Hodgetts, S., Hausmann, M. (2022). Sex/Gender Differences in Brain Lateralisation and Connectivity. In: Current Topics in Behavioral Neurosciences. Springer, Berlin, Heidelberg. https://doi.org/10.1007/7854_2022_303

Sex/gender differences in brain lateralisation and connectivity

Sophie Hodgetts[a] and Markus Hausmann[b]
[a] School of Psychology, University of Sunderland, Sunderland, United Kingdom.
sophie.hodgetts@sunderland.ac.uk
[b] Department of Psychology, Durham University, Durham, United Kingdom.
markus.hausmann@durham.ac.uk

Abstract

There is now a significant body of literature concerning sex/gender differences in the human brain. This chapter will critically review and synthesise key findings from several studies that have investigated sex/gender differences in structural and functional lateralisation and connectivity. We argue that while small, relative sex/gender differences reliably exist in lateralisation and connectivity, there is considerable overlap between the sexes. Some inconsistencies exist, however, and this is likely due to considerable variability in the methodologies, tasks, measures, and sample compositions between studies. Moreover, research to date is limited in its consideration of sex/gender-related factors, such as sex hormones and gender roles, that can explain inter-and interindividual differences in brain and behaviour better than sex/gender alone. We conclude that conceptualising the brain as "sexually dimorphic" is incorrect, and the terms "male brain" and "female brain" should be avoided in the neuroscientific literature. However, this does not necessarily mean that sex/gender differences in the brain are trivial. Future research involving sex/gender should adopt a biopsychosocial approach whenever possible, to ensure that non-binary psychological, biological, and environmental/social factors related to sex/gender, and their interactions, are routinely accounted for.

1. Introduction

Recent decades have seen a substantial increase in the number of studies investigating sex/gender differences in the brain. These studies have generally supported the notion that sex/gender differences in the brain exist at multiple levels, including structural and functional lateralisation and connectivity (e.g., Cahill 2017; Jäncke 2018; Hodgetts and Hausmann 2020b). Historically, many cognitive neuroscientists have conceptualised sex/gender differences in brain structure and function as large and "hard-wired". Consequently, explanations for such differences typically emphasised early genetic factors and prenatal hormonal influences (Jäncke 2018). Recent evidence has prompted a shift away from such ideas, and a growing number of neuroscientists now agree that while sex/gender differences in the brain do exist they are small in size, and thus it cannot be argued that the brain is 'sexually dimorphic' (Joel et al. 2015; Hirnstein and Hausmann, 2021, Hodgetts and Hausmann 2020b; Eliot et al. 2021). Moreover, findings from several recent studies support taking a biopsychosocial approach to the study of sex/gender differences in the brain, such that both the influence of biological and environmental factors and their complex interaction(s) are investigated (Halpern 2013; Cahill 2017; Jäncke 2018; Hausmann 2020; Hodgetts and Hausmann 2020b; Joel 2021).

This chapter will review the findings from current research into sex/gender differences in brain lateralisation and connectivity. In this chapter, we will argue that some sex/gender differences reliably exist in both lateralisation and connectivity and that they are not trivial, while at the same time they are not "sexual dimorphisms" (see also Galea 2021; Hirnstein et al. 2021). We will argue that some sex/gender differences exist regarding both brain lateralisation and connectivity, but that there is a high level of inter-and intra-individual

variability resulting in a considerable amount of overlap between the sexes at population level. We will also argue that future research should adopt a biopsychosocial approach (Hausmann 2020), to ensure that environmental factors and intra-individual variation related to sex/gender are considered more routinely.

The term 'sex' is typically used when referring to the biological classification of an individual as male or female, based on their reproductive organs (e.g., genitalia) while 'gender' refers to the psychosocial constructs typically associated with sex (e.g., masculinity, femininity). However, the two terms are often misleadingly conflated in previous research, and it is not always clear whether a given study is investigating sex, gender, or both. Therefore, to account for this inconsistency, this chapter will use sex/gender, rather than 'sex' or 'gender' separately. It should also be noted that we are discussing data from averages of groups, not individuals. This chapter will also focus primarily on large-scale studies and meta-analyses, meaning several, high-qualities studies will not be reviewed in detail here. Finally, we explicitly avoid the term "sexual dimorphism" as this term implies two distinct brains in a binary sense: one male and one female, as all empirical evidence suggests that such dual categorisation is incorrect in the context of the brain.

2. Sex/gender differences in lateralisation

Sex/gender has been extensively investigated concerning cerebral lateralisation, a fundamental principle of functional brain organisation referring to the asymmetrical representation of a specific cognitive process to either the left or right cerebral hemisphere. For example, in the healthy adult human brain, the left hemisphere is typically dominant for some language processes (Broca, 1861; Kimura, 1967), while the right hemisphere is dominant for some visuospatial processes (Hellige 1993; Hugdahl and Westerhausen 2013).

Cerebral lateralisation can be assessed at both the structural level (i.e. asymmetry with regards to size/volume/shape of specific brain areas) and at the functional level (see Section 3.3).

