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Hypnosis, hypnotic suggestibility and meditation: An integrative review of the associated brain regions and networks

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Abstract

The number of neuroimaging studies on hypnosis and meditation has multiplied rapidly in recent years. The methods and analytic techniques that are being applied are becoming increasingly sophisticated and approaches focusing on connectomics have offered novel ways to investigate the practices, enabling brain function to be investigated like never before. This chapter provides a review of the literature on the effects of hypnosis and meditation on brain network functional connectivity. Numerous cross-sectional as well as longitudinal studies have also reported enduring transformations in brain structure and function in practitioners of meditation, while evidence is mounting which demonstrates a relationship between hypnotic suggestibility and variations in neuroanatomy/functional connectivity that may facilitate hypnosis. The similarities (and differences) between the brain regions and networks associated with each type of practice are highlighted, while links are tentatively made between these and the reported phenomenology.

Overview

This chapter focuses on functional and structural neuroimaging studies of hypnotic suggestibility, hypnosis, and meditation. The content emphasises functional Magnetic Resonance Imaging (fMRI) studies, and draws reference to Positron Emission Tomography (PET) and Single Photon Emission Tomography (SPECT), whereas the literature on temporal dynamics using electroencephalography and magnetoencephalography has not been included. The studies detailed within are not intended to be an exhaustive review of the literature, but should nonetheless provide a comprehensive and up to date overview of those that appear relevant when comparing the practices of hypnosis and meditation. A number of functional neuroimaging studies, with traditional designs (e.g., block design) are described, often as a preface to those which have applied functional connectivity (FC) analyses. Readers should note that the FC studies that are included predominantly focus on the assessment of baseline (resting) states in those that are hypnotically suggestible and in meditators, and on the changes associated with hypnosis and meditation themselves, as opposed to the effects that those states might have on the brain networks which underpin particular tasks (e.g., how FC in the pain matrix may be modulated). Three brain networks in particular are discussed within the chapter: The executive-control network (Seeley et al., 2007), the salience network (Seeley et al., 2007) and the Default Mode Network (DMN; Greicius, Krasnow, Reiss, & Menon, 2003; Raichle et al., 2001). Structural neuroimaging research is reviewed which reports neuroanatomical variations in high suggestible people (Highs), as are studies which appear to demonstrate structural differences linked to meditative practice. Within this review, readers will also be exposed to the wide range of neuroimaging methods that are employed within these fields of research.

As a preview to the chapter, activity within brain regions such as the anterior cingulate cortex (ACC) and the dorsolateral prefrontal cortex (DLPFC), which are components of the salience and executive-control networks, is frequently modulated as

people engage in hypnosis and meditation. These are structures that have been linked to attentional and executive function, absorption and metacognitive processes. Hypnosis and meditation also both tend to lead to alterations in FC and deactivation of the DMN, which is associated with mind-wandering and spontaneous thought. Expansion of FC within the salience and executive-control networks may underpin hypnotic suggestibility and reflect long-term changes due to meditation. In terms of brain structure, variations within the ACC, DLPFC and insular cortices are associated with hypnotic suggestibility/response to hypnosis and meditative practice. These findings paint a small part of a greater picture that is certainly not so simplistic however. A range of methodological differences, which appeared to especially impact the more numerous meditation studies (e.g., the type of meditation, length of practice, task and analysis technique), often severely limited the conclusions that could be drawn from between study comparisons. The same problems can be seen in studies of hypnosis, with different suggestibility scales, tasks and analytic methods, likely impacting the results. While attempting to interpret the neuroimaging findings many authors (including me and my colleagues) have suggested potential links between

phenomenology/cognition/behaviour and associated brain function/structure. Throughout the chapter, the worthwhile endeavour of performing contemporary confirmatory assessments of these relationships in the same study samples is highlighted (see also the chapter by Cardeña, this volume).

Phenomenology of Hypnosis and Meditation

The phenomenology associated with hypnosis and various kinds of meditation will be addressed in richer detail within other chapters of this volume. A brief description is however provided here so that these qualitative aspects can be explored in relation to the neuroimaging results. During hypnosis, people may experience a range of phenomena. These include increased absorption, dissociation, decreased self-agency and self-monitoring, mental relaxation, reduced spontaneous thought and a suspension of orientation toward time and place (Cardeña, 2005; Grant & Rainville, 2005; Rainville, Hofbauer, Bushnell, Duncan, & Price, 2002; Rainville & Price, 2003; Tart, 1970). Experiential accounts of hypnotic phenomena also relate to the level of suggestibility of the participant (Cardena, Jonsson, Terhune, & Marcusson-Clavertz, 2013).

The term "meditation" is used to refer to a wide range of mental training practices with varied goals and techniques. Lutz, Slagter, Dunne, and Davidson (2008), in relation to Buddhist traditions, describe two main styles of meditation: Focused Attention (FA) and Open Monitoring (OM). FA refers to the maintenance of attention (sustained attention; narrow field) on a chosen internal or external object (e.g., a thought, a mantra, breathing). This type of meditation also involves identifying distractors, disengaging attention from them and redirecting attention back to the object of focus. OM on the other hand captures the practice of passive monitoring (wide field of attention) of the self or environment (acknowledging, but not evaluating extensively or responding) and of emotional and internal bodily awareness. Combinations of these meditative styles can be found in Zen, Tibetan Buddhism, Vipassana and Mindfulness-Based Stress Reduction (Lutz, Slagter, et al., 2008). These attention-oriented practices were chosen for review, as opposed to, for example, compassion-based meditation, because attentional modulation is often theorized as central to hypnosis and hypnotic suggestibility (e.g., Gruzelier, 1998; Raz, Kirsch, Pollard, & Nitkin-Kaner, 2006).

Brain networks

Many functional neuroimaging studies on hypnosis and meditation, especially those carried out at an earlier point in time (e.g., prior to 2010), tended to employ traditional designs and methods of data analysis which enabled brain regions to be identified that were more (or less) active during the states of hypnosis and meditation. The results of these studies provided important contributions to the literature and a number of key findings will be detailed during the course of this chapter. Revealing how different brain regions communicate with each other, however, provides another level of understanding about the effects of meditation and hypnosis, and interest in the networks of the brain has grown steadily over recent years. This shift towards networks is necessary to further understand how discrete sets of functional units within the brain result in the emergence of higher level cognition and states of consciousness. A number of multi-region brain networks can be isolated from fMRI data through FC analyses. This is possible due to low frequency oscillations in the Blood Oxygenation Level Dependent signal, which have a physiological basis (Biswal, Yetkin, Haughton, & Hyde, 1995). Methods such as independent components analysis (ICA) or setting of seed regions and subsequent correlation assessment enable the extraction of these networks (which are comprised of brain regions activated in a coordinated fashion). A major benefit of these types of analysis is that participants need not complete a task in the scanner and the networks can be isolated from data acquired during periods while participants do nothing but rest. It should be noted that FC analysis of data collected during tasks is also commonplace. For networks isolated through FC analysis, the term "restingstate networks" has often been applied. The term "intrinsic connectivity networks" (ICNs; Seeley et al., 2007) will instead be used in this chapter as it is applicable to networks extracted during rest or during the period in which a participant completes a task.

