be observed.

EEG has been widely used to assess FC in depression, however, no systematic account of these differences exists to date. Thus, the nature of EEG FC alterations in depressed versus healthy individuals remains unclear. This systematic review aimed to assess studies comparing healthy individuals' EEG FC to that of individuals with depression. With the four elements outlined here: (1) individuals with depression as the population of interest (P); (2) brain activity via EEG as the methodology of observation (I); (3) healthy individuals as a comparison group (C); and (4) changes in FC as a specific outcome of interest (O), our review met the PICO framework for a clear and focused research topic/question (Huang et al., 2006).

After a preliminary review of the literature, it was apparent that large variability was present in the methods used to study EEG FC measures in depression, making assessment of the quality of included studies difficult, and evaluation of the consistency of findings across different methodologies complicated. To address this issue, concurrent with the present review, we developed a novel checklist to allow for quantification of the quality of EEG studies accounting for important methodological variables relevant to FC assessment (Miljevic et al., 2021), and implemented this checklist in the current review assessing EEG FC differences in depression.

2. Methods

2.1. Protocol and search strategy

This systematic review was performed according to PRISMA Guidelines (Moher et al., 2009; Page et al., 2020). A comprehensive electronic literature search was performed in Medline and Embase via Ovid, Scopus, and Web of Science. Keywords used for the search are provided in supplementary material Table S1. A combination of title, abstract, keywords and database trees (where terms are organised by broader and narrower headings, and the broader subject headings will retrieve most associated synonyms, i.e., narrower headings for the entered terms), were used to find papers from which more key search terms were derived. These key search terms were then adapted to the requirements of each database.

The final search was run in November 2021. Following this, titles and abstracts were independently assessed against the selection criteria. Further, reference lists of potentially eligible articles were checked for missing studies. In the instances that it was unclear if an article met the inclusion criteria, reviewing authors (AM and MPNP) conferred and examined the full-text article. All studies were assessed for inclusion and exclusion according to the PICO framework highlighted in the introduction. A summary of the PICO inclusion/exclusion process and a list of the articles that were double-checked are depicted in Supplementary Table S2. Lastly, full texts of selected articles were examined and summarised for the purposes of this paper (Table 1).

2.2. Selection and inclusion criteria

Peer-reviewed journal articles, preprints, and grey literature published in English from 2000 to November 2021, were examined for inclusion. Studies were required to compare EEG FC between individuals with depression and healthy controls (HCs).Conference paper articles were included given the usefulness of the data for this review. All studies were required to include at least a baseline EEG recording (where no treatment for depression had been applied) and comparison of baseline EEG FC between healthy and depressed individuals. Case studies or case series were excluded, due to small sample size and the potential lack of reliability/general applicability of their findings. Studies with samples of individuals with postpartum depression or a primary diagnosis other than depression or severe comorbidities such as stroke, substance abuse, dementia, and schizophrenia were excluded. Additionally, studies from whom the full text was not able to be obtained or was not available in English were not included.

Further, our laboratory has previously published results on differences within three independent samples of participants on EEG measures taken before participants received any treatment: responders, non-responders, and healthy controls (Bailey et al., 2018). The primary author of that study (NWB) conducted FC analyses on the depressed sample versus the healthy controls (unpublished p values are included in summary Table 3). Fig. 1 depicts PRISMA study selection process.

In addition, to facilitate the transparent, accurate and complete presentation and standardised reporting of the current systematic review, a completed 2020 PRISMA checklist (Page et al., 2020) can be found in Supplementary Table S3.

2.3. Study quality assessment

As highlighted and explained in Miljevic et al. (2021), the interpretation and comparability of EEG FC results is greatly confounded by the

Table 1
A definition of power-based and phase-based measures, and brief summaries of EEG connectivity metrics used in identified articles.

Connectivity measure categories	Measure summary/definition
Power-based connectivity measures	Power-based connectivity measures first convert the EEG signal into the time-frequency domain, then assess whether there is a relationship in the changes to power of a specific oscillation between two different electrodes or brain regions (Cohen, 2014).
Phase-based connectivity measures	Phase-based connectivity measures assess whether the phase angle of voltage shifts is related between two electrodes or brain regions (Cohen, 2014).

Connectivity measure	Studies using the measure	Measure summary/definition
Magnitude Squared Coherence (Coh)	Ahn et al., 2017; Knott et al., 2001; Leuchter et al., 2012; Li et al., 2017; Li et al., 2016; Markovska-Simoska et al., 2018; McVoy et al., 2019; Orgo et al., 2017; Park et al., 2007; Suhhova et al., 2009; Sun et al., 2019	Coh is a widely used measure of connectivity. It was developed to quantify the linear relationship between two signals (Bakhshayesh et al., 2019). Coh allows for these relationships to be measured in different frequency domains, making it sensitive to both changes in power and phase relationships. Coh is generally represented as an estimate between 0 (no linear relation) and 1 (maximum linear relation). Coh only gives information on the stability of relationships and does not give information on the directional, true nature of a noted relationship (Sakkalis, 2011). Coh is sensitive to volume conduction (VC) which can increase the Coh values especially in electrodes that are close to one another (Khadem and Hossein-Zadeh, 2014; van Diessen et al., 2015). This is also because Coh is sensitive to both changes in power and phase relationships and the strength of signals can distort its synchronisation measurements at the scalp-level, depending on the relative powers of the sources (Dominguez et al., 2007; Schoffelen and Gross, 2009). The dipolar nature of neural activity can create spurious connectivity at electrodes which detect activity from distant sources due to VC (Dominguez et al., 2007), blurring phase estimates obtained in Coh, increasing false identification of connectivity, and decreasing the accuracy of interpretation.
Imaginary Coherence (iCoh)	Sun et al., 2019	iCoh uses the same basic principle as Coh. However, it eliminates all sources of instantaneous activity leaving only the "imaginary" values which are thought to reflect true source interactions at a given lag time (Nolte et al., 2004). Thus, the measure is made to be insensitive to volume conduction.
Partial Directed Coherence (PDC)	Damborská et al., 2020; Sun et al., 2008, 2011	Partial coherence quantifies the relationship between two electrodes, while avoiding the effects of volume conduction. PDC measures the directional influence of this relationship. PDC ranks the relative strength of causal interactions with respect to the given electrodes while fulfilling the statistical assumption for normality. PDC avoids the effect of volume conduction by subtracting the recorded activity of neighbour electrodes that may be contributing to the shared activity at the two electrodes of interest. It is reasoned that the coherence left behind by this subtraction is the true activity between the two electrodes, that cannot be accounted for by the activity recorded by neighbour electrodes (Cohen, 2014; Joffe, 2008).
Correlation coefficient (Pearson's; Corr)	Holmes and Pizzagalli, 2008; Knyazev et al., 2018; Sun et al., 2019; Zhang et al., 2018	Corr is a power-based connectivity measure which assesses linear synchrony or quantifies the linear correlation between two time-series signals. The measure is sensitive to volume conduction and the violation of the assumption of normality. However, power data is non-normally distributed so outliers significant inflate or deflate the result (Cohen, 2014). When using this measure data needs to be inspected carefully for normality violations and/or outliers.
Amplitude envelope correlation (AEC)	Benschop et al., 2021	Similar to Corr, AEC assesses amplitude envelopes which are energy fluctuations in oscillations over time, thus the measure assesses the degree to which the two envelope fluctuations are temporally correlated.
Synchronisation likelihood (SL)	Fogelson et al., 2020; Leistedt et al., 2009; Orgo et al., 2016; Park et al., 2007	SL describes dynamic interdependencies or how strongly one channel is synchronised to all the other channels. SL detects both linear and non-linear dependencies. The basic principle of SL is that time series are divided into series of patterns, the recurrence of which is then searched for. Then the SL is the chance that the pattern recurring in one time series signal will coincide with patterns recurring in a second signal under investigation. The measure can be computed for each time sample thus it is able to track time-dependent changes of

(*continued on next page*)

Table 1 (*continued*)