2.1. Sex/gender differences in structural cerebral asymmetries

Given that a body of literature has supported the existence of sex/gender differences in specific language processes, research into sex/gender differences in structural cerebral asymmetries has focused on cortical areas known to be involved in language processes such as the planum temporale, a region that overlaps with Wernicke's area and is involved in language comprehension (Shapleske et al. 1999).

An early study with only 24 healthy participants revealed that the left planum temporale is bigger in men compared to women (Kulynych et al. 1994). Moreover, men showed an asymmetry (i.e., larger left PT compared to right), but women did not. A recent study of three large magnetic resonance imaging (MRI) datasets (n = 2337, 935, and 888) found a stronger leftward asymmetry in the planum temporale for men compared to women (Guadalupe et al. 2015). However, this finding is inconsistent. For example, a meta-analysis of 13 studies (n = 807) investigating structural asymmetry of the PT revealed no sex/gender difference (Sommer et al., 2008). In addition, two reviews of clinical data suggest that aphasia following left-hemispheric damage is not associated with sex/gender (Plowman et al. 2012; Watila and Balarabe 2015). Taken together, these findings suggest that (i) a sex/gender difference in the structure of the planum temporale might exist, (ii) the effect size is small, and (iii) a significant difference will only be detected with larger samples.

3. Sex/gender differences in connectivity

3.1. Structural connectivity

One of the most consistently reported sex/gender differences in brain macrostructure is brain size and volume. These studies suggest that the average male brain is larger and heavier than the average female brain (Peters 1991), even if sex/gender differences in body size are controlled for (Ruigrok et al. 2014). However, several authors have argued that this finding is a false positive that results from the specific analysis method and the specific method by which sex/gender differences in body size are controlled (Schluter 1992; Forstmeier 2011). For example, a recent study Sanchis-Segura et al. (2019) demonstrated that sex/gender differences in regional grey matter volumes were significantly reduced when the total intracranial volume was controlled for. As such, the authors argued that male-female differences in brain size are better conceptualised as size differences resulting from variation in total intracranial volume as opposed to sex/gender effects *per se.* The authors further argued that not all methods of controlling for total intracranial volume are equally valid/reliable, and some methods may produce misleading results.

Further MRI studies have demonstrated sex/gender differences in measures that are associated with within- and between-hemisphere structural connectivity, such as the relative composition of grey and white matter (GM, WM) volumes. Such studies have shown that WM volume is generally larger across the cerebrum in men compared to women (Allen et al., 2003; Filipek et al., 1994; Gur et al., 1999; Lentini et al., 2013; Passe et al., 1997). However, inconsistencies exist in the literature when several potentially confounding factors are considered. For example, when sex/gender differences in cranial size are controlled for, women typically yield a higher volume of GM compared to men (Gur et al. 1999; Goldstein 2001), while sex/gender differences in the relative proportions of GM and WM were

considerably reduced when differences in brain size are controlled (Lüders et al. 2002; Leonard et al. 2008; Jäncke et al. 2015). Furthermore, Allen et al. (2003) reported that women had a higher GM:WM ratio consistently across all brain structures and lobes analysed. This study with a relatively small sample size (n = 36) also showed that the effect of sex/gender was greater on WM than GM; that is, the higher GM:WM ratios in women were a result of reduced WM in women compared to men. More recently, a large MRI study (n = 900, van der Linden et al., 2017) also reported that women yielded a higher GM:WM ratio throughout the cortex compared to men, even after controlling for sex/gender differences in body size. However, it should be noted that van der Linden et al. (2017) used body height to control for body size differences, a measure previously suggested to lead to an overestimation of sex/gender differences in brain size (Jäncke et al., 2015). It is also likely that age is a relevant factor to consider regarding sex/gender differences in GM:WM, as several studies have shown that WM volume typically decreases during the perimenopause phase and throughout menopause itself (Brinton 2016; Rahman et al. 2020). Nevertheless, sex/gender differences in GM:WM proportions have been reported in two recent studies with large sample sizes (n = 1400, Joel et al. 2015; n = 2838, Lotze et al. 2019). Together, these findings suggest that while brain/body size may explain some of the variance in GM:WM ratio, it is likely that sex/gender effects are also present.

The size and/or shape of the corpus callosum is one of the most frequently cited examples of sex/gender differences in structural connectivity (Eliot et al. 2021). Several early studies reported that the posterior subsections of the corpus callosum were larger in women compared to men, including the splenium (e.g., Allen et al., 1991; DeLacoste-Utamsing & Holloway, 1982), posterior midbody (Habib et al. 1991), and the isthmus (Witelson, 1989). Such findings are inconsistent, with some studies demonstrating larger corpus callosum