This chapter will focus in particular on three well documented networks: The Executive-control network (Seeley et al., 2007), the Salience Network (Seeley et al., 2007) and the DMN (Greicius et al., 2003; Raichle et al., 2001). Questions to consider throughout the coming sections are: 1) Which brain regions are jointly activated (and deactivated) during hypnosis and in different types of meditation? 2) In terms of networks, are there similarities or differences between the effects of hypnosis and meditation on FC within and between ICNs? 3) Is ICN FC associated with hypnotic suggestibility or meditative practice, and if so, do network alterations correspond? 4) Can neuroanatomical variations be seen in association with hypnotic suggestibility or as a consequence of meditative practice? 5) What are the likely implications of any variation in activity/FC/brain structure?

Executive-control network and salience network

The brain regions that comprise the executive-control network are commonly activated during tasks that require focused and sustained attention (see e.g., Corbetta, Patel, & Shulman, 2008). The executive-control network incorporates the left and right lateral fronto-parietal cortices and the dorsomedial PFC (Seeley et al., 2007). The salience network is involved with sensory filtering and integration, pain, interoception, autonomic functioning, and emotional processing, and includes brain regions such as the dorsal ACC (dACC) and fronto-insular cortices (Critchley, 2005; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Seeley et al., 2007). The salience network has also been proposed as an interface that enables switching between the more task relevant executive-control network and the more introspective DMN (Sridharan, Levitin, & Menon, 2008), which has been linked to internal processes such as mind-wandering and thinking about the past and present (Buckner, Andrews-Hanna, & Schacter, 2008). It should be noted that the neuroimaging literature also refers to "extrinsic" (or task positive) systems and "intrinsic" (or task negative) systems.

These systems typically correspond on the one hand to combinations of the salience and executive-control networks in addition to task relevant sensory networks (extrinsic / task positive) and on the other hand to the DMN (intrinsic / task negative) (M. D. Fox et al., 2005; Tian et al., 2007). Anti-correlation has been demonstrated between those systems (M. D. Fox et al., 2005).

Executive-control network and salience network: Hypnosis and hypnotic suggestibility

Hypnosis-related activation has been observed within components of both the executive-control and salience networks. For example, activity has been detected within the ACC (Maquet et al., 1999; Rainville et al., 2002; Rainville, Hofbauer, et al., 1999), the lateral frontal cortical regions (Deeley et al., 2012; Maquet et al., 1999; Rainville et al., 2002; Rainville, Hofbauer, et al., 1999) and the insular cortex (Rainville et al., 2002; Rainville, Hofbauer, et al., 1999). The involvement of the ACC and PFC presumably reflects processes such as focused/sustained attention and executive functions (Grahn & Manly, 2012; Posner & Rothbart, 2007), whereas activation of the insular cortex is more unclear and may be related to the perceived salience of the object of attention, or to processes such as interoception, and the modulation of sensory integrative processes (Critchley, 2005; Critchley et al., 2004; V. Menon & Uddin, 2010; Seeley et al., 2007).

Discrepancies between study designs are likely to be of major importance to the results obtained. For example, whether hypnosis leads to activation of the fronto-parietal network may depend on the content of the induction and/or the task requirements. A simple visual display such as that used by Deeley et al. (2012) may promote focused and sustained attention (even if participants are instructed only to look at the screen), which could explain their findings of greater activity in fronto-parietal regions in relation to hypnotic depth, whereas decreased activity in the parietal cortices found by Rainville et al. (2002; 1999) might relate to their induction which included "specific instructions for decreased orientation to, and interest in, irrelevant external sources of stimulation" (p 897). These are of course speculations as to the sources of activation and deactivation, but these subtle distinctions in experimental design are likely to be extremely important. Variations such as these are also expected to contribute to the FC modulations in relation to hypnosis and meditation. For interpretation the devil is likely to be in the detail.

Demertzi and colleagues (2011) compared FC during hypnosis to a mental imagery condition in Highs. An informative feature of their study was the use of participant self-report data on level of dissociation (from the environment), absorption, and external thoughts. During hypnosis, participants reported greater dissociation and FC mirrored these reports, revealing a reduction in lateral cortical regions associated with executive control and external processing (Demertzi et al., 2011). This association appears to be appropriate as the hypnotic induction required revivication of autobiographical memories, which would require an internal rather than external focus. In another FC study, which instead used a regression approach, McGeown, Mazzoni, Vannucci, and Venneri (2015) found that reports of greater hypnotic depth were linked to decreased FC within portions of the salience and executive-control networks, such as the left insula and right DLPFC (but increased FC within the ACC). Clearly additional research with larger sample sizes is needed to further refine the complex changes in FC that may occur during hypnosis.

Turning now from the features of the hypnotic state to the trait of hypnotic suggestibility, Hoeft et al. (2012) found that Highs (during rest, without the use of hypnosis) had greater FC between the dorsal ACC and DLPFC bilaterally, but particularly within the left hemisphere. This pattern of FC illustrates an expansion of the salience network in Highs

to incorporate part of the executive-control network. The authors suggest that this association may underpin hypnotisability (Hoeft et al., 2012). A recently published study by Huber, Lui, Duzzi, Pagnoni, and Porro (2014) did not replicate the findings of Hoeft et al. (2012) exactly, but showed that people higher in suggestibility also had an expansion of the salience network (described differently in their article as the "executive-control network", but similarly comprised of the ACC and bilateral insula) this time in connection with the right inferior parietal lobule (IPL) and postcentral gyrus. Higher suggestibility was also associated with higher FC between the left fronto-parietal network and the precuneus and PCC (and lower FC between the right fronto-parietal network and the right thalamus and caudate). Huber et al. suggest that the pattern of results may reflect greater absorption, use of self-monitoring and imagery, and less distractibility at rest, in those that are more suggestible. While neither set of authors studied the effects of hypnosis on FC in Highs, the findings of Demertzi et al. (2011) described above demonstrate a reduction of FC within these networks (which it would appear are expanded at baseline), following a hypnotic induction. A related point is that activity within the DLPFC has been shown to be suppressed during hypnosis, when no external focus is required (McGeown, Mazzoni, Venneri, & Kirsch, 2009). Moreover, interventions such as with Transcranial Magnetic Stimulation, which have targeted neural activity within the PFC/left DLPFC have been shown to increase response to suggestion (e.g. Dienes & Hutton, 2013; Semmens-Wheeler, Dienes, & Duka, 2013). These results suggest that disruption of the expanded network may underpin hypnotic response.

Executive-control network and salience network: Meditation

Across various studies on meditation (involving FA, OM or a combination) either the dACC, the DLFPC, or more generally both are activated (Baron Short et al., 2010; Brefczynski-Lewis, Lutz, Schaefer, Levinson, & Davidson, 2007; Farb et al., 2007; Hasenkamp, Wilson-Mendenhall, Duncan, & Barsalou, 2012; Lazar et al., 2000; Manna et al., 2010; Newberg et al., 2001). Activation of the fronto-parietal networks (that underpin the executive-control network) has been observed (Brefczynski-Lewis et al., 2007; Hasenkamp et al., 2012; Lou et al., 1999). The insular cortices have also been a common site of activation (Brefczynski-Lewis et al., 2007; Farb et al., 2007; Hasenkamp et al., 2012).