Connectivity measure	Studies using the measure	Measure summary/definition
		the synchronisation level (Stam and Van Dijk, 2002). SL is often used in conjunction with graph theory analyses to identify networks.
Phase synchronisation	Aiba et al., 2019; Lagged-phase synch: Olbrich et al., 2014; Whitton et al., 2018	Phase synchronisation measures for similarities in phase between two times-series independent of their amplitude. To avoid the effects of volume conduction, the method can be lagged or biased away from zero phase synchronisation (Pascual-Marqui, 2007). The lag between the electrodes is not important for this measure rather, the consistency across time in the phase lag is what matters.
Phase locking value (PLV)	Sun et al., 2019	PLV assesses the significance of the phase covariance between two signals and depends on the instantaneous phase of the signals. It can separate the phase and amplitude components (Lachaux et al., 1999). PLV first requires filtering data in the frequency of interest and then extracting instantaneous phase via Hilbert transformation. The measure depends on the assumption that regions of connectedness have a constant phase difference, which may not be the case. Further, given that the measure depends on instantaneous phase, this makes it more vulnerable to the effects of volume conduction (Lachaux et al., 1999).
Phase lag index (PLI)	Iseger et al., 2017; Sun et al., 2019	PLI measures the extent to which a distribution of phase angles is pointing towards positive or negative sides of an imaginary axis. It is expected that positive connectivity measures that are not affected by volume conduction will predominantly be on one side (positive or negative) of the axis, away from 0. Volume conduction affected measures on the other hand, are known to be distributed around 0 (Stam et al., 2007). PLI underestimates the connectivity at small time lags and low signal-to-noise ratio. Frequency non-stationarities are a common issue for measures such as PLI - if there is a mismatch in the frequency of oscillation between the two sources, then the distribution of the phase differences will fluctuate around 0 which will naturally cause PLI give a value of 0 (Stam et al., 2007).
Weighted phase lag index (wPLI)	Bailey et al., 2017, 2018	wPLI is an extension of PLI where angle differences are weighted according to their distance from 0 so that vectors further away from 0 have a larger influence on the estimates of connectivity (Vinck et al., 2011). PLI is positively biased, so wPLI was developed as a de-biasing tool. Thus, wPLI is a conservative measure of phase synchronisation between two channels. wPLI has the advantage of robustness against the effects of volume conduction, an artefact that is unrelated to brain activity, and common reference activity. This is thought to be the case because time lags of near zero contribute minimally to the wPLI measure, thus preventing the detection of false positive connectivity due to the aforementioned artefacts and the described mismatch in the frequency of oscillations between the two sources, which is an influencing factor on the PLI (Vinck et al., 2011).
Operational synchrony/ Structural Synchrony Index (SSI)	Fingelkurts and Fingelkurts, 2017; Fingelkurts et al., 2007	Operational synchrony/SSI identifies rapid transition periods (RTPs) in the electrode's signals. Where RTPs occur in the same time window across pairs of electrodes being compared, and if they meet certain criteria (above a pre-determined threshold) of statistical significance, the RTPs and EEG segments are said to be coupled. Thus, synchronisation of brain operations is occurring (Fingelkurts et al., 2005; Fingelkurts et al., 2007). The measure assesses brain connectivity according to 9 categories: short left/right, short anterior/posterior, long left/right, long anterior/ posterior, long interhemispheric. The authors propose that operational synchrony controls for volume conduction because it specifically identifies RTPs in the EEG trace, according to strict requirements within specific time-windows of the time-series (for more detail see Fingelkurts et al., 2007).
Dynamic Time Warping (DTW)	Guo et al., 2018	DTW warps the path of comparison between voltage points, rather than comparing signals based on time (i.e., the straight-line distance between two points in time, known as Euclidean distance). Rather DTW compares points that are most likely to fit with one another. This is achieved by creating a matrix and finding the shortest points form one point to the other through the

(*continued on next page*)

Table 1 (*continued*)

Connectivity measure	Studies using the measure	Measure summary/definition
		matrix (Dinov et al., 2016). Because the measure does not use Euclidean distance it limits the incorrect comparison of signals that are out of phase.
Phase transfer entropy (PTE)	Hasanzadeh et al., 2020	PTE is a measure of directed phase interactions. The measure quantifies the transfer entropy (which estimates whether including the past of both source and target time-series influences the ability to predict the future of the target time-series) between phase time-series extracted from neuronal signals by filtering for instance (Lobier et al., 2014). PTE is model-free in so far as it makes no assumptions on signal or interaction structure. PTE may be computed across collapsed trials as well as across continuous data, using a simple binning method for state-space reconstruction.

Note. Phase synchronisation and amplitude correlations are functionally independent phenomena which reveal distinct neuronal networks (Cohen, 2014).

wide variety of methodological steps undertaken and the choices made between methodological options, which commonly vary between studies. Different methodological approaches have been demonstrated to vary in their ability to control false positives and false negatives, and as such can be used to assess the quality of the study against a checklist (Miljevic et al., 2021). Thus, we applied the EEG FC checklist to assess the quality of the identified studies, this evaluation of included studies according to the checklist is presented in Supplementary Table S4; authors AM and MPNP applied the checklist independently, which were combined to provide each study a final quality rating (QR).

Briefly, the checklist assessed studies based on the following six criteria: 1) the EEG reference montage used (which can artificially inflate FC if an inferior reference montage is chosen, as the signal at all electrodes is simultaneously influenced by the reference signal); 2) the length of EEG epochs used to compute FC measures (short epochs can produce less reliable measures of FC, especially in lower frequencies); 3) the number of epoch used to compute FC (a higher number produces a more robust estimate); 4) which EEG artefact rejection methods were applied (these can artificially inflate FC measures without actual neural FC being present); 5) the controls implemented for the volume conduction (VC) of EEG signal (which can artificially inflate FC as the signal at all electrodes is almost simultaneously influenced by the same signal from a single underlying source); 6) which multiple comparison controls were used (which are generally essential in FC research, as statistical comparisons can be performed on every pair of electrodes, so comparisons can number in the 1000's), *or* if a FC network metric was used, studies were judged not on multiple comparison controls but on the quality of threshold setting (i.e., if arbitrary or if data-driven/weighted; where the former is not preferred as it is based on subjectivity, which can produce more biased and non-replicable findings).

Following assessment of the individual steps, a cumulative score was calculated based on how many of the checklist criteria each study met. Studies were then assigned a QR of 1 for high quality, 2 for moderate quality, and 3 for low quality. For specific details for each of these steps and the final scoring, please see the checklist development article (Miljevic et al., 2021). Application of this checklist enabled the current review to categorize findings with confidence, based on the quality of the studies supporting each finding.

3. Results

3.1. Summary of study characteristics

A total of 52 studies were identified: 36 assessed differences between a depressed and HC group in resting-state EEG FC and 16 assessed differences in task-related and '*other*' FC, including sleep or pain-related EEG FC (summarised in the Supplementary Materials due to significant inconsistency in results and methods leading to limited discussion and interpretation). Overall, six of the studies assessed un-medicated individuals with depression and one assessed an adolescent sample, while the rest of the studies assessed a mix of medicated and unmedicated individuals with depression or included only medicated participants. Most of the research articles included samples of individuals diagnosed with Major Depressive Disorder (MDD) following standardised criteria using the Diagnostic and Statistical Manual of Mental Disorders (American Psychiatric Association, 2013), or the International Classification of Disease (World Health Organization, 2015). Five studies, however, did not disclose the relevant information as to diagnosis: thus, participants in these studies are referred to as simply as depressive disorder (DD). As such, the terms 'depression' and 'MDD' will be used to denote separate meanings; '*depression*' will be used as a general term encompassing all studies that assessed aspects of depression, depressive symptoms, and depressive severity. Whereas '*MDD*' will be used to refer to specific the specific studies where a clinical diagnosis for was implemented.

A further two studies assessed populations of remitted MDD (rMDD) individuals. Whitton et al. (2018) included both HC and MDD groups with a third rMDD group, thus making the study eligible for consideration. However, Benschop et al. (2021) only assessed rMDD and HC individuals and were thus not included.

Several publications assessed FC using the same sample population as other studies included in the review but using different analytic approaches: Sun et al. (2008, 2011) used the same participant sample and FC measure in both studies, however the 2011 study included extra steps for control of VC; Khadem and Hossein-Zadeh (2014) and van Diessen et al. (2015), used the same participant sample but assessed a different frequency in each study. Fingelkurts et al. (2007) and Fingelkurts and Fingelkurts (2017) also used the same participant sample and measure in both studies; however, the 2007 paper assessed alpha and theta frequency differences across the whole EEG montage, whereas the 2017 study assessed only alpha frequency for nine DMN-specific channel locations, to determine if DMN activity specifically could be used to distinguish between MDD and HC groups. Lastly, Orgo et al. (2016, 2017) used the same participant sample but two different FC measures in each of the studies and maintained the same findings for theta and alpha differences across the two. The impacts of these differences in methodologies on the results are discussed specifically in each of the relevant sections.