sections in men compared to women (e.g., Allen et al., 2002; Westerhausen et al, 2011), or no sex/gender differences (Oppenheim et al. 1986). Moreover, evidence from meta-analyses of such studies has demonstrated that larger callosal indices in women become evident only when sex/gender differences in brain size are controlled for (Bishop and Wahlsten 1997; Smith 2005; see also Cahill 2017). Consequently, more recent studies have investigated sex/gender differences in the corpus callosum while statistically controlling for variation in brain size and/or by matching male and female samples for brain size. Using both methods, a larger study (n = 316) by Ardekani et al. (2013) found that the whole corpus callosum was larger in women compared to men (see also, Shiino et al., 2017). In contrast, Luders et al. (2014) found in a smaller sample (n = 96) that sex/gender differences in callosal thickness were reduced when male/female samples were matched for intracranial volume. Another possible explanation for these inconsistencies is the small sample sizes used in most individual studies. Indeed, in a recent review, Eliot et al. (2021) argued that since most studies on sex/gender differences in the corpus callosum included less than 100 participants they are likely underpowered and not able to detect the estimated effect size (d = 0.22, as reported in an earlier meta-analysis by Smith, 2005).

Aside from the corpus callosum, two other inter-hemispheric connections have been shown to differ in size between men and women: the anterior commissure and interthalamic adhesion, also known as massa intermedia (Eliot et al., 2021). To date, findings regarding the anterior commissure are inconsistent with some evidence suggesting it is bigger in men (Demeter et al., 1988), some reporting a larger anterior commissure in women (Allen and Gorski 1991), while others showed no sex/gender difference (Lasco et al. 2002). More recently, an MRI study by Choi et al. (2011) included correction for sex/gender differences in intracranial volume (ICV) and reported larger anterior commissure volumes in middle-aged

(but not young adult) women. Findings regarding a sex/gender difference in the size of the interthalamic adhesion are more reliable with studies typically showing it is larger in women compared to men (Allen and Gorski 1991; Damle et al. 2017). However, it should be noted that the number of studies of this structure is limited. For example, it is unclear to what extent the size of the interthalamic adhesion is sensitive to brain size, and more importantly, its functional relevance is largely unknown (Damle et al., 2017).

More recent studies have used diffusion tensor imaging (DTI) to investigate sex/gender differences in microstructural connectivity. Studies of microstructure typically report measures of fractional anisotropy (FA) and mean diffusivity (MD) as indices of white matter (WM) fibre organisation and structural integrity, respectively. Several studies investigated sex/gender differences in WM microstructure of the corpus callosum, which allows for inferences to be made regarding structural interhemispheric connectivity (Westerhausen et al. 2003, 2011; Hsu et al. 2008; Schmithorst et al. 2008; Kanaan et al. 2012). For example, Westerhausen et al. (2003) found higher FA throughout the corpus callosum in men compared to women, possibly reflective of thicker myelination and/or less inter-fibre space in the average male corpus callosum. In a further study, Westerhausen et al. (2011) reported greater FA and lower MD in the anterior genu subregion of the corpus callosum in men. Given that this subregion facilitates interhemispheric connectivity between the two frontal lobes, these results were interpreted as evidence for stronger, more efficient callosal-frontal connectivity in men. While both studies are limited by relatively small samples, Westerhausen et al. (2011) concluded that this may be related to sex/gender differences in lateralisation (see Section 3.3 of this chapter). An alternative interpretation of these findings is that the stronger callosal connectivity in males may be due to the greater distance between the hemispheres, resulting from their larger overall brain size. Other studies reported

inconsistent results, with some demonstrating higher FA in the corpus callosum in women compared to men (Schmithorst et al. 2008; Kanaan et al. 2012) while others suggested there are no sex/gender differences in global FA and MD (Eluvathingal et al. 2007; Hsu et al. 2008; Clayden et al. 2012). Moreover, evidence suggests that sex/gender differences in WM microstructure become non-significant after controlling for differences in intracranial volume (Takao et al. 2014). Overall, there is an ongoing debate regarding whether sex/gender differences in the macro-and microanatomy of the corpus callosum truly exist, as well as whether sex/gender differences in WM exist in the brain globally.

Further DTI studies have investigated sex/gender differences in the structural connectivity via whole-brain analysis (Iturria-Medina et al. 2007, 2008; Tian et al. 2011; Ingalhalikar et al. 2014). For example, across two smaller sample studies (n = 5 and 20, respectively), Iturria-Medina et al. (2007; 2008) reported no sex/gender differences in the small-world attributes (high clustering of network nodes, short paths between nodes) of the whole brain. In contrast, Yan et al. (2011) found that women exhibited greater clustering within several specific brain regions, such as the precuneus, precentral gyrus, lingual gyrus, and the calcarine fissure, suggesting sex/gender differences in local network efficiency. Ingalhalikar et al. (2014) investigated sex/gender differences in structural connectivity across the whole brain in a large sample of healthy participants (n = 949), including children and young adults (8–22 years of age). Results showed that men exhibited greater intra-hemispheric structural connectivity compared to women, particularly between the frontal, temporal, and parietal lobes. In contrast, women exhibited greater inter-hemispheric structural connectivity. Such differences in structural connectivity were not seen in similar studies (Duarte-Carvajalino et al. 2012; Dennis et al. 2013).