Careful consideration of the processes involved during focused (and sustained) attention can shed more light on the underlying neural systems that are utilized. Using fMRI on experienced meditators who practiced FA, Hasenkamp and colleagues (2012) showed that focused attention activated the right DLPFC; mind-wandering (indicated with a button press), the DMN; becoming aware of a distraction, the dACC and anterior insula bilaterally; and shifting attention away from the distraction and back to the object of attention, the right DLPFC and bilateral inferior parietal cortex (see article for a full details). These findings fit closely with research unrelated to meditation, which has described the neuroanatomical correlates of sustained attention, alerting and orienting (e.g., Corbetta et al., 2008; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Posner & Rothbart, 2007). Hasenkamp et al. (2012) demonstrate that FA meditation involves a complex interplay between attentional sub-systems. A certain degree of overlap with the neural systems recruited by OM meditation is likely, although different demands may be placed on the attentional sub-systems, with Lutz et al. (2008) instead indicating for OM, reliance on monitoring, vigilance, and attentional disengagement.

In the previous section, evidence was presented for trait related expansion of ICNs in high suggestible people. Research has also shown expansion of ICNs in meditators both while meditating and during rest. We will turn first to the studies that have demonstrated expansions of ICNs in meditators engaged in practice (Froeliger et al., 2012; Kilpatrick et al., 2011). Kilpatrick et al. (2011) found that when instructed to be mindfully aware and to pay attention to the noise of the scanning environment, compared to waiting list controls, a meditation group trained for 8 weeks on Mindfulness-Based Stress Reduction (MBSR; involves FA and OM) had greater FC within a merged network the authors refer to as the "auditory/salience" network; named as such due to its inclusion of brain regions from other ICNs that have been documented (Seeley et al., 2007; Smith et al., 2009). Froeliger et al. (2012) instead examined the Dorsal Attention Network (DAN), which is comprised bilaterally of the frontal eye fields (FEFs), intraparietal sulcus and MT (Corbetta et al., 2008; M. D. Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Raichle, 2011) and overlaps with the executive-control network. Meditation (in experienced practitioners of Hatha yoga) versus rest was associated with increased FC between the DAN (right FEF) and DMN nodes; and multiple nodes of the DAN and the salience network (right anterior PFC). Both of these studies suggest that increased FC may reflect a shift towards a more functionally integrated network, which incorporates attentional, self-referential and salience processing (but additional decreases in FC reported in the latter study suggests that this interpretation is incomplete).

Expanding on these meditation state related changes there is evidence of greater anticorrelation between the extrinsic and intrinsic systems during FA (versus rest), in Tibetan Buddhist meditators (Josipovic, Dinstein, Weber, & Heeger, 2011). Alternatively, as the participants practiced Nondual Awareness (NDA) meditation (which operates through the integration of external and internal experience) weaker anti-correlation was observed between the networks. The results highlight the importance of the type of meditation and the malleability of the organisation of FC within ICNs. Taking all of these findings together they suggest that greater integration of ICNs is possible if meditation task demands require it (e.g., Froeliger et al., 2012; Josipovic et al., 2011; Kilpatrick et al., 2011) and that greater separation may also occur during meditative styles that predominantly require activation and coordination of the extrinsic network (Josipovic et al., 2011).

As alluded to above, repeated activation of the brain networks utilized during meditation may lead to long-term trait related changes during rest (when participants have not been directed to meditate). Hasenkamp and Barsalou (2012) showed that FC defined from a seed region within the right DLPFC, the area previously found to be associated with focused attention (Hasenkamp et al., 2012), was observed to be higher in more experienced meditators (mixed styles), in relation to the mid-cingulate gyrus, the left DLPFC and three regions within the right insula. The authors suggest that this pattern of increased FC might explain the reports of superior attentional skills in meditators (including both short-term trainees and more experienced practitioners) versus controls (e.g., Chan & Woollacott, 2007; Hodgins & Adair, 2010; Jha, Krompinger, & Baime, 2007). Furthermore, they propose that the increased FC to the insula might afford experienced meditators additional access to present moment awareness and the perception of internal states when engaging executive functions, or provide the ability to more efficiently switch between the executive network and the DMN. Yet, without assessing the mental activities of participants during rest or their attentional skills outside of these periods, there are major difficulties in interpreting the meaning of ICN modifications (and it remains unclear whether these alterations persist while meditators are performing the same mental tasks as controls).

A further point that should be taken from these studies is that meditation appears to decouple visual cortical areas from those associated with the salience network, both as a short term state feature during meditation and as a trait change observable at rest in long-term practitioners (Hasenkamp & Barsalou, 2012; Kilpatrick et al., 2011). This could reflect a decrease in the attentional resources allocated to unnecessary visual processing or may

indicate capacity for better cross modal inhibition (Hasenkamp & Barsalou, 2012; Kilpatrick et al., 2011).

Providing stronger evidence for long-term causal effects of meditation on ICNs, Xue, Tang, and Posner (2011) demonstrated with a randomised longitudinal design (with an active control group) that engaging a meditation regimen labelled Integrative Body-Mind Training (IBMT) for 11 hours increased network efficiency and connectivity degree in the left ACC (assessed with graph theory) during rest. IBMT aims to develop relaxation, FA and mindfulness (Tang et al., 2007). The increased network efficiency could reflect the capacity of the ACC to integrate information from across brain regions, whereas the increase in connectivity degree demonstrates that the ACC had more direct connections to other nodes (Xue et al., 2011).

Executive-control network and salience network: Summary

As described above, key regions of the executive control and salience networks, such as the ACC, DLPFC and insular cortices are consistently activated in studies both on hypnosis (Deeley et al., 2012; Maquet et al., 1999; Rainville et al., 2002; Rainville, Hofbauer, et al., 1999) and meditation (Baron Short et al., 2010; Brefczynski-Lewis et al., 2007; Farb et al., 2007; Hasenkamp et al., 2012; Lazar et al., 2000; Manna et al., 2010; Newberg et al., 2001). The activity in these brain regions may reflect processes such as attentional and affective regulation and saliency processing (V. Menon & Uddin, 2010; Posner & Rothbart, 2007). Where discrepancies between studies occur, careful examination of the content of the hypnotic induction (and the requirements during the hypnotic period), and the type of meditation practiced is likely to help explain the patterns of activation and deactivation, and may generate testable hypotheses for future studies.