Eleven different methodologies or techniques for assessing EEG FC were identified across all the studies, these are summarised in Table 1. Table 1 also provides brief definitions of power versus phase -based FC estimates, which are important for understanding EEG FC measures and their discussion. The most common measure of FC across the studies was Coherence (Coh), a non-directional (functional) FC measure based on correlations, which does not control for the effects of VC (Bastos and Schoffelen, 2016; Sakkalis, 2011). Additionally, a variety of EEG acquisition methods, processing steps, statistical methods and analyses methods were used. Furthermore, a variety of different cognitive tasks were employed in the task-related studies. As such, there was a high degree of variability in methods across study parameters (all study characteristics and results are summarised in Table 3).

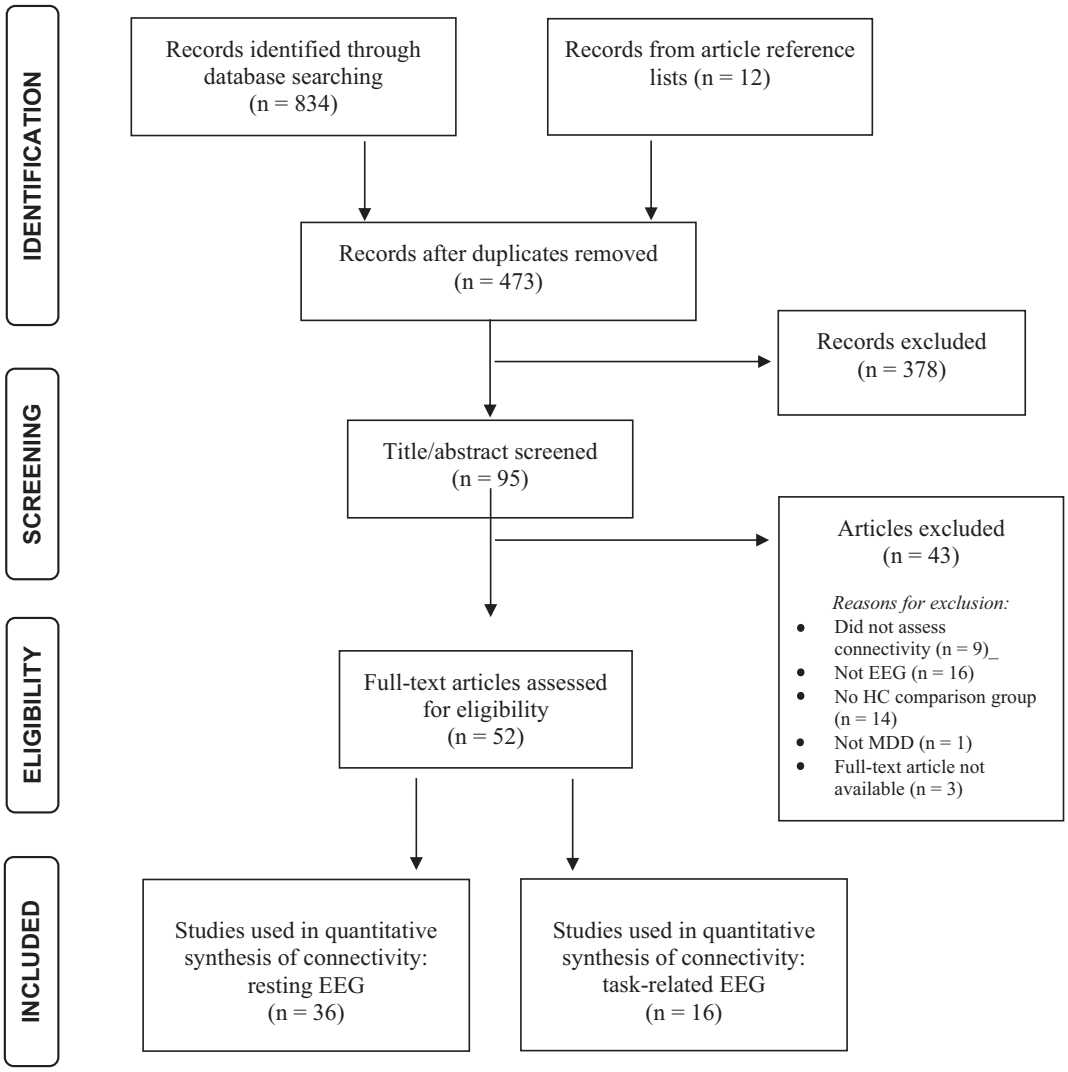

Fig. 1. PRISMA diagram of the study selection process.

3.2. Resting-state EEG FC findings and study quality

A total of 36 studies assessing resting-state FC were identified (all study information and findings are summarised in Table 2). Most studies (N = 31) assessed resting-state while the participants kept their eyes-closed. While assessing EEG FC, three studies did not discuss specific frequency related findings, and only mentioned general trends of higher brain FC in individuals with depression with no significance values reported (Khan et al., 2021; Movahed et al., 2021; Sun et al., 2020). We note these studies here but do not include them in the breakdown of the findings by EEG oscillation frequencies below.

The identified studies were assessed according to the checklist criteria briefly outlined in Section 2.3 of the Methods and explained in detail in Miljevic et al. (2021). The QRs are included in the study summary Table 2 (and for task-related and other studies in Supplementary Table S5). Of the identified studies, only two met the highest level of quality (QR 1): Fingelkurts and Fingelkurts (2017), and Fingelkurts et al. (2007). Further, three studies met a QR of 2: Khan et al. (2021), Movahed et al. (2021), and Sun et al. (2019). Unfortunately, several studies did not report sufficient detail to determine the QR for specific methodological aspects and were by default awarded a QR 3 (worst score). Overall, the three criteria that were the least reported overall across the studies were epoch number, epoch length, and re-reference choice.

A more accessible summary of the number and studies that noted differences at each of the frequencies is presented in Table 2, a full summary including methodological details, results, and quality-ratings can be found in Table 3.

3.2.1. Alpha EEG FC differences

The alpha frequency band (oscillations between ~8–13 Hz) was among the most commonly investigated oscillatory frequency, with 24 studies examining alpha FC. Most studies found higher alpha FC in depression (Table 2), including the only study with a QR of 1 which investigated alpha FC (Fingelkurts and Fingelkurts, 2017). Further, inspection of the results based on regions revealed an interesting trend for individuals with depression, where higher alpha FC was evident between all frontal sites specifically (i.e., Duan et al., 2020; Khan et al., 2021). This was especially apparent in studies where FC was assessed at pre-determined frontal sites (Aiba et al., 2019; Del'Acqua et al., 2021; Olbrich et al., 2014; Fingelkurts and Fingelkurts, 2017; Zhang et al., 2021), and where source localisation techniques were used (mathematical estimation or prediction of the origins of a particular signal within the recorded EEG activity, for a review see Jatoi et al., 2014). Additionally, lower alpha FC was commonly found between parieto-occipital regions (Hasanzadeh et al., 2020; McVoy et al., 2019).

Further, the studies that assessed alpha FC globally reported most of the non-significant results (Bailey et al., 2018; Li et al., 2017). This

Table 2
Summary of connectivity differences and the number of studies noting differences across the five EEG frequencies.