Ingalhalikar et al. (2014) argued that the inconsistency between their results and previous studies may be due to small effect sizes, meaning the effects will only be detected by larger samples. However, Hänggi et al. (2014) revealed similar differences in inter-and intra-hemispheric connectivity using a smaller sample (n = 138), suggesting that the inconsistent results are not entirely due to small effect sizes and underpowered studies. Critically, Hänggi et al. (2014) demonstrated that differences in inter-and intra-hemispheric connectivity were driven by differences in brain size, not sex/gender per se. That is, larger brains were more often associated with more intra-hemispheric connectivity and smaller brains were more often associated with more inter-hemispheric connectivity, even when the sample was pooled according to sex/gender. It should also be noted that the study reported by Ingalhalikar et al. (2014) has been subject to multiple criticisms concerning the authors' methodology and interpretations of their data (Joel and Tarrasch 2014). Regarding methodology, this study did not control for brain size, a factor known to both vary according to sex/gender and to influence structural connectivity. Moreover, as noted by Joel and Tarrasch (2014), it is important to place the significant results in context as Ingalhalikar et al. (2014) only found sex/gender differences in a small subsample of the 9000 connections assessed in their study. Moreover, Ingalhalikar et al. (2014) argued that such sex/gender differences in structural connectivity suggested that "male brains are structured to facilitate connectivity between perception and coordinated action, whereas female brains are designed to facilitate communication between analytical and intuitive processing modes." (p. 1), despite the study lacking behavioural measures. In contrast, an earlier, larger study (from which Ingalhalikar et al.'s participants were sampled) demonstrated that although sex/gender differences in social cognition and spatial processing were present, the effect sizes were small (Gur et al. 2012), suggesting that the conclusions drawn in 2014 are highly speculative at best.

A further study aimed to investigate whether structural sex/gender differences in functionally defined cortical networks such as auditory, visual, and motor networks, are related to behavioural sex/gender differences (Tunç et al. 2016). In this study, a large sample of healthy participants (n = 900) underwent both DTI and neurocognitive testing. The results demonstrated more structural connectivity in men within the motor, sensory, and executive function networks, while women exhibited greater connectivity within networks associated with memory, attention, and social cognition. The results suggest that sex/gender differences in structural connectivity can predict some sex/gender differences in cognition. A further recent structural connectivity study with a sample of 312 males and 362 females, aged 9–22 years, suggested that "the degree to which a given participant's cognitive profile was "male" or "female" was significantly related to the masculinity or femininity of their pattern of brain connectivity" (Satterthwaite et al., 2015, p. 2383). Although these studies indicated sex/gender differences in structural connectivity, the overall picture is inconsistent because other studies with large samples revealed no sex/gender differences (e.g., Nielsen et al., 2013) as well as substantial variability and overlap both within and between men and women.

3.2. Functional connectivity

Several studies have investigated sex/gender differences in functional connectivity using functional MRI paradigms (fMRI), in which participants are scanned while completing a specific cognitive task. Most studies using such paradigms to investigate sex/gender differences have focused on differences in task-related activity in specific cortical regions (for a review see Eliot et al., 2021), while other studies investigated sex/gender differences in task-related functional connectivity by examining the temporal correlation of activity between brain areas during a given task. Other studies have focused on sex/gender differences in

resting-state functional connectivity, defined as the temporal correlation of activity between brain regions generally in the absence of a specific cognitive task (Tomasi and Volkow 2012a; Mao et al. 2017; Ritchie et al. 2018; Zhang et al. 2018; Weis et al. 2019; Wheelock et al. 2019). Further resting-state fMRI studies have investigated sex/gender differences in the resting functional connectivity of several task-related cortical networks in the absence of a specific task.

3.2.1. Task-related connectivity

Sex/gender differences in task-related functional connectivity have been investigated using fMRI during sex/gender-sensitive visuospatial tasks, such as mental rotation. These studies typically showed that sex/gender differences exist in the networks that underpin mental rotation. For example, it was shown that accurate mental rotation performance was associated with deactivation of the parieto-insular vestibular cortex in men only (Butler et al. 2006), whereas accurate performance in women was underpinned by functional connectivity between frontal and parietal cortical regions (Thomsen et al. 2000; Weiss et al. 2003; Hugdahl et al. 2006), though contradictions have also been reported (see Eliot et al., 2021, for a tabulated review). In an earlier review, Cahill (2006) noted a common misconception regarding sex/gender differences in brain and behaviour which assumes that no sex/gender differences in (cognitive) behaviour imply no sex/gender differences in the underlying neural network. Several studies have shown that this is incorrect. For example, Jordan et al. (2002) demonstrated significant sex/gender differences in mental rotation-related brain activity, despite similar task performance between men and women in the same study. Together, these findings indicate that the lack of a sex/gender effect in task performance cannot necessarily be used to infer a lack of sex/gender effects at the neural level (Cahill, 2006).