On the whole, higher suggestibility appears to be associated with an expansion of the salience network (Hoeft et al., 2012; Huber et al., 2014), although the regions that have higher FC vary between studies. Enhanced FC within the salience network and the executive network can also often be seen in meditators (Froeliger et al., 2012; Hasenkamp & Barsalou, 2012; Xue et al., 2011). These functional organisations may reflect more unitary and integrated networks that provide additional control over attentional and affective processing, assist the goals of the meditative practices, and confer on Highs the ability to substantially modulate attention. The effect of hypnosis on FC was a decrease within brain regions that underpin the extrinsic system; a finding that fits closely with reported phenomenology such as dissociation (Demertzi et al., 2011). Meditation on the other hand was associated with increased FC within components of this system (Froeliger et al., 2012; Kilpatrick et al., 2011), which probably reflects task requirements (e.g., paying attention to the scanner noise in the study by Kilpatrick et al. 2011). Further evidence indicating that the flexibility of ICNs depends on the type of meditation was provided by Josipovic et al. (2011).

Finally, meditation led to decreased interaction between brain regions associated with attention and visual areas (Hasenkamp & Barsalou, 2012; Kilpatrick et al., 2011). Hypnotic suggestibility on the other hand was associated with increased FC to visual regions, which may underpin reports of mental imagery in hypnosis (Maquet et al., 1999; Rainville, Hofbauer, et al., 1999). Previous research has also shown that during hypnosis, spontaneous mental imagery (even when not requested) has occurred in participants, in addition to corresponding brain activity in relevant regions (Rainville, Hofbauer, et al., 1999).

Default Mode Network

The DMN has featured frequently in FC studies on hypnosis and meditation. It is composed of brain regions such as the ACC and posterior cingulate cortex (PCC), the ventral

and dorsal medial frontal cortex, the hippocampal formation, lateral temporal cortex, lateral parietal cortex and precuneus (Buckner et al., 2008). As described above, this network is usually active during self-referential thought, autobiographical memory, future planning, day-dreaming, and social cognition (Buckner & Carroll, 2007; Gusnard, Akbudak, Shulman, & Raichle, 2001; Mason et al., 2007).

Default mode network: Hypnosis and hypnotic suggestibility

McGeown et al. (2015) demonstrated that after a hypnotic induction, greater levels of self-reported hypnotic depth were associated with reduced FC within the anterior DMN in a group of participants which varied from high to low in hypnotic suggestibility. Further evidence for a decrease in DMN connectivity due to hypnosis comes from Lipari et al. (2012) who examined the effects of hypnosis in a single hypnotic virtuoso using Regional Homogeneity (ReHo) analysis. ReHo provides a measure of the similarity of the time-series in adjacent voxels and as opposed to FC which examines inter-regional relationships it offers a measure of coherence among voxels in localized regions (Zang, Jiang, Lu, He, & Tian, 2004). Decreased ReHo was apparent within the medial PFC and middle PFC (with increased ReHo in the occipital cortex). The findings across both studies appear to support previous observations of suppressed DMN activity during hypnosis (Deeley et al., 2012; McGeown et al., 2009), and the occipital ReHo increases may reflect the use of visual imagery as reported in other previous hypnosis studies (Maguet et al., 1999; Rainville et al., 2002). Some degree of caution must be applied to ReHo findings however, given the single case approach, and the fixed order, single repetition, of the conditions of no hypnosis and hypnosis.

In the study by Demertzi et al. (2011) mentioned above, a complex picture emerges in which hypnosis related decreases in DMN FC were seen within the left parahippocampal gyrus and PCC, whereas increases occurred within the medial prefrontal cortex and angular gyrus, bilaterally. The apparent discrepancy between the increased anterior DMN connectivity observed in the study by Demertzi et al. (2011) and the decreased FC/ReHo reported above (Lipari et al., 2012; McGeown et al., 2015), could result from Demertzi and colleagues' comparison of hypnosis to a mental imagery control condition as opposed to rest. Although the direct statistical comparison of hypnosis versus rest was not reported in the Demertzi et al. study (despite the networks being displayed individually), examination of the supplied figure (Fig. 2, p 316) suggests that hypnosis reduced both the anterior and posterior DMN substantially in relation to the rest condition. During hypnosis, participants also reported significantly less external thoughts (mind-wandering), which suggests suppression of the DMN. An explanation for higher FC in some elements of the DMN in the Demertzi et al. study, during hypnosis versus mental imagery, might relate to the requirements of the hypnosis condition. This involved revivication of autobiographical memories, which is a task requirement that is likely to depend upon the DMN (Andreasen et al., 1995) and neuroimaging research on autobiographical memory retrieval has indeed indicated involvement of the medial PFC (Buckner et al., 2008; Cabeza & St Jacques, 2007).

Focusing now on hypnotic suggestibility, and the FC differences that might facilitate the experience of hypnosis, Hoeft et al. (2012) and McGeown et al. (2015) did not find any significant relationship between hypnotic suggestibility and DMN FC. Huber et al. (2014) on the other hand found a number of interactions between the DMN and regions that comprise other ICNs. For example, people higher in suggestibility had increased FC between the lateral visual network and the cuneus, precuneus and PCC. The authors interpreted the increased FC to cortical regions relating to vision as congruent with reports that high suggestibility is associated with vivid imagery and fantasy proneness (e.g., Lynn & Rhue, 1986). The differences between the FC studies could relate to a range of factors, including the scales used to measure hypnotic suggestibility. These were inconsistent across the three studies. As item composition differs across scales (e.g. in the number relating to motor challenge, perceptual alteration), this is likely to impact the number of suggestions people respond to in each class, and due to the relationship with neuroanatomy that each type of suggestion has, this might result in the identification of slightly different brain/behaviour relationships. Another factor contributing to discrepancies in the findings could be the composition of the participant samples (in distribution of suggestibility, gender, etc.).

Default mode network: Meditation

A study by Brewer and colleagues (2011) offers insight into the effects of meditation on DMN FC both during meditative practice and in relation to the putative long-term changes observed during rest. Concentration (FA), loving-kindness, and mindfulness (involving FA and OM) in experienced mindfulness/insight meditators led to less self-reported mindwandering and lower activity within anterior and posterior areas of the DMN (collapsed across all three types of meditation) versus the controls. The findings parallel others which have demonstrated lower levels of activity within the DMN during meditation, more effective inhibition of the network in meditators compared to controls, and that capacity to inhibit correlates with attentional performance outside of the scanner (e.g., Farb et al., 2007; Garrison et al., 2013; Pagnoni, 2012). The FC analyses added to this picture, showing expansion of the DMN to the dACC (during meditation and rest) and left posterior insula (during meditation). Providing additional evidence for trait related changes, during rest, meditators were found to have increased FC between the posterior DMN and the DLPFC, bilaterally. The increased FC between the DMN and the other brain regions may reflect greater cognitive control over the DMN, which may reduce interference (Brewer et al., 2011). Despite being consistent with the theory that meditation leads to long-term changes in resting state FC, practitioners might have assumed a state of meditation during rest (spontaneously, with or without awareness), even when it was not required.