	Alpha	Theta	Beta	Delta	Gamma
Total studies	24	24	17	13	5
High connectivity observed in MDD	10 Aiba et al., 2019; Damborská et al., 2020; Del'Acqua et al., 2021; Duan et al., 2020; **Fingelkurts et al., 2007; Fingelkurts et al., 2017** [counted as one]; Leuchter et al., 2012; Markovska-Simoska et al., 2018; Olbrich et al., 2014; Orgo et al., 2016, 2017 [counted as one]; Zhang et al., 2021	8 Damborská et al., 2020; Del'Acqua et al., 2021; **Fingelkurts et al., 2007**; Hasanzadeh et al., 2020; Leuchter et al., 2012; Li et al., 2017; Orgo et al., 2016, 2017 [counted as one]; Zhang et al., 2021	6 Duan et al., 2020; Hasanzadeh et al., 2020; Knyazev et al., 2018; Leuchter et al., 2012; Markovska-Simoska et al., 2018; Whitton et al., 2018	1 Leuchter et al., 2012	–
Low connectivity observed in MDD	8 Hasanzadeh et al., 2020; Imperatori et al., 2019; Knott et al., 2001; McVoy et al., 2019; Park et al., 2007; Sun et al., 2011, 2019 [when CST used]; Zhang et al., 2018	5 Ahn et al., 2017; Iseger et al., 2017; Knott et al., 2001; McVoy et al., 2019; *Sun et al., 2019* [both when CST and MST assessed]	3 Knott et al., 2001; McVoy et al., 2019; Sun et al., 2008	5 Hasanzadeh et al., 2020; Knott et al., 2001; Markovska-Simoska et al., 2018; McVoy et al., 2019; Park et al., 2007	–
No differences observed in connectivity in MDD	5 Bailey et al., 2018; Iseger et al., 2017; Knyazev et al., 2018; Li et al., 2017; Whitton et al., 2018	9 Bailey et al., 2018; Duan et al., 2020; Hill et al., 2021; Knyazev et al., 2018; Markovska-Simoska et al., 2018; Olbrich et al., 2014; Park et al., 2007; Suhhova et al., 2009; Whitton et al., 2018	6 Damborská et al., 2020; Hill et al., 2021; Li et al., 2017; Olbrich et al., 2014; Park et al., 2007; Suhhova et al., 2009	4 Damborská et al., 2020; Knyazev et al., 2018; Olbrich et al., 2014; Whitton et al., 2018	4 Knyazev et al., 2018 Park et al., 2007; Whitton et al., 2018
Studies with non-specified differences/ inconsistent findings	–	2 *Movahed et al., 2021*; Sun et al., 2020	2 Sun et al., 2020/Orgo et al., 2016, 2017 [counted as one due to use of same sample but 2016 notes no differences using SL, 2017 noted higher using Coh]	3 *Movahed et al., 2021*; Sun et al., 2020/Orgo et al., 2016, 2017 [counted as one due to use of same sample but 2016 notes no differences using SL, 2017 noted higher using Coh]	1 Orgo et al., 2016, 2017 [counted as one due to use of same sample but 2016 notes no differences using SL, 2017 noted higher using Coh]

Note. Level 1 quality studies (higher quality) are presented in bold and underlined; Level 2 (medium quality) quality studies are presented in italics and underlined; all other studies are Level 3 (lowest quality). The 24th study by Khan et al. (2021), was a level 2 quality study that specified that individuals with MDD had significantly higher connectivity in DMN nodes, but did not give an indication for what frequency these changes are observed.

pattern was also present within the studies that assessed alpha FC both globally and between pre-determined electrode pairs, for example McVoy et al. (2019) found significantly higher FC in MDD at electrode pairs (F7-P7 and T8-P8), but, when "global" Coh (the averaging of FC values for one frequency across all electrode pairs) was compared between depressed and healthy volunteers, no differences were observed. This could suggest that the ways in which FC is assessed (pairs versus global activity) may result in a lower likelihood of detecting significant differences.

Of the studies that assessed alpha, those that found higher alpha in MDD did not have differences in the quality of metrics when compared to studies which found lower alpha in MDD. As can be observed, sample sizes were equal, as was the quality of FC measures, with studies in none of the 3 QRs using higher quality metrics over the other. When our synthesis was restricted to studies that scored higher quality ratings (QR of 1 or 2), the results indicated that 2 studies showed MDD had higher alpha FC while only 1 noted decreases and 2 showed null results. The selected epoch length and sample size were found to be typically greater in studies noting higher alpha as compared to studies noting lower alpha FC in MDD, however. Both epoch length and epoch number have been noted to lead to more robust FC estimates; FC values and *patterns* of activity have been shown to be better detected by longer epochs (David et al., 2004; Fraschini et al., 2016), and larger sample sizes overall are generally more robust. However, the contrasting findings do not appear to be obviously explained by differences in common methodological variables.

Different alpha band limits were used to assess FC across the different studies, which further complicated the comparability of the assessed studies, and calls for further standardization of frequency assessments. Overall, the reviewed studies demonstrate broad inconsistency in findings related to alpha FC.

3.2.2. *Theta EEG FC differences*

Theta (oscillations between ~4–8 Hz) was the other most investigated FC frequency, with 24 studies reporting theta FC related findings (Table 2). Like the alpha FC results, inspection of the results based on regions revealed an interesting trend towards individuals with depression displaying lower theta FC within frontal regions (Del'Acqua et al., 2021; Fingelkurts et al., 2007; Iseger et al., 2017; Hasanzadeh et al., 2020; McVoy et al., 2019), and higher theta FC between temporal-posterior regions (Del'Acqua et al., 2021; Leuchter et al., 2012; Orgo et al., 2016; Zhang et al., 2021).

Overall, there was considerable heterogeneity in the review findings (Table 2), and several study methodological differences can be observed; with studies finding significantly higher theta typically using higher quality methodological steps including robust FC estimates (i.e., PDC and operational synchrony) and longer epochs (Damborská et al., 2020; Orgo et al., 2016, 2017). In contrast, studies that found no differences in

Table 3
Summary of studies' analyses assessing resting-state EEG connectivity and their quality rating (n = 36).

Article	Sample	Conn. Measure	Analysis specifics	Acquisition	Artefact rejection/ reference	Epoch length & number	MCC	Results (in comparison to HCs)	QR
Ahn et al. (2017)	15 MDD, 25 HC, 15 SSD	Coh	Bivariate interactions	10 min, eyes-closed, 21 channels	Visual rejection, Mastoid reference	N/A, n = N/A	Yes	**Theta** Coh sig. ↓ T5-P3 (p = 0.0067)	3
Aiba et al. (2019)	4 DS, 16 HC	Phase synch	Bivariate interactions – eLORETA	3 min, eyes-closed, 62 channels	N/A rejection, Mastoid reference	2 s, n = N/A	N/A	**Alpha** (8–10 Hz) sig. ↑ (p = 0.036), between mPFC and PCC. No differences in alpha2 (10–13 Hz), beta1 (13–16 Hz), beta2 (16–20 Hz), beta3 (20–24 Hz), beta4 (24–30 Hz).	3
Bailey et al. (2019)	39 MDD, 20 HC	wPLI	Bivariate interactions – assessed with NBS	3 min, eyes-closed & open 30 channels	Automated then visual rejection, Average reference	2 s, n = 20+	Yes	No differences in alpha (p = 0.20) or theta (p = 0.17)	3
Damborská et al. (2020)	26 MDD, 25 HC	iPDC	Bivariate interactions – LAURA & network metrics	15 min, eyes-closed, 128 channels	Visual rejection, Average reference	2 s, n = 30	N/A	Sig. ↑ values found in MDD in network measure at 4–12 Hz (**theta** and **alpha**). At *population* level, the local efficiency measured in MDD was ↑ in all examined subcortical ROIs and at *individual* level, global efficiency was sig. ↑ ($p < 0.05$) in MDD mainly at right precentral, amygdala and caudate regions. No differences in traditional delta or beta bands found.	3
Del'Acqua et al. (2021)	26 DD, 28 HC	Phase Coh of PLV	Bivariate interactions	4 min eyes-closed, 32-channels	Visual (w/ ICA), Average reference	N/A s, n = N/A	Yes	Sig. ↑ **theta** in DD group in right frontal with central electrodes (C2 – C7, p = 0.047) and right temporal with left occipital (C4 – C5, p = 0.042), found. Also, sig. ↑ **alpha** in DD group in right and left central electrodes (C1 – C2, p = 0.010) and between frontal and central-temporal areas bilaterally (C5 – C1, p = 0.040; C6 – C2, p = 0.009; C7 – C2, p = 0.027; C7 – C6, p = 0.028) but sig. ↓ **alpha** in right frontal to temporal area (C2-C4, $p < 0.05$).	3
Duan et al. (2020)	16 MDD, 12 HC	Cross-corr.	Bivariate interactions	3 min, eyes-open, 64 channels	Semi-automated (w/ICA), Mastoid reference	1, 2, 3 s, n = N/A	No	Sig. ↑ **alpha** in all but occipital regions (C3-C4, P7-P8, AF7-AF8, AF3-AF4, TP9-TP10, F5-F6, FC1-FC2, CP1-CP2), and sig. ↑ **beta** in parietal and central regions (P1-P2, C5-C6), $p < 0.05$. No significant differences in theta.	3
Fingelkurts et al. (2007)	12 MDD*, 10 HC	Operation synch	Bivariate interactions	20 min, eyes-closed 20 channels	Automated, then visual rejection, Nose reference	1000 s, n = 233 MDD & 189 HC	Yes	Sig. ↑ **alpha and theta** in short left ($p < 0.01$) posterior ($p < 0.05$), anterior ($p < 0.001$) connections; and long left ($p < 0.05$), right, and anterior ($p < 0.05$) connections. Sig. ↑ **theta** found in long posterior ($p < 0.05$) and ↑ **alpha** in short right ($p < 0.01$) connections. DD had sig. ↑ number of connections in **alpha and theta** in short anterior ($p < 0.001$), right, left, and posterior ($p < 0.05$) connections. Sig. ↑ number of connections found in **alpha** in long posterior and ↓ number of connections observed in **theta** in long left and anterior connections ($p < 0.05$).	1
Fingelkurts and Fingelkurts (2017)	12 MDD*, 12 HC	Operation synch	Bivariate interactions – pre-determined "sub-nodes" of DMN	20 min, eyes-closed, 20 channels	Automated, then visual rejection, Nose reference	1000 s, n = 233 MDD & 189 HC	Yes	**Alpha** operational synchrony sig. ↑ within F3-Fz-F4 ($p < 0.000001$), and P3-T5-O1 ($p < 0.05$).	1
Hasanzadeh et al. (2020)	26 MDD, 23 HC	PTE	Bivariate interactions –	5 min, eyes-closed, 19-channels	Semi-automated (w/ ICA),	N/A s, n = N/A	Yes	Sig. ↑ **beta 1, 2, and 4 GE** in MDD; the strength of prefrontal nodes ↑ **in theta** band; both degree and	3