Additional studies have investigated sex/gender differences in task-related functional connectivity associated with the integration of cognitive and emotional processes (Weissman-Fogel et al. 2010). These studies revealed sex/gender differences in the underlying mechanisms associated with cognitive control and emotion (Butler et al., 2007; Cahill, 2003; Hamann & Canli, 2004; Koch et al., 2007 for a review see Cahill, 2017). For example, in an fMRI study, Butler et al. (2007) demonstrated in a small sample (n = 32) that performing a cognitively demanding task was associated with a suppression of activity in the ventral anterior cingulate cortex, a region associated with affect regulation (Stevens et al. 2011) and emotion recognition (Etkin et al., 2011) among other processes related to social cognition (Rigney et al., 2018), in women only. Butler et al. (2007) also reported negatively correlated functional connectivity between the ventral and dorsal anterior cingulate cortices in women only. Consequently, and similar to Cahill (2006), Butler et al. (2007) suggested that sex/gender differences in task-related functional connectivity that may partly reflect sex/gender differences in the neurocognitive strategies used to complete the task do not necessarily result in sex/gender differences in task performance. Specifically, Butler et al. argued that suppression of the ventral anterior cingulate likely reflects the greater cognitive effort, consistent with a "top-down" approach to mental rotation in women. Taken together, findings from studies of task-related connectivity support the notion that sex/gender differences reflect different neural correlates of the behaviour – i.e., comparable task performance underpinned by different patterns of neural activity (De Vries 2004; Becker and Koob 2016; Hirnstein et al. 2021).

3.2.2. Resting-state connectivity

Several recent studies have investigated sex/gender differences in functional connectivity using resting-state fMRI (rs-fMRI) paradigms, in which awake participants are scanned

without a specific cognitive task to complete. Smaller early studies yielded no (n = 49, Weissman-Fogel et al., 2010) or small sex/gender differences (n = 40, Bluhm et al., 2008), with the latter finding demonstrating greater connectivity in the default-mode network (DMN) of women. The DMN is comprised of the dorsal and ventral medial prefrontal cortex, the posterior cingulate cortex, precuneus, and lateral parietal cortex (Laird et al. 2011). The function of the DMN was initially thought to be 'spontaneous cognition', such as daydreaming or mind-wandering, but more recent findings suggest that it is involved in fundamental processes such as the functional integration of multiple cortical regions (for a review, see Raichle, 2015). Unlike other resting-state networks, which become more active during cognitive processing, activity in the DMN typically reduces (Raichle 2015b). In line with this suggestion, hyperconnectivity and hyperactivity in the DMN has been demonstrated in psychiatric disorders such as schizophrenia (Whitfield-Gabrieli et al. 2009).

Several large rs-fMRI studies have revealed stronger functional connectivity in the DMN of women compared to men (Biswal et al. 2010; Allen et al. 2011; Tomasi and Volkow 2012b; Ritchie et al. 2018; Zhang et al. 2018; De Lacy et al. 2019; Weis et al. 2019), though contradictions also exist (Weissman-Fogel et al. 2010). This finding is important, as atypical organisation and function of the DMN has been demonstrated in clinical populations where men are overrepresented, such as schizophrenia and bipolar disorder (Garrity et al. 2007; Whitfield-Gabrieli et al. 2009; Öngür et al. 2010). It should be noted, however, that if schizophrenia is associated with higher DMN activity, and women have higher resting DMN activity than men, then it seems contradictory that schizophrenia is more prevalent in men. This might suggest that the relationship between connectivity and psychopathology differs between men and women. Similar contradictions apply to sex/gender differences in lateralisation as reduced cerebral asymmetries have been frequently reported in

schizophrenic samples compared to healthy controls, and in women compared to men (see below).

In a recent review, Eliot et al. (2021) noted that several inconsistent findings exist when the whole connectome is considered (see Table 1). For example, the specific regions of difference, as well as the direction of the sex/gender difference, varies depending on the chosen analysis method. Evidence supporting this claim can be found in studies that applied different analysis methods to the same data sets, such as those reported by Tomasi and Volkow (2012a) and Zuo et al. (2012). Although both studies used data from the "1000 Functional Connectomes Project" (Biswal et al. 2010), differences in analysis methods resulted in differing conclusions; Tomasi and Volkow (2012a) showed that women had higher local functional-connectivity density across multiple cortical regions compared to men, while Zuo et al. (2012) found that women had higher functional connectivity density in some areas while men had higher functional density connectivity in other areas. Still further studies suggest that sex/gender differences in functional connectivity exist, but they are small and there is considerable overlap between men and women (e.g., Weis et al., 2020). Taken together, these findings suggest that sex/gender differences exist, but studies are quite inconsistent in terms of sample size, specific resting-state networks investigated, and findings. Comparisons between studies are further complicated as only a very few studies (e.g., Hjelmervik et al. 2014; Weis et al. 2019) included sex hormonal factors in their analyses. Further caution is warranted as many fMRI studies are underpowered and significant results may be subject to publication bias (David et al. 2018).

Table 1: Studies investigating the effect of sex/gender on connectivity of different resting state networks.