The study by Hasenkamp et al. (2012) described previously adds to the findings of enhanced connectivity between the DMN and other brain regions at baseline. During rest increased FC was detected between the DMN and the orbitofrontal cortex/ventromedial PFC (and a decoupling was observed between anterior and posterior DMN regions of the experienced meditators). Jang et al. (2011) also investigated FC in the DMN at baseline in meditators (who practiced Brain-Wave Vibration Meditation, the goals of which are to quiet the mind and reduce negative emotions through FA). Greater FC was found within the ventromedial PFC in meditators compared to controls. The higher connectivity involving the ventromedial PFC may reflect greater control over the regulation of emotional processing, inhibition of emotional response (Carretie, Lopez-Martin, & Albert, 2010; Winecoff et al., 2013) and/or the internalisation of attention (Jang et al., 2011).

Providing further support that DMN FC appears to undergo long-term modulation in relation to sustained meditative practice, Taylor et al. (2013) examined FC between particular nodes of the DMN, during rest, comparing a group of Zen meditators who were experienced in mindfulness (which involves both FA and OM) to beginner meditators. The experienced group had less connectivity between the dorsomedial PFC (dmPFC) and ventromedial PFC (vmPFC), and between the dmPFC and left IPL. The authors point out the role these anterior components of the DMN play in analytic self-referential processing and emotional judgement (Buckner et al., 2008; Taylor et al., 2013). The experienced meditators also had instances of increased FC, for example, between the dmPFC and the right IPL, and between the right IPL and the PCC and left IPL. The results of this study alone can highlight the complexity of ICN interactions and the associated interpretative difficulties.

The wide range of neuroimaging studies reported throughout this chapter are provided to highlight the similarities across studies where possible e.g., such as expansion of ICNs, but the results of these studies have been provided in sufficient detail to raise awareness that the findings are often complex and that both increases and decreases in FC between elements of different ICNs often occurs. Attempting to map the patterns of FC across brain regions to the abilities of meditators or those who are hypnotized often leads only to speculative interpretations of the meaning of the patterns, such as those suggested above, that may have theoretical support from a wide range of scientific literature, but the proposed relationships are rarely assessed directly. In the future, the inclusion of subjective measures could be extremely useful in understanding FC findings (Taylor et al., 2013), as could data collection pertaining to the abilities that are assumed to be superior in the participant (e.g., in regulating aspects of their emotions or cognition). Collection of this type of data would also aid interpretation of putative long-term changes to the resting state. To reinforce a point I made earlier, when meditators are asked to rest in a scanner, given the context of the study, they might partially engage in meditative practices (despite being instructed not to), meaning that their mental content is not representative of their resting cognitive state in everyday life. The possibility is also there that during rest periods (in a scanner or elsewhere), people highly experienced in meditation spontaneously engage in meditative processes (rest becomes more meditation like). A third alternative is that the mental processes utilized during rest might not differ from controls while FC patterns in the ICNs have undergone long-term changes.

Default mode network: Summary

Brain activity appears to be reduced within the DMN during meditation (e.g., Brewer et al., 2011; Farb et al., 2007) and hypnosis (Deeley et al., 2012; McGeown et al., 2009). Suppression of DMN activity in both may reflect reduced elaboration during the processing of self-referential thoughts should they occur, and less mind-wandering (Buckner et al., 2008).

A complicated pattern of DMN FC emerges in experienced meditators during rest, which may be characterised by an expansion of the DMN (Brewer et al., 2011; Taylor et al., 2013) to include areas associated with attention and executive control. Other findings include increased FC within the anterior DMN (Jang et al., 2011), but others instead report a reduction (Taylor et al., 2013). Divergent findings such as these may relate to the different requirements of the meditation under study. Further to this, as the studies on meditation tend to focus on many different styles (with little convergence on a particular type), this may present particular problems for the interpretation of FC analyses, where multiple relationships between nodes (positive and negative) may exist. Interpretative errors may well occur, especially without more insight into the mental state of practitioners (during the meditation and rest periods). Other factors that differ among studies which may restrict interpretation include the level of experience of meditators and the analytic techniques that are applied.

Hypnosis, compared to rest, led to reduced FC (and ReHo) within the DMN (Demertzi et al., 2011; Lipari et al., 2012) and increased depth of hypnosis was associated with greater decreases within the anterior DMN (McGeown et al., 2015). Taken together, these alterations to the DMN may be interpreted as reduced spontaneous thought and mind-wandering during hypnosis, but again the conclusions remain speculative. Of the beforementioned studies on hypnotic suggestibility, neither the findings of Hoeft et al. (2012), nor of Huber et al. (2014) or McGeown et al. (2015) appear to parallel the DMN FC findings in meditators. Associations between the DMN and the visual cortices may assist in imagery (Huber et al., 2014), but to date, hypnotic suggestibility appears to be more strongly linked to the salience and executive-control networks (Hoeft et al., 2012; Huber et al., 2014).

Structural Analyses

Investigations of regional grey matter (GM) have steadily multiplied over recent years. Cross-sectional and longitudinal studies in this area suggest the occurrence of plasticity related changes across a host of activities. To name but a few examples, variation in GM corresponds to navigation skills (Maguire et al., 2000), musical abilities (Gaser & Schlaug, 2003), learning to juggle (Draganski et al., 2004), picking up a second language (Mechelli et al., 2004) and extensive learning (Draganski et al., 2006). Interestingly macroscopic changes to regional GM can occur over very brief time periods, such as a number of days (May et al., 2007). Given the short time period over which GM changes can occur, the underlying neural changes are more likely associated with dendritic branching or synaptic plasticity, as opposed to glial or neuro-genesis (May et al., 2007). Typically, greater skill acquisition is related to greater GM volume/density/concentration/cortical thickness in associated brain regions, but this does not always appear to be the case. For example, decreased GM in brain regions could reflect higher automaticity (see Granert, Peller, Jabusch, Altenmuller, & Siebner, 2011; Hanggi, Koeneke, Bezzola, & Jancke, 2010; James et al., 2014). Another point to note is that GM cannot indefinitely expand with the acquisition of each new skill or with prolonged practice, and an inverse u-shaped curve relating to GM volume changes in association with skill learning over time has been demonstrated (Driemeyer, Boyke, Gaser, Buchel, & May, 2008).

Structural Analyses: Hypnotic suggestibility and hypnosis

The degree of susceptibility to suggestions provided in hypnosis appears relatively stable throughout one's life. For example, a study by Piccione, Hilgard, and Zimbardo (1989) showed that susceptibility scores between a test and retest period had a correlation of 0.82 after a 15 year retest, and 0.71 after 25 years. Additional studies also suggest a role for genetics (Morgan, 1973) and have highlighted an association between polymorphisms in the Catechol-O-Methyltransferase (COMT) gene and hypnotisability (Lichtenberg, Bachner-Melman, Gritsenko, & Ebstein, 2000; Raz, 2005; Szekely et al., 2010). Given these findings that high and low suggestible participants appear to vary in their behavioural capabilities and genetic profile it might be that individual differences in response to hypnosis or suggestions are associated with variance in the neuroanatomy/neurobiology of brain structures (McGeown et al., 2015).