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Table 3 (*continued*)

Article	Sample	Conn. Measure	Analysis specifics	Acquisition	Artefact rejection/ reference	Epoch length & number	MCC	Results (in comparison to HCs)	QR
			using weighted network metrics		Average referenced			strength of nodes in occipital region were sig. ↓ **in alpha**; and LE ↓ but the degree and strength of nodes in occipital region ↑ **in delta** (all $p < 0.05$). **Note*. Overall, the MDD group sig. ↑ higher GE and ↓ LE.	
Hill et al. (2021)	21 MDD, 22 HC	wPLI	Bivariate interaction	10 min, eyes-closed, 64 channels	Semi-automated (w/ ICA) Average referenced	3 s, N = N/A	Yes	No significant differences between MDD & HC in theta or beta.	3
Imperatori et al. (2019)	18 DD 95 HC	LPS	Bivariate interactions – eLORETA	5 min, eyes-closed, 31 channels	Visual rejection, ICA, Mastoid reference	180 s, n = N/A	N/A	**Frontal alpha asymmetry (FAA):** Sig. ↓ FAA scores between mPFC-sgACC in DD participants, (all $p < 0.05$). **Note.* FAA calculated by subtracting lagged phase synch. Values at left ROIs from right ROIs & diving their sum (ROIs: mPFC-sgACC and mPFC-ACC).	3
Iseger et al. (2017)	447 MDD, 336 HC	PLI	Bivariate interactions – eLORETA	2 min, eyes-closed, 26 channels	N/A rejection, Mastoid reference	4 s – 50 % over, n = N/A	N/A	Sig. ↓ **theta** connections only for sgACC-lDLPFC ($p < 0.003$) and sgACC-DMPFC ($p < 0.010$). No differences in alpha	3
Khan et al. (2021)	30 MDD, 30 HC	PDC	Bivariate interactions – specified to 6 "DMN" electrodes°	5 min eyes-closed, 19-channels	Automated, Mastoid reference	2 s, n = N/A	Yes	Connectivity found to be sig. ↑ in MDD vs HC at: Fz → F3 ($p = 0.03$); F3 → F4 ($p = 0.036$); Fz → F4 ($p = 0.048$); P3 → P4 ($p = 0.028$); F3 → Pz ($p = 0.043$); P3 → Pz ($p = 0.03$); and P4 → Pz ($p = 0.03$). **Note.* No frequency specific differences were assessed or discussed.	2
Knott et al. (2001)	70 MDD*, 23 HC	Coh	Bivariate interactions	20 min, eyes-closed, 21 channels	Visual rejection, Mastoid reference	2.5 s, n = 48	Yes	Sig. ↓ coherence across all inter-hemispheric pairs (Fp1-Fp2, F3-F4, C3-C4, P3-P4, O1–02, F7-F8, T3-T4, T5-T6) in **delta** ($p < 0.0001$), **theta** ($p < 0.0001$), **alpha** ($p < 0.02$), **and beta** ($p < 0.001$)	3
Knyazev et al. (2018)	57 MDD, 36 HC	Corr – Pearson	Bivariate interactions – fMRI identified "sub-nodes" of 3	6 min, eyes-closed, 118 channels	Semi-automated rejection, Average reference	1 s, n = N/A	Yes	**Beta** connectivity sig. ↑ ($p < 0.01$) at all ROIs, including areas of the left middle frontal gyrus and left inferior frontal gyrus. No differences in delta, theta, alpha, and gamma.	3
Leuchter et al. (2012)	121 MDD*, 37 HC	Coh	Bivariate interactions – using weighted network metrics	10 min, eyes-closed, 35 channels	Semi-automated rejection, Pz reference	2 s, n = N/A	N/A	Sig. ↑ coherence in all frequencies: **beta** ($p < 0.001$, across most EEG pairs), **delta** ($p = 0.041$, mostly in frontal to temporal left regions), **theta** ($p = 0.0024$ across some EEG pairs, mostly in frontal region and around midline), **alpha** ($p = 0.017$, across all EEG pairs).	3
Li et al. (2017)	23 MDD, 15 HC	Coh	Bivariate interactions – averaged & network analyses, threshold & with MST	5 min, eyes-closed, 72 channels	Semi-automated rejection, Cz reference	N/A, n = N/A	No	Sig. ↑ global **theta** coherence, especially in the left hemisphere (parietal and temporal, and left hemisphere) (all $p < 0.05$). No differences in alpha and beta.	3
Markovska-Simoska et al. (2018)	5 DD, 10 HC 7 GAD, 10 ADHD, 3 TTH, 5 AS	Coh	Bivariate interactions – averaged	5 min, eyes- closed & open, 19 channels	Automated, then visual rejection, Mastoid reference	4 s, n = N/A	Yes	Interhemispheric: sig. ↑ **alpha** ($p < 0.01$) **and beta** ($p < 0.05$) coherence in C3-C4 electrode pairs during eyes open. Intrahemispheric: sig. ↓ **delta** in O2-P4 during eyes open ($p < 0.05$). No differences in theta.	3
McVoy et al. (2019)	24 MDD, 14 HC (Adolescent sample)	Coh	Bivariate interactions – averaged	– min, eyes-closed, 32 channels	Semi-automated rejection, N/A reference	2 s, n = N/A	No	Average **theta** coherence sig. ↓ ($p = 0.049$), also sig. ↓ in frontal-only areas ($p = 0.046$), and between P3-O1 and Fp2-F4 (p unspecified). Seven node pairs also sig.	3

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Table 3 (*continued*)