Study	Number of participants (M:F)	Mean age (± SD)	Sex/gender-related factors considered	Resting state network(s) investigated	Main results
Allen et al. (2011)	603 (298:305)	23.4 (9.20)	None	Attentional, Auditory, Basil ganglia, Default mode, Frontal, Sensorimotor, Visual	Increased within-network connectivity in women, particularly in default mode network and some nodes of the frontal networks (including Broca's area) Increased between-network connectivity in men, particularly between motor and sensory networks.
Biswal et al. (2010)*	1093 (not reported)	30.18 (6.40)	None	Default mode (and whole brain connectome)	Increased functional connectivity in the default mode network in women compared to men.
De Lacy et al. (2019)	670 (335:335)	Not reported	None	Cerebellar, Control, Default mode, Language, Sensorimotor, Visual	Sex/gender differences present in majority of resting state networks, most robust differences were increased connectivity in the default mode network of women compared to men.
Filippi et al. (2013)	104 (48:56)	Not reported	None	Attention, Auditory, Control, Default mode, Fronto-parietal	Men showed increased connectivity in parietal and occipital regions across most networks

				working memory, Salience, Sensorimotor, Visual	compared to women. Women showed increased connectivity in frontal and temporal regions across networks compared men. Women also showed increased connectivity between attention and fronto-parietal working memory networks compared to men.
Hjelmervik et al. (2014)	31 (15:16)	23.19 (3.72)	Menstrual cycle (women tested three times, cycle phase verified via saliva assays of estradiol and progesterone)	Fronto-parietal	Women showed increased connectivity in two of four fronto-parietal networks investigated.
Ritchie et al. (2018)	5216 (2466:2750)	61.72 (7.51)	None	Default mode, Frontal, Sensorimotor, Visual	Men showed increased connectivity between the sensorimotor, visual, and rostral lateral prefrontal areas compared to women. Women showed increased connectivity within the default mode network compared to men.
Scheinost et al. (2015)	103 (52:51)	34.1 (11.20)	None	Auditory, Default mode, Fronto-parietal, Sensorimotor,	Men showed increased connectivity in sensorimotor network compared to women.

				Subcortical-limbic, Visual	Women showed increased connectivity in subcortical and limbic networks compared to men.
Smith et al. (2014)	188 (85:103)	21.85 (SD not reported)	Testosterone levels included as a covariate; type of sample (i.e., blood or saliva) not reported	Auditory, Frontal-parietal, Visual	Compared with women, men showed increased connectivity between the visual network and the intracalcerine cortex, cuneus, supracalcerine and lingual gyrus. Men also showed increased connectivity between the auditory network and Heschl's gyrus, planum temporale, insula, and temporal pole. Finally, men also showed increased connectivity between the frontal-parietal network and the middle, superior, and inferior frontal gyrus. Testosterone levels did not correlate with any of the above measures.
Tomasi & Volkow (2012b)*	561 (225:336)	Not reported	None	Whole brain	Women had 14% higher connectivity compared to men, even after differences in total brain volume, grey matter, white matter, and age

					were controlled for. Largest differences were seen in the anterior thalamus.
Weis et al. (2019)	38 (19:19)	24.73 (3.58)	Menstrual cycle (women tested three times, cycle phase verified via blood assays of estradiol and progrestone)	Auditory, Default mode	No sex/gender differences present in connectivity of the default mode network. For the auditory network, men showed increased connectivity between the superior temporal gyrus and the postcentral gyrus compared to women.
Weissman-Fogel et al. (2010)	49 (23:26)	30.00 (7.00)	None	Control, Default mode, Salience	No sex/gender differences present in functional connectivity in any of the networks investigated.
Zhang et al. (2018)	820 (366:454)	Not reported	None	Whole brain	Functional connectivity of the default mode, fronto-parietal, and sensorimotor networks contributed most to predictions of sex/gender.
Zuo et al. (2012)*	1003 (434:569)	28.10 (12.70)	None	Whole brain	Women showed increased functional connectivity in the hippocampus and medial occipital regions compared to men. Men showed increased functional connectivity in pre-and postcentral lobules compared to men.

	Findings were inconsistent across analysis methods.

*indicates data sampled from the *1000 Functional Connectomes Project* (http://fcon_1000.projects.nitrc.org/)
Auditory: superior temporal gyrus, auditory cortices
Attentional: inferior parietal lobule, middle and superior frontal gyrus, precuneus, middle and superior temporal gyrus, angular gyrus, cingulate gyrus, insula
Basal ganglia: left and right putamen
Cerebellar: anterior and posterior lobe
Control: anterior cingulate, anterior prefrontal cortex, dorsolateral and ventrolateral prefrontal cortex, inferior parietal cortex, insula
Default mode: dorsal and ventral medial prefrontal cortex, posterior cingulate cortex, precuneus lateral parietal cortex
Frontal: inferior and middle frontal gyrus, supramarginal gyrus, middle temporal gyus, caudate, pyramis, superior medial gyrus, superior parietal lobule
Fronto-parietal/frontro-parietal working memory: dorsolateral prefrontal cortex, intraparietal sulcus, posterior parietal sulcus
Salience: dorsal interior cingulate and bilateral fronto-insular cortices
Sensorimotor: precentral gyrus, cerebellum, postcentral gyrus, precuneus, inferior frontal gyrus, middle temporal gyrus, insula, supramarginal gyrus, supplementary motor area, inferior parietal lobule
Subcortical-limbic: parahippocampal gyrus, hippocampus, thalamus, insular cortex, amygdala
Visual: lingual gyrus, calcarine gyrus, visual cortices, inferior parietal lobule, inferior temporal lobule