Hypnotic suggestibility and hypnosis: ACC and PFC

Two studies have assessed the relationship between hypnotic suggestibility and regional GM volume using regression (Huber et al., 2014; McGeown et al., 2015). Huber et al. found that those higher in suggestibility had greater GM volume in the left superior and medial frontal gyrus. The authors interpreted the frontal correlations mainly in terms of the overlap with SMA/pre-SMA areas and cited the roles of these regions in the control of movement, postural stability, and in sensory-motor association (pointing out that Highs have been shown to have more effective sensory-motor integration (Menzocchi et al., 2010)). The findings of McGeown et al. (2015) did not replicate these results precisely, but did however find that greater self-reported depth of hypnosis was associated with more GM in the ACC, superior frontal gyrus and medial PFC, bilaterally. As shown above, these brain regions have been implicated in attentional and affective regulation and there is also overlap with the DMN. The larger volume of these cortical regions may facilitate hypnosis by enabling the suspension of spontaneous thought/self-referential processing. Interactions between the ACC

and superior frontal gyrus may also perhaps enable the modulation of metacognition during hypnosis. Refer to the cold control theory of hypnosis (Dienes & Perner, 2007; see also the chapter by Dienes & Semmes-Wheeler within this volume; Semmens-Wheeler & Dienes, 2012).

Hypnotic suggestibility and hypnosis: Insular cortices

Huber et al. (2014) found that suggestibility correlated negatively with GM volume within the left posterior insula and superior temporal gyrus. The role of the insula in interoception and in integrating external information was flagged, as were the associations between insular and temporal GM abnormalities in people with schizophrenia, and the related symptoms such as hallucinations and difficulties identifying stimuli which is self-generated (e.g., R. R. Menon et al., 1995; Wylie & Tregellas, 2010). McGeown et al. (2015) instead identified a *positive* correlation between suggestibility and volume within the left superior temporal gyrus, and at a less conservative statistical threshold, the left insula. It is unclear why this discrepancy has arisen and further research is required. Despite controversy as to direction of the relationship, both sets of authors pointed out the roles one or both of these brain regions appear to have in the formation of hallucinations and in determining agency. A positive relationship was also observed between reports of hypnotic depth and insular volume, but again only when a more liberal threshold was adopted (McGeown et al., 2015). As there are very few studies reporting neuroanatomical variation in relation to hypnotic suggestibility it is unclear whether there is a file-drawer problem. Future studies should consider much larger sample sizes to increase statistical power, gather convergent evidence using different suggestibility scales, and could assess the neuroanatomical variation between sub-types of Highs (such as those reported by, e.g., Terhune & Cardena, 2010).

Hypnotic suggestibility and hypnosis: White matter tracts

The first study to address the potential relationship between suggestibility and neuroanatomy focused on white matter (WM) and was provided by Horton, Crawford, Harrington, and Downs (2004). By manually measuring the subdivisions of the corpus callosum, Highs were found to have greater volume within the rostrum when compared to Lows. Higher volume within this WM tract that provides inter-hemispheric information transfer might facilitate hypnosis and increase attentional and inhibitory capabilities (Horton et al., 2004). In the first whole brain analysis, Hoeft et al. (2012) detected structural differences (WM/GM) between Highs and Lows within parietal, temporal and cerebellar brain regions, but the differences did not satisfy the primary statistical threshold set by the researchers and no further information was supplied on these within the publication. WM microstructure was also assessed with diffusion tensor imaging (DTI) but no between-group differences were detected.

Structural Analyses: Meditation

Compared to the dearth of neuroanatomical analyses concerning hypnotic suggestibility, there is an extensive literature on meditation. A very comprehensive systematic review and meta-analysis on this topic has been recently published by K. C. Fox et al. (2014) and readers may want to refer to this. Given the extent of the literature in this area, reporting the full set of brain regions that appear to undergo meditation related change is beyond the scope of this chapter and instead the focus will be placed on those studies and sets of brain regions that appear also to be relevant to hypnosis and/or suggestibility.

Meditation: ACC and PFC

As the ACC and lateral aspects of the PFC have been shown above to be consistently activated during meditation (see e.g., Hasenkamp et al., 2012; Manna et al., 2010), these brain regions (which are central to attentional and executive processing), might be anticipated to undergo long-term neuroanatomical change in meditators. The first assessment of structural neuroanatomy in relation to meditation by Lazar et al (2005) revealed significantly greater cortical thickness in the right middle and superior frontal sulci and insula of Buddhist Insight meditators (who practice FA and OM) compared to controls. Similarly, Vestergaard-Poulsen et al. (2009) found that meditators who practised Tibetan Buddhism (Dzogchen) had higher GM density in the left superior frontal gyrus, compared to controls. Later studies identified increased cortical thickness in the superior frontal, ventromedial, and orbitofrontal cortices in those who practice Brain Wave Vibration meditation, which involves FA on bodily sensations and emotions (Kang et al., 2013) and in the right dACC in Zen meditators, who practice mindfulness (Grant, Courtemanche, Duerden, Duncan, & Rainville, 2010). The findings of these studies support the assumption that repeated meditative practice (e.g., involving FA) leads to modulation of structure in brain regions such as the ACC and DLPFC, which play key roles in attentional regulation (Corbetta et al., 2008; Fan et al., 2005). As mentioned above, the ACC and DLPFC also seem to have increased volume in those who are higher in hypnotic suggestibility (Huber et al., 2014) and who report deeper levels of hypnosis (McGeown et al., 2015), findings which appear to highlight the similarities across practices in their utilization of these brain regions.

In a further analysis (which illustrates the utility of collecting additional information on participants that may be incorporated into the designs of future neuroimaging studies), Grant et al. (2013) showed that participant scores on the Tellegen Absorption Scale (Tellegen & Atkinson, 1974) were higher in meditators, were associated with the number of days of practice per week, and were positively related to cortical thickness in regions which included the left ACC, superior frontal gyrus, and the middle frontal gyrus bilaterally. Note that a PET study on hypnosis by Rainville et al., (2002) complements these results closely, showing a positive relationship between regional cerebral blood flow in the ACC and ratings of absorption, and that other functional neuroimaging studies demonstrate high levels of absorption during hypnosis (Deeley et al., 2012; Demertzi et al., 2011). For an in depth discussion of how absorption is related to both practices, see the chapter by Ott, this volume.

Activation of the dACC has also been reported during pain perception (Rainville, Carrier, Hofbauer, Bushnell, & Duncan, 1999), and Grant et al. (2010) suggest that greater cortical thickness in the dACC might enhance attentional control over pain and/or decrease emotional reactivity to pain. This is an interesting point as both hypnosis and meditation can be effective at modulating perceptions of pain (Grant et al., 2010; Grant & Rainville, 2009; Horton et al., 2004).

An alternative explanation for the enlargement of the left superior PFC in meditators might reflect a goal of certain types of meditation, namely the development of mindfulness or metacognition. Semmens-Wheeler and Dienes (2012) argue that hypnosis involves a disruption of metacognition (or higher order thoughts), whereas meditation attempts to promote metacognition. While meditative practice might be expected to lead to greater development of the left DLPFC, the theory that hypnosis disrupts metacognition does not necessarily translate into an expectation for decreased cortical thickness in the left DLPFC in Highs. It might instead be that greater development of the DLPFC, such as in the finding mentioned above by Huber et al. (2014) who found greater GM volume in the left DLPFC in association with suggestibility, or by McGeown et al. (2015) who reported larger GM volume

in the PFC in association with reports of deeper levels of hypnosis, may enable fractionation of meta-cognition. A functional explanation for the modulation would also be sufficient, possibly in terms of decreased activation (McGeown et al., 2009) or decreased FC (Demertzi et al., 2011; McGeown et al., 2015). For more information on the contrast between hypnosis and meditation in terms of metacognition and the links to the left DLPFC, see the chapter by Dienes et al. in this volume.