Article	Sample	Conn. Measure	Analysis specifics	Acquisition	Artefact rejection/ reference	Epoch length & number	MCC	Results (in comparison to HCs)	QR
								different: **alpha** coherence sig. ↓ between F7-P7 and T8-P8 electrode pairs, **beta** coherence ↓ between P3-O1 and Fp2-F4, and **delta** coherence ↓ between P3-O1 and Fp2-F4, (all $p < 0.05$).	
Movahed et al. (2021)	34 MDD, 30 HC	SL	Bivariate interactions	N/A min, eyes-closed and eyes-open, 19 channels	Semi-automated (w/ ICA) rejection, mastoid reference	1 min, n = 249 MDD, n = 261 HC	Yes	Significant difference observed between MDD and HC in connectivity between frontal and temporal regions. However, the frequency in which this was observed is unspecified.	2
Olbrich et al. (2014)	60 MDD, 60 HC	LPS	Bivariate interactions – eLORETA	15 min, eyes-closed, 31 channels	Visual rejection, Average reference	2 s, n = N/A	Yes	**Alpha** connectivity sig. ↑ between sgPFC-lDLPFC and sgPFC-lMPFC (*p* unspecified). No differences in delta, theta, and beta.	3
Orgo et al. (2016)	37 MDD*, 37 HC	SL	Bivariate interactions – averaged	6 min, eyes-closed, 30 channels	Visual rejection, Mastoid reference	20 s, n = N/A	N/A	Sig. ↑ **theta and beta** for short connections in posterior regions ($p < 0.05$). No differences in delta, alpha, gamma.	3
Orgo et al. (2017)	37 MDD*, 37 HC	Coh	Bivariate interactions – binarized using network metrics with threshold	6 min, eyes-closed, 30 channels	Visual rejection, Mastoid reference	20 s, n = 10	N/A	Sig. ↑ connectivity (at all bands – **delta, theta, alpha, beta,** and **gamma** – exact connectivity pairs of differences unspecified, all $p < 0.05$)	3
Park et al. (2007)	12 MDD, 16 HC	SL & Coh	Bivariate interactions	NA, 16 channels	N/A	N/A, n = N/A	N/A	Values of mean/whole SL sig. ↓ in MDD for **delta** ($p < 0.05$), **alpha** ($p < 0.05$). No significant differences in theta, beta, or gamma.	3
Shim et al. (2018)	87 MDD, 58 HCC	PLV	Bivariate interactions – min-norm estimation – using weighted network metrics	5 min, eyes-closed, 62 channels	Visual rejection, Cz (online) reference	4.096 s, n = 10	Yes	Overall, the strength ($p = 0.031$), CC ($p = 0.037$), and efficiency were sig. ↓ in MDD vs HCs in **theta** and **alpha** (strength: $p = 0.010$; CC: $p = 0.010$; efficiency: $p = 0.013$). PL was sig. longer in MDD vs HCs only in **alpha** ($p = 0.019$).	3
Suhhova et al. (2009)	18 MDD, 18 HC	Coh	Bivariate interactions – average	– min, eyes-closed, – channels	Visual rejection, Cz reference	N/A, n = N/A	No	No differences in theta, beta1 (12–20 Hz), or beta2 (20–49 Hz) ($p > 0.05$).	3
Sun et al. (2011)	12 MDD, 12 HC (Females only)	PDC	Bivariate interactions – binarized using network metrics with threshold	5 min, eyes-closed, 16 channels	Visual rejection, Mastoid reference	N/A, n = N/A	N/A	Sig. ↓ **alpha** connectivity ($p < 0.01$). But sig. ↑ overall connectivity in left hemisphere ($p < 0.01$).	3
Sun et al. (2008)	12 MDD, 12 HC	PDC	Bivariate interactions	5 min, eyes-closed, 16 channels	Visual rejection, Mastoid reference	N/A, n = 24	N/A	Sig. ↓ **beta** in frontal areas during resting specifically, interactions between left to right interhemispheric: F3- > F4, C3- > C4, F3- > C4, C3- > F4 ($p < 0.001$), and right to left interhemispheric: F3 < -F4, C3 < -C4, F3 < -C4, C3 < -F4 ($p < 0.001$), and in left hem: Fp1 < −>F3, F7 < ->F3, and C3 < ->F3 ($p < 0.001$), and in the right hem. Fp2 < −>F4, F8 < ->F4, C4 < ->F4 ($p = 0.014$).	3
Sun et al. (2019)	16 MDD, 15 HC	Corr, Coh, iCoh, PLI, PLV	Bivariate interactions – using network metrics: MST, CST, ECO, and density	5 min, eyes-closed, 128 channels	Semi-automated rejection, REST reference	4 s – 50 % over, n = 16	N/A	For **theta** assessed with iCoh, CPL, EBC, and NBC in networks of MDDs were sig. ↓ when CST used but sig. ↑ when MST and Density used. iCoh with CST and density noted sig. ↓ in CC of MDDs. With Corr, CPL, EBC, and NBC in networks of MDDs was sig. ↓ when density used. For **alpha** assessed with iCoh, CPL, EBC, NBC sig. ↓ when CST used, MDDs also showed reduced CC in iCoh when ECO used (all $p < 0.05$). **Most sig. findings noted when	2

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Table 3 (*continued*)

Article	Sample	Conn. Measure	Analysis specifics	Acquisition	Artefact rejection/ reference	Epoch length & number	MCC	Results (in comparison to HCs)	QR
								iCoh with CST used and noted to be best for MDD identification.	
Sun et al. (2020)	24 MDD, 29 HC	wPLI	Bivariate interactions – using network metrics	5 min eyes-closed, 128-channels	Semi-automated rejection, REST reference	N/A s, n = N/A	Yes	All frequencies sig. differed between MDD and HC: for **delta** in frontal and temporal lobes; **theta** in frontal and parietal lobes; **alpha** in parietal-occipital and central-temporal lobes; and **beta** in temporal and parieto-occipital lobes, (all $p < 0.05$).	3
Whitton et al. (2018)	65 MDD, 30 rMDD 79 HC	LPS	Bivariate interactions – eLORETA	8 min, eyes-open & eyes-closed, 128 channels	Visual rejection, Average reference	2 s, n = 40	Yes	Sig. ↑ LPS right SGF and the right PHG in the **beta 2** frequency band (18.5–21 Hz; $p < 0.05$) for MDD. Stronger LPS between left SFG and right MTG in **beta 1** band (12.5–18 Hz; $p < 0.001$ uncorrected) for MDD. No differences in delta (1.5–6 Hz), theta (6.5–8 Hz), alpha 1 (8.5–10 Hz), alpha 2 (10.5–12 Hz), and beta 3 (21.5–30 Hz).	3
Zhang et al. (2018)	13 MDD, 13 HC	Corr (Pearson's)	Bivariate interactions – binarized using network metrics with threshold	4 min, eyes-closed, 64 channels	Semi-automated rejection, Average reference	8 s, n = 10	N/A	**Alpha** connectivity sig. ↓ (all $p < 0.05$). No differences in delta, theta, beta, and gamma.	3
Zhang et al. (2021)	24 DD, 29 HC	PLI	Bivariate interactions – using network metrics	5 min eyes-closed, 128-channels	Semi-automated, N/A reference	N/A s, n = N/A	N/A	Sig. ↑ **theta** mostly in regions of left hemisphere and some left-temporal and right-temporal regions, and ↑ **alpha 2** (10–13 Hz) mostly in the two temporal regions and some left-frontal, left-temporal, and left partial-occipital (all $p < 0.05$).	3

Note. °6 "DMN" electrodes = F3, F4, P3, P4, Fz, and Pz. Further, all differences where *p* is not specified are assumed to be significant at $p < 0.05$. *Abbreviation*: ADHD = attentional deficit hyperactivity disorder; AEC = amplitude envelope correlation; AS = Asperger syndrome; CC = cluster coefficient; Coh = magnitude squared coherence; Corr = correlation coefficient; CPL = characteristic path length; CST = cluster-span threshold; DD = depressive disorder (used in instances where not made clear if clinical diagnosis took place); DS = depressive symptoms/state; DMPFC = dorsomedial prefrontal cortex; EBC = Edge between centrality; ECO = Efficiency Cost Optimisation threshold; eLORETA = exact low resolution brain electromagnetic tomography; fMRI = functional magnetic resonance imaging; GAD = generalised anxiety disorder; GE = global efficiency; HC = healthy control; iCoh = imaginary coherence; LAURA = Local AutoRegressive Average; lDLPFC = left dorsolateral prefrontal cortex; LE = local efficiency; LLC = lagged linear connectivity; LNC = lagged nonlinear connectivity; LPS = lagged phase synchronisation; MCC = multiple comparisons controlled; MDD = major depressive disorder; MDD* = unmediated participants with MDD; MST = minimum spanning trees; MTG = middle temporal gyrus; N/A = Not available or specified by authors of article (in the affirmative or negative); NBC = node betweenness centrality; NBS = network based statistics; PDC = partial directed coherence; PHG = parahippocampal gyrus; PLI = phase lag index; PLV = phase locking value; PTE = phase transfer entropy; QR = Quality Rating (1 = high, 2 = moderate, 3 = low); REST = reference electrode standardization technique; rMDD = remitted MDD; SCZ = schizophrenia; sgACC = sub-genial anterior cingulate cortex; SGF = superior frontal gyrus; sgPFC = sub-genial prefrontal cortex; SL = synchronisation likelihood; SSD = somatic symptom disorder; ROIs = regions of interest; TTH = tension type headaches; wPLI = weighted phase lag index.

theta varied greatly in the FC techniques used. Thus, there may be some differences between depressed individuals and controls in theta FC, but this will need to be investigated further. However, when our synthesis was restricted to studies that scored higher quality ratings *overall* (QR of 1 or 2), despite better individual steps for FC analysis, the results indicated that an equal number of studies noted bother higher and lower theta FC differences.