3.3. Sex/gender differences in functional cerebral asymmetries

In addition to structural cerebral asymmetries and structural/functional connectivity, sex/gender differences have been extensively investigated with respect to functional cerebral asymmetries (FCAs, Hodgetts & Hausmann, 2020). Although it has been shown that FCAs are relatively stable over time (e.g., Vingerhoets 2019), several factors have been shown to contribute to variations and dynamic changes in FCAs (e.g., Hausmann, 2019; Hausmann et al., 2016), including biological sex and sex hormones (e.g., Hausmann 2017).

In healthy adults, a large body of research showed sex/gender differences in FCAs related to language (Hausmann et al., 1998; Shaywitz et al., 1995), spatial ability (Chiarello et al. 1989; Hausmann and Güntürkün 2000), and face recognition (Rizzolatti and Buchtel 1977; Borod et al. 2005). While contradictions exist (Boles, 2005; Sommer et al., 2004), these studies suggest that women show reduced FCAs (i.e. greater bilateral brain activity) relative to men. Several reviews, meta-analyses, and large-scale behavioural studies have been conducted to quantify the size of sex/gender effects on FCAs across a range of lateralised processes (e.g., Bless et al., 2015; Hausmann et al., 2019; Hiscock et al., 1994; Vogel et al., 2003; Voyer et al., 1995). A recent systematic review summarised these findings spanning 40 years (Hirnstein et al. 2019) and concluded that a small but robust effect size regarding greater FCAs in men ($d = 0.05 – 0.15$). This suggests that such sex/gender differences in FCAs do exist at population level but may only be detected in studies with larger samples.

Several MRI studies also investigated the effect of sex/gender on FCAs. For example, using rs-fMRI Liu et al. (2009) found small but significant sex/gender differences for both left- and right-lateralised resting-state networks, with men showing stronger FCAs than women. However, both sexes showed strong FCAs in this study, and there was much overlap between

them. In a larger rs-fMRI study (n = 913), Tomasi and Volkow (2012a) reported that men had stronger rightward FCAs for short-range connectivity in specific regions of the superior temporal, inferior frontal, and inferior occipital cortices, while women had stronger leftward FCAs for long-range connectivity in the inferior frontal cortex. Furthermore, in a large rs-fMRI study (n = 1011), Nielsen et al. (2013) identified several resting-state networks characterised by lateralisation (e.g. the DMN and language network included several left-lateralised regions), but the patterns of FCAs did not differ between men and women. Finally, a recent structural MRI study used measures of cortical thickness to create 'hemispheric morphological networks' in a sample of 285 participants (Choi et al., 2020). Results showed that the patterns of FCA differed between men and women in several cortical regions, with men showing stronger FCAs in the cingulate and superior parietal gyrus, and women showing stronger FCAs in the temporal pole.

In sum, although inconsistencies exist regarding specific brain areas and methodologies used, several meta-analyses and large-scale studies suggested that sex/gender differences in FCAs do exist and that interactions with sex/gender should be considered when investigating lateralisation and brain connectivity. Sex/gender and FCAs have also been identified as potentially relevant factors with regards to several clinical disorders (e.g., schizophrenia and other psychotic disorders, for a review see Hodgetts and Hausmann 2020a). Although the relationship between sex/gender, lateralisation, and psychopathology is not well understood, and therefore remains speculative, future research investigating these relationships might help to better understand individual differences in clinical populations, which in turn will support the development of stratified treatments for disorders characterised by sex/gender differences and/or atypical FCAs.

3.4. Hormonal influences on lateralisation and connectivity

Considering the evidence presented above, sex/gender differences exist concerning both connectivity and lateralisation. However, it is incorrect to refer to brains as 'sexually dimorphic' as there is clear empirical evidence showing that prototypical 'male brains' or 'female brains' do not exist. Instead, there is overlap in brain structure and function between the sexes, and there is substantial within-sex/gender variation. As such, an increasing number of studies support the notion that sex/gender differences are best conceptualised as a product of several non-binary factors, including biological (e.g. sex hormones) and environmental influences.