Meditation: Insular cortices

Many functional neuroimaging studies of meditation have highlighted the involvement of the insular cortices (e.g., Brefczynski-Lewis et al., 2007; Hasenkamp et al., 2012; Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008). In meditators, FC also appears to be altered between the insular cortex and the executive control and/or DMN regions during meditation (Froeliger et al., 2012; Kilpatrick et al., 2011) and during rest (Froeliger et al., 2012).

The study described above by Lazar et al. (2005) showed that meditators had greater cortical thickness in the right insula, when compared to controls. Additional support for meditation related adaptations to the insular cortex is provided by Holzel et al. (2008) who found that Vipassana (involving OM) meditators had greater GM concentration in regions that included the right anterior insula (compared to controls). In association with experience, a cluster within the right anterior insula also approached significance. Adopting a different methodological approach, Luders, Kurth, et al. (2012) demonstrated that meditators had greater cortical gyrification (the degree of cortical folding - in which a higher index equates to more surface area) in the insula bilaterally (with years of meditation experience correlating with gyrification in the right insula). Activities practiced during meditation, such as FA on interoceptive stimuli and awareness of emotion, cognition and external stimuli are likely causes of insular cortical development (Holzel et al., 2008; Lazar et al., 2005). Not all studies have provided evidence for adaption of the insular cortex due to meditation however. For example, a short-term training course (8 weeks) on MBSR meditation (which involves both FA and OM) and a subsequent ROI analysis focused on the insular cortices (and hippocampus), did not detect adaptations in grey matter concentration in either the left or right insula, but did detect change within the hippocampus (Holzel et al., 2011). Findings such as this may reveal the temporal dynamics of plasticity in some brain regions over others (or alternatively may highlight differential effects of contrasting meditative practices).

The insular cortex seems to be relevant to both meditation (Holzel et al., 2008; Luders, Kurth, et al., 2012) and suggestibility/depth of hypnosis (Huber et al., 2014; McGeown et al., 2015). Posterior portions of the insula have been linked to interoceptive processes, anterior aspects to exteroceptive processes (Farb, Segal, & Anderson, 2013), and middle portions have been suggested to provide sites for the integration of each input and a more unified experience of present moment awareness (Craig, 2009; Farb et al., 2013). Insular function also differs between hemispheres (e.g., in emotional processing, and autonomic control (Craig, 2005; Craig, 2009)). Of note, Critchley et al. (2004) demonstrate the role of the right insula in awareness of interoceptive processes, which appears to be particularly relevant to meditation. In future studies of meditation and hypnosis, more detailed analysis of insular function should be illuminating, both for our understanding of the practices and for higher order brain functions themselves.

Meditation: White matter

Cross-sectional studies, using DTI, have revealed higher fractional anisotropy (DTI-FA) in many of the major fibre tracts in the brains of meditators. For example, Luders, Clark,

Narr, and Toga (2011) found differences within the superior longitudinal fasciculus temporal component, superior longitudinal fasciculus, uncinate fasciculus, corticospinal tract and forceps minor of meditators of mixed practices versus controls. Higher DTI-FA values usually reflect enhanced connectivity, presumably due to greater numbers of fibres, changes in axonal structure or increases in myelination (Luders et al., 2011). Additional studies have demonstrated higher DTI-FA in meditators in regions such as the ventromedial PFC (Kang et al., 2013) and the anterior portion of the corpus callosum (Luders, Phillips, et al., 2012). Others have shown that very short periods of practice can influence DTI measures. For example, Tang, Lu, Fan, Yang, and Posner (2012) showed that only 5 hours of IBMT training led to a reduction in DTI axial diffusivity (which reflects axonal morphological changes), whereas a longer training regimen of 11hrs had a similar effect, but in addition showed a reduction in radial diffusivity (which reflects increased myelination) and an increase in DTI-FA within multiple fibre pathways including the genu and body of the corpus callosum (Tang et al., 2012; Tang et al., 2010).

The higher DTI-FA values in experienced meditators (and those that have undergone short-term training), for example, in the corpus callosum may reflect superior interhemispheric transfer capabilities (Luders, Phillips, et al., 2012; Tang et al., 2010). These findings appear to be congruent with the findings and interpretations of Horton et al. (2004), who found that Highs had greater WM volume in the rostrum of the corpus callosum than Lows. Differences such as these may underpin the enhanced emotional regulation and attentional skills that have been reported in meditators (e.g., Hodgins & Adair, 2010; Jha et al., 2007), and the attentional skills in Highs (e.g., Castellani, D'Alessandro, & Sebastiani, 2007). The meditation studies appear to be paving the way in this area and a much wider investigation of how WM varies macroscopically and in terms of microarchitecture in relation to hypnotic suggestibility and the capacity to experience hypnotic phenomena is necessary.

Overall summary and future directions

This chapter has included a range of neuroimaging studies that relate to meditation, hypnotic suggestibility and hypnosis. The most salient similarities between the practices have been highlighted, as have to a lesser extent, the differences.

The studies on meditation have included participants of many types of practices (sometimes even within the same study) and of varying levels of experience, different requirements during the scanning period, and various analytic techniques. The diversity of results, not always conveyed in their entirety in this chapter, appears to reflect these changeable factors, and although discovering the neural underpinnings of each particular style of meditation may be informative, well designed studies to replicate and build upon previous findings are necessary. Similar considerations should be made in relation to hypnosis studies. For example, various screening scales for hypnotic suggestibility are adopted, different analytic approaches used, and baseline comparison periods may vary (e.g., resting state, mental imagery). Even subtle changes in methodology can lead to substantially different findings, and sometimes it can be difficult to pool results. A number of key findings have however emerged from the literature and these will be explored below.

Drawing upon the functional neuroimaging literature on meditation, the ACC and the PFC were repeatedly activated (Baron Short et al., 2010; Brefczynski-Lewis et al., 2007; Farb et al., 2007; Hasenkamp et al., 2012; Lazar et al., 2000; Manna et al., 2010; Newberg et al., 2001), which may reflect processes such as focused attention, attentional control, conflict resolution and absorption (Egner, Jamieson, & Gruzelier, 2005; Fan et al., 2005; Grant et al., 2013). As a possible consequence of the repeated application of processes such as these,

meditation appears to be linked to greater GM density/cortical thickness in these brain regions (Grant et al., 2010; Grant et al., 2013; Kang et al., 2013; Lazar et al., 2005; Vestergaard-Poulsen et al., 2009). On a related point, FC studies illustrate increased connectivity between the cingulate cortex and DLPFC, and their connectivity to ICNs such as the DMN and executive-control network, both during meditation and rest (Brewer et al., 2011; Hasenkamp & Barsalou, 2012), which may reflect more integration of brain networks, with coordination possibly leading to greater attentional control. Note that most evidence comes from cross-sectional comparison rather than well controlled randomised longitudinal designs, however, and future investigations should take this into account to more firmly establish the causal effects of meditation.