3.2.3. Beta EEG FC differences

A total of 17 studies assessed differences in beta FC (oscillations between 25 and 35 Hz). The findings in beta FC were complicated however due to differing beta band classification across studies, with some studies defining beta from 12 to 30 Hz while others assessed beta across multiple frequency components (i.e., beta 1, 2, 3, and 4) with varying ranges. For example, Hasanzadeh et al. (2020) separated beta into four sub-bands and observed contrasting findings, with the MDD group demonstrating higher FC for "beta 1" (13–16 Hz), "beta 2" (16–20 Hz), and "beta 4" (25–30 Hz), whereas no differences were observed for beta 3 "beta 3" (20–25 Hz). This highlights the need for clear reporting of the measures being assessed, the need to communicate a clear and logical rationale for frequency sub-band division, and the resulting outcomes, as well as a greater consistency between studies and potentially a more consistent consideration of beta sub-bands in analyses given the significant differences that exist between them.

Interestingly, the 2016 and 2017 Orgo et al. studies reported contrasting results when assessing the same sample, using two different FC metrics. Specifically, the 2016 article employed the synchronisation likelihood measure of FC and observed no differences in activity, and the 2017 article examined Coh (with network metrics) and observed higher beta FC in the general 25–35 Hz range. These findings could point to a difference in the outcomes that these EEG FC measures provide, given that the EEG pre-processing methodology was carried out equally for both. This provided further evidence that a combination of suboptimal pre-processing steps and variability in FC metrics could be contributing to the contradictory findings observed here.

Overall, when viewing all the studies on beta together, no consistent findings can be observed (Table 2). Very few studies localised activity to specific brain areas (as for alpha and theta) and the studies assessing beta were overall of lower quality than the studies that had assessed alpha and theta, with no studies of beta FC scoring above the worst

quality rating. The studies noting no differences and those noting higher beta FC in depression however differed in methodological steps. For example, those that reported higher beta FC in individuals with depression were studies that controlled for multiple comparisons and used source localisation. Thus, possibly suggesting higher beta in depression is likely, as studies of slightly higher quality reported positive results compared to those reporting null results.

3.2.4. Delta EEG FC differences

Delta frequency FC (oscillating between ~1–4 Hz) was assessed in 13 studies (Table 2), with little consistency in the results. Interestingly, when looking at differences in the delta frequency FC, the studies assessing FC with higher quality measures of FC, including PLI and iPDC noted no differences at this frequency (Damborská et al., 2020; Sun et al., 2020). Meanwhile, studies which noted significant but contradictory findings were more likely to use FC measures which have been suggested to be confounded by VC and affected by Type 1 errors (for example, FC measures such as Corr and Coh) (McVoy et al., 2019; Markovska-Simoska et al., 2018; Leuchter et al., 2012; Knyazev et al., 2018; Knott et al., 2001; Orgo et al., 2017; Park et al., 2007; Zhang et al., 2018).

Overall, none of the studies assessing delta FC scored in the higher quality range. Given the limited number of studies, the heterogeneity and poor quality of the studies, and differing methodologies used in the assessment of delta frequency changes in MDD, there is insufficient evidence to confidently suggest for differences in delta FC.

3.2.5. Gamma EEG FC

Finally, five studies assessed FC differences in the gamma frequency (oscillating ~35+ Hz). These studies all obtained lower quality scores and noted no differences in gamma FC in MDD. Most of these studies assessed gamma FC globally (where, as stated in our previous section, it may be that actual differences may be less likely to be detected), using Coh estimates of FC, with only a small number of trials, and no controls for VC. Coh has been found to be significantly affected by Type 1 error, especially where no VC is employed (Cohen, 2014) thus, increasing false identification of FC, and decreasing the accuracy of interpretation.

4. Discussion

This systematic review aimed to assess studies comparing EEG FC between individuals with depression and HCs. Overall, 52 studies assessing EEG activity were identified; 36 studies assessed resting-state EEG FC, and 16 assessed task-related FC (summarised in the Supplementary Materials). Comparisons between individuals with depression and controls were made within both resting-state and task-related categories. Significant methodological differences were observed in study reporting and quality that made it difficult to synthesise the results and come to any clear conclusions. However, reasonably consistent suggestions for higher alpha FC in depression (especially at frontal sites) during resting-sate EEG recordings can be observed. Meanwhile, inconsistencies across other frequencies are still quite prevalent, these same inconsistencies were observed in a recent review of EEG oscillations across several psychiatric disorders (Newson and Thiagarajan, 2019).

4.1. Resting-state alpha and theta FC

In the present review, EEG FC was most assessed in the alpha and theta frequencies, with the majority of studies noting higher alpha FC in the depressed group, and no consistent findings for theta. Among the more consistently observed findings was the depressed group demonstrating higher alpha FC within frontal regions, and lower alpha within parietal-occipital regions of the brain. However, this finding may be complicated by several studies assessing alpha FC across the whole brain, an approach which showed the most inconsistency in findings across the studies. This suggests the ways in which FC is assessed (between specific electrode-pairs versus globally) may affect the likelihood of detecting true significances.

This might be because of the nature of FC. As discussed above, previous research has shown that the brain is separated into a number of networks, most of which are activated during various processes. For example, task-positive networks (TPNs) are activated in response to external stimuli and include regions of the brain such as the DLPFC. On the other hand, task-negative networks (TNNs) are decreased in response to external stimuli and are driven more by self-referential processes, the primary region of which is the DMN (Fox et al., 2005; Knyazev et al., 2018). Previous work has indicated that in depression, higher FC in certain networks (i.e., the DMN), and lower FC in other networks (i.e., the TPN) is observed and that the increased activity in the DMN may dominate over the TPN (Hamilton et al., 2011; Kaiser et al., 2015). As such, the global examination of FC may not be ideal for characterising differences in FC in depression, as the averaging of these FC networks across cortical regions may result in the cancelling out of effects (or regression towards the mean) since some networks may show increased activation while others may show decreases activity in MDD. Thus, it could be beneficial for future research to focus on FC contained within specific, known networks to further assess this trend for increased alpha FC in depression.

In contrast, the overall pattern across theta FC research suggests that theta FC may be lower in frontal regions in depression and higher in temporal-posterior regions. This is a trend opposite to that of alpha and may have to do with the functional differences of the two frequencies (which might further link to differing network activation). Given what we know about the physiology of EEG and its relation to white matter, it may be that EEG FC measures in the alpha and theta bands link to synaptic signal times (Nunez et al., 2015). Further still, EEG research suggests that alpha relates to long-range brain FC and theta to short-range FC (Fingelkurts and Fingelkurts, 2017; Knyazev et al., 2011). Nunez et al. (2015) report that when structural white matter is violated, FC is significantly reduced for high frequency bands compared to lower ones. Perhaps white matter dysfunction might partially explain why EEG studies in depression predominantly report theta and alpha changes. Indeed, studies have reported some white matter dysfunction in depression (Tham et al., 2011; H.E. Wang et al., 2014; L. Wang et al., 2014).

More specifically, the synaptic signal times of the EEG frequencies have been related further to top-down inhibitory processes (Nunez et al., 2015), especially in the lower EEG frequencies including alpha and theta (Greicius et al., 2007; Klimesch, 1996, 1999, 2012; Klimesch et al., 2007; Sadaghiani et al., 2010). Key evidence for the role of alpha oscillations in attention suggests that regions or networks of the brain which are unrelated to a task often display higher alpha power (i.e., inhibition; Klimesch, 2012; Yuk et al., 2020); and long-range alpha FC patterns have been shown to organise resting-state networks (i.e., the DMN) during internal mental processes (Jann et al., 2009; Knyazev et al., 2011). To support this further, research studies assessing resting-state EEG alpha activity have suggested that higher alpha power (with some suggestion for FC) within specific brain regions may reflect an individual's ability to build up a highly efficient attentional 'filter' (Klimesch, 2012; MacLean et al., 2012; Zanto et al., 2011). This filter is suggested to operate when the discrimination and detection of a target are required (i.e., top-down control of attention to focus on specific external stimuli thus, activation of TPNs).

Within this article, it could be that the observed dysfunctions in alpha FC, with higher FC within frontal regions, is due to a lack of ability to regulate and synchronise internal neural processes, such that individuals with depression show a broad spread alpha rather than the alpha power increases that are constrained to specific regions that may be required for optimal function, disrupting the ability of depressed individuals to engage attention and executive functions which are mediated by these frontal regions.

Similarly, theta has been posited to be involved in cognitive control (Cavanagh et al., 2009; Cavanagh and Frank, 2014), which is known to be guided by attention and inhibition. In Nakao et al. (2012) it was noted that internally guided decision-making (i.e., not based on stimuli or prompts) was also correlated with resting-state brain activity in the theta (and beta) frequency bands. Further, lower theta in depression has been demonstrated to reflect a lowering in cognitive control efficacy of the associated top-down processes. Deficits in cognitive control have been noted in depression (Hwang et al., 2015), and lower theta FC has been observed to link to more sever presence of depressive symptomology (McVoy et al., 2019). Thus, alpha and theta may play a similar role in the resting-state.

It is important to consider that these differences in alpha and theta were observed during *resting EEG* (predominantly with eyes closed). Oscillatory activity is dynamic and context-dependent, higher theta FC in a region may be considered beneficial in one context but detrimental in another. When individuals are sitting, at rest (particularly with eyes closed), the typical EEG pattern is that of increased posterior alpha activity and decreased posterior theta activity (Klimesch et al., 1998). This aligns with the top-down inhibition framework, as posterior visual processing regions are inhibited if the eyes are closed, reflected as increased alpha (i.e., inhibition) and decreased theta (i.e., active information processing). Thus, the pattern observed here in individuals with depression could be viewed as a failure to properly modulate alpha and theta FC in response to external/environmental demands (i.e., to inhibit posterior regions perhaps, TPNs, when they are not being used).

However, most of the theories presented above are speculative, as considerable differences and inconsistencies are present across the literature as to the exact links between EEG activity/FC and function, and a complete understanding of the functional meaning of EEG FC in different frequencies remains elusive. Very few studies have assessed resting-state theta in relation to depressive symptoms, neurophysiology, and cognition. Fewer still have assessed the specific differences, similarities, or relations between EEG oscillations and FC. Thus, to provide sensible interpretations of potential differences in depression in theta and alpha EEG FC, more robust research will need to be conducted to ascertain true differences in FC in individuals with depression, and the underlying neurophysiology of depression.

4.2. Resting-state beta, delta, and gamma FC

A total of 18 studies assessed beta FC, and demonstrated heterogenous results, with studies finding increased, decreased, or no significant differences: thus, limiting any conclusions as to the differences. This inconsistency was further complicated by differing beta bands (i.e., beta 1, 2, 3, and 4). Overall, there was not enough evidence to suggest for differences in delta FC in MDD due to highly conflicting findings.

Lastly, only five studies assessed gamma differences, with only one noting higher gamma FC in depression and the remaining studies noting no FC differences. Thus, as with delta, there is insufficient evidence to support a clear conclusion as to gamma FC differences in relation to MDD. Physiologically, while theta and alpha have been noted to be altered when white matter integrity is compromised, other frequency bands have been related to both direct and indirect signalling (Chu et al., 2015). It could be that lower frequencies relate to indirect signalling and possibly through less myelinated pathways compared to higher frequencies. Overall, there is a need for more studies in beta, delta, and gamma FC, in addition to clear reporting of EEG methodologies, results as well as greater consistency between studies.

4.3. The quality of FC studies assessed in this review

Overall, most studies reported results based on suboptimal processing choices for EEG FC analysis methodologies (only five studies scored in the recommended range for quality of FC assessment as determined by Miljevic et al., 2021). Further, most studies assessed FC through metrics known to be significantly influenced by noise and error such as Coh and Corr. To demonstrate the potential difficulties posed by different FC metrics across the studies, we note that the two studies by Orgo et al. (2016, 2017) assessed two different FC metrics on the same sample based on the same EEG processing methodology. However, different patterns of results in the comparisons between the two groups were observed across the five frequencies assessed. Thus, indicating the significant impact that analysis decisions can have on the results.

In addition, more than half of the studies did not report or account for multiple comparison controls. Given the potential number of electrode pairs that could be included in a comparison (e.g., >1000 comparisons for caps with >46 electrodes), multiple comparison controls are vital in FC research. If multiple comparisons are not controlled for, the number of comparisons can almost guarantee false positives (Miljevic et al., 2021). Despite this risk, many studies have neglected to control for multiple comparisons.

Lastly, despite the application of network metrics designed to identify significant connections more accurately, the findings by Sun et al. (2019) further highlight the potential for varying methodological approaches to confound the results when differing binarization techniques are used, as contradictory findings can be obtained depending on the approach. Sun et al.'s (2019) results therefore highlight that studies employing binarization techniques need to be mindful of how different settings could affect their results and suggest that the inconsistency in findings relating to alpha FC in depression may be the result of methodological confounds.

4.4. Task-related FC

This review noted no reliable conclusions for task-related FC differences in depression. Generally, theta and gamma frequencies have been found to be *much* more prevalent during task-related processes, with some overlap in the tasks. For example, theta has been proposed to be involved in both attentional and working memory processes (Cavanagh and Frank, 2014; Klimesch, 1999), but this needs to be examined further. However, this may be somewhat confounded by the fact that it could be difficult to distinguish between the '*resting-state*' and '*task-related*' states of the brain in MDD. Individuals with MDD experience higher levels of rumination (a cognitive symptom of depression) and therefore may be unable to truly be "at rest" (Papageorgiou and Wells, 2004). Whereas, during specific task-directed recordings, a researcher may be able to confirm with behavioural data that both groups of interest are performing the same cognitive process.

Future studies should aim to address this perhaps by assessing and/or controlling for the cognitive symptoms of depression in EEG recordings. Further, assessing differences in FC within a single task is still a necessary step for deeper understanding and the replicability of observed differences. Lastly, future research would benefit from the development of clear, evidence-based rationales for why a certain task was chosen for the assessment of EEG FC in depression, and how it relates to the understanding of cognition, neuropsychology, and the changes in these because of depression. Doing so will provide clearer interpretation of the functional meaning of potential differences in FC between individuals with depression and healthy individuals.

Future research should aim to standardise FC assessment and EEG pre-processes using robust and validated steps as discussed in Miljevic et al. (2021), as well as assessing FC and frequencies beyond theta and alpha, as most studies were found to do. Further, beyond EEG, the specific elements of (major) depression also need to be considered as depression is a multifaceted disorder and differences across individuals may be generated by underlying electrophysiological, biological, and neurochemical differences (Ferdek et al., 2016), these may affect the results being obtained in the different studies included in this review.

5. Conclusion

Overall, there are reasonably consistent suggestions for higher alpha FC in depression (especially at frontal sites) during resting-state EEG recordings. However, the presence of broad heterogeneity in methodologies between the studies prevents drawing firm conclusions regarding the presence, direction, and anatomical location of FC differences in MDD versus HCs. There are several methodological features which are likely to contribute to this: 1) variability in several EEG preprocessing steps, the FC metrics used, and in overall methodology quality; and 2) where some studies assessed the strength of relationships between electrode pairs, others used binarization and graph theory to assess the topographic distribution of the connections (i.e., CPL and clustering). Thus, these methodological inconsistencies limited the comparability of the studies assessed and the overall conclusions around EEG FC differences in depression.

More research is needed to explore whether alterations in frequencies beyond alpha and theta are present. Furthermore, the FC findings in the alpha frequency need to be confirmed to demonstrate consistency within and across varying EEG measures of FC, particularly since most previous research has used Coh to measure FC, a measure that has been suggested to lead to false positives. Thus, future research should employ measures of FC that have been demonstrated to be most reliable.

CRediT authorship contribution statement

All who meet authorship criteria are listed as authors, and all certify that they have participated sufficiently in the work to take public responsibility for the content. With AM contributing to conceptualization, design, literature search and study inclusion/exclusion, writing – preparation, creation, writing – editing, and revision; MPNP contributing to literature search and study inclusion/exclusion, writing – editing, and revision; NWB to conceptualization, design, writing – editing, and revision; and OWM and PBF contribution to the conceptualization, writing – editing, and revision.

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No other acknowledgments of significance to note.

Conflict of interest

Authors AM, NWB, OWM, and MPNP report no financial or potential conflicts of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jad.2023.01.126.

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