Interestingly there are reports of ACC and PFC activity during hypnosis as well (Deeley et al., 2012; Maquet et al., 1999; Rainville et al., 2002; Rainville, Hofbauer, et al., 1999) and studies that have used different hypnotic inductions and different experimental designs have led to similar reports of phenomenology, e.g., increased absorption and reduced spontaneous thought (Deeley et al., 2012; Demertzi et al., 2011; Rainville et al., 2002). As in meditation, the activity within the ACC and the PFC may relate to attentional regulation and phenomena such as absorption, and neuroanatomical variations within these brain structures may underpin hypnotic suggestibility and facilitate hypnosis (Huber et al., 2014; McGeown et al., 2015). In sum, the interaction between the ACC and PFC appears to be highly relevant to both practices and as mentioned above structural adaptations within the left DLPFC in particular may be associated with improved metacognition in meditators, and/or enhanced flexibility to modulate that system in those that are suggestible and capable of deep levels of hypnosis (for additional discussion see Dienes et al., this volume).

In many of the studies, reverse inference is used in an attempt to back translate activity or link an alteration in FC to a cognitive process that is assumed to take place, but which has not been explicitly tested. Careful measurement of the phenomenology of hypnosis and meditation within future neuroimaging studies, and of the characteristics of people that vary in hypnotic suggestibility/meditative experience (e.g., attentional abilities) may help to avoid this problem, as it would allow relationships between these variables and neurophysiology/neuroanatomy to be explored (see the chapter by Cardeña, current volume).

The insular cortex is another brain region of interest for meditation and hypnosis. Activation of the insular cortices has been reported in both practices (Brefczynski-Lewis et al., 2007; Farb et al., 2007; Hasenkamp et al., 2012; Rainville et al., 2002; Rainville, Hofbauer, et al., 1999). Greater GM concentration/cortical thickness/gyrification of the insular cortices have been reported in those that meditate, with the extent of the differences relating to experience (Holzel et al., 2008; Lazar et al., 2005; Luders, Kurth, et al., 2012), and associations have been shown with hypnotic suggestibility and those who report deeper levels of hypnosis (Huber et al., 2014; McGeown et al., 2015). Studies on meditation (Froeliger et al., 2012; Kilpatrick et al., 2011) and hypnotic suggestibility (Hoeft et al., 2012) show alterations in FC between the salience network, which includes the insular cortices, and regions underpinning executive control and/or the DMN. The neuroanatomical variance and modified FC within the insular cortices may contribute to alterations in the perceived salience of environment or internal stimuli, sensory integration or interoception (Craig, 2009, 2011; Critchley, 2005; Critchley et al., 2004; Seeley et al., 2007). The insular cortex also appears to play a crucial role in supporting a sense of embodied presence (Craig, 2009, 2011), which may have significance for both practices, and has been linked to feelings of agency (Farrer et al., 2003; Farrer & Frith, 2002), which may be especially important for hypnosis and hypnotic suggestibility. Given the anatomical and functional connections between the insula and the ACC (Medford & Critchley, 2010), the coordination of activity within these brain regions (each heterogeneous in function) is likely to be a large contributor to the effects and

phenomenology of both hypnosis and meditation. The relationship between the ACC and insula may also assist the effective modulation of pain perception that has been reported both in meditators (Grant et al., 2010; Grant & Rainville, 2009) and in high suggestible people (Derbyshire, Whalley, & Oakley, 2009; Horton et al., 2004). For more information on the effects of meditation and hypnosis on pain perception see the chapter by Grant and Zeidan in this volume.

Investigations of WM suggest that meditation related modifications are widespread and are especially prominent within anterior brain regions. Higher suggestibility has also been linked to increased WM volume in the corpus callosum (Horton et al., 2004). Both of which may explain reports of superior attentional skills in meditators (e.g., Hodgins & Adair, 2010; Jha et al., 2007) and in Highs (e.g., Castellani et al., 2007; Raz et al., 2006; Raz, Shapiro, Fan, & Posner, 2002). Future neuroimaging studies should further investigate associations between WM microstructure and hypnotic suggestibility, as well as the capacity to experience certain hypnotic phenomena.

Alterations in activity and FC are present within the DMN during both hypnosis (Demertzi et al., 2011; Lipari et al., 2012; McGeown et al., 2015; McGeown et al., 2009) and meditation (Brewer et al., 2011; Froeliger et al., 2012), as well as in experienced meditators during rest (Brewer et al., 2011; Hasenkamp & Barsalou, 2012; Jang et al., 2011; Taylor et al., 2013). Decreased activity tends to be seen during both practices, which may reflect a decrease in mind-wandering or a reduction in the further processing of spontaneous or self-referential thoughts should they have occurred. With hypnosis, decreased FC/ReHo has been recorded within the anterior DMN (Demertzi et al., 2011; Lipari et al., 2012; McGeown et al., 2015), which again may relate to decreased mind wandering and spontaneous self-referential thought. Within the meditation literature, however, there are discrepant reports both of increased (Jang et al., 2011) and decreased FC (Taylor et al., 2013) within the anterior DMN in meditators during rest, the reasons behind which remain highly speculative, especially in the absence of information relating to the mental activities of the meditators.

FC within the extrinsic system (which involves salience/executive control regions such as the lateral fronto-parietal cortices) decreases during hypnosis (Demertzi et al., 2011), whereas it has been shown to increase during meditation (Froeliger et al., 2012). These differences are likely to reflect what is required from participants in each study; for example, dissociation from the environment in hypnosis, and attentional focus (FA) and monitoring of the environment or internal sensations in meditation (mindfulness).

Conclusion

Studies exploring the neural basis of meditation with FC and structural neuroimaging methods have multiplied faster than those focusing on the effects of hypnosis and the potential underpinnings of hypnotic suggestibility. Analytic techniques such as ICA, seed-based analyses and DTI-FA are beginning to be applied more frequently to the study of hypnosis and suggestibility, however, and future studies will further elucidate the commonalities and differences between the practices. Components of the salience and executive-control networks – the ACC, DLPFC and insula – often undergo functional modulation in both practices. Alteration in brain structure within these regions can also often be seen in meditators, and variations in these structures may likewise be associated with hypnotic suggestibility, and the ability to experience deep levels of hypnosis and phenomena such as absorption. The DMN is affected during meditative practice and hypnosis, and its activity appears to be supressed in both cases. In terms of FC, the majority of evidence seems to suggest that this network is expanded at rest in meditators, but it does not appear to be as strongly linked to suggestibility. Finally, many studies apply reverse inference to their

findings and future neuroimaging studies which apply phenomenological measures, and cognitive/behavioural/affective/physiological assessments, are likely to be hugely informative in our understanding of both practices and of brain function in general.

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