Several studies have shown that an individual's distinct hormonal profile can be an important factor in the generation and maintenance of sex/gender differences in lateralisation (i.e. FCAs) and connectivity (Weis and Hausmann 2010; Hodgetts and Hausmann 2018, 2020a). However, sex hormone levels are dynamic, both across short-time intervals (e.g., fluctuating during the menstrual cycle), across the lifespan (e.g., reducing after menopause). Indeed, many studies investigating menstrual cycle-related effects of sex hormones on lateralisation have revealed reduced FCAs during the follicular phase (high levels of estradiol) and/or during the postovulatory luteal phase and increased FCAs during menstruation (lowest levels of estradiol and progesterone, (Hausmann 2017; Hodgetts and Hausmann 2018). In contrast, other studies showed larger FCAs during the follicular and/or luteal phase in combination with reduced FCAs during menstruation (e.g., Cowell et al., 2011; Mead & Hampson, 1996; Sanders & Wenmoth, 1998; Wadnerkar et al., 2008). The conflicting results, sometimes occurring even in the same study (e.g., Mead and Hampson 1996; Sanders and Wenmoth 1998), may suggest that some studies are reporting false positives, or they indicate that size and direction of the

effects partially depend on the specific task and test modality (Hausmann and Bayer 2010; Hodgetts et al. 2015, 2017).

Although different explanations on how sex hormones might influence lateralisation have been proposed, one explanation takes the neuromodulatory properties of sex hormones into account and hypothesised that sex hormones affect lateralisation via their effects on functional connectivity. The *hypothesis of progesterone-mediated interhemispheric decoupling* (Hausmann and Güntürkün, 2000) stated that high levels of progesterone lead to a reduction in interhemispheric inhibition (i.e., activity in the non-dominant hemisphere is no longer suppressed by the dominant hemisphere). Specifically, it was hypothesised that higher levels of progesterone can reduce interhemispheric inhibition by suppressing the excitatory responses of neurons to glutamate (Smith et al. 1987) and by enhancing their inhibitory responses to GABA (Smith 1991), leading to increased bilateral activation and reduced FCAs (e.g., Cook, 1984; Regard et al., 1994). This mechanism presumes that FCAs arise because the hemisphere dominant in a particular task inhibits the non-dominant hemisphere via the corpus callosum (Cook 1984; Chiarello et al. 1989). Although cortico-cortical transmission is primarily excitatory, callosal projections terminate on pyramidal neurons, which subsequently activate GABAergic interneurons (Toyama & Matsunami, 1976), inhibiting the contralateral hemisphere (Innocenti, 1980). Moreover, it has been shown that callosal projections terminate directly on GABAergic interneurons (Conti and Manzoni 1994). Both mechanisms would result in widespread inhibition of homotopic regions of the nondominant hemisphere by the dominant hemisphere. This hypothesis was supported empirically by several behavioural studies of FCAs (e.g., (Hausmann and Güntürkün 2000; Hausmann et al. 2002, 2013; Bayer et al. 2008), transcranial magnetic stimulation experiments (Hausmann et al., 2006), and fMRI (Weis et al., 2008; Weis et al., 2011).

Further research revealed that high estradiol levels may also be capable of reducing FCAs via an effect on interhemispheric inhibition (Hausmann 2005, 2017; Hausmann et al. 2006; Weis et al. 2008; Hausmann and Bayer 2010). For example, Weis et al. (2008) used fMRI to scan a sample of naturally cycling women while completing a word-matching task. Results revealed that high levels of estradiol during the follicular phase were associated with reduced interhemispheric inhibition, and in turn, reduced FCAs. Hausmann et al. (2013) used electroencephalography to directly measure interhemispheric connectivity by using visual-evoked potentials to estimate interhemispheric transfer time (IHTT). The results showed that IHTT from right-to-left was longer during the luteal phase as compared to the menstrual phase and that this effect was related to high levels of estradiol, as opposed to progesterone. Further research has investigated the effect of sex hormones on intrahemispheric activity. For example, Weis et al. (2011) used fMRI to scan natural cycling women as they completed a figure-matching task. The results revealed cycle-phase related reduced functional connectivity within right hemispheric networks during the luteal phase, as compared to both the menstrual and the follicular phase. Consequently, the authors suggested that sex hormones modulate not only interhemispheric inhibition between homotopic areas (Weis et al., 2008) but can also influence intrahemispheric integration, and interhemispheric connectivity between heterotopic brain regions (Weis et al., 2011).

Considering the evidence presented in this chapter, it seems that sex/gender differences in lateralisation and connectivity exist, but there is much overlap between the sexes (Joel et al. 2015; Weis et al. 2020). Moreover, the detection of sex/gender differences seems to partly be dependent on individuals' sex hormonal environment. Indeed, it has been argued that FCAs are double-coded by stable characteristics (e.g., genetics) and temporary situational aspects (e.g., sex hormones, environmental influences) (e.g., Hausmann, 2019). It is

noteworthy in this context that sex hormones have been shown to have antipsychotic properties, for example in schizophrenia (Kulkarni et al. 2015; McGregor et al. 2017; Riecher-Rossler et al. 2018). However, if sex hormonal effects on FCAs contribute to these clinical observations is not known, as is the causality in the relationship between sex hormones, FCAs, and psychiatric symptoms (see Figure 1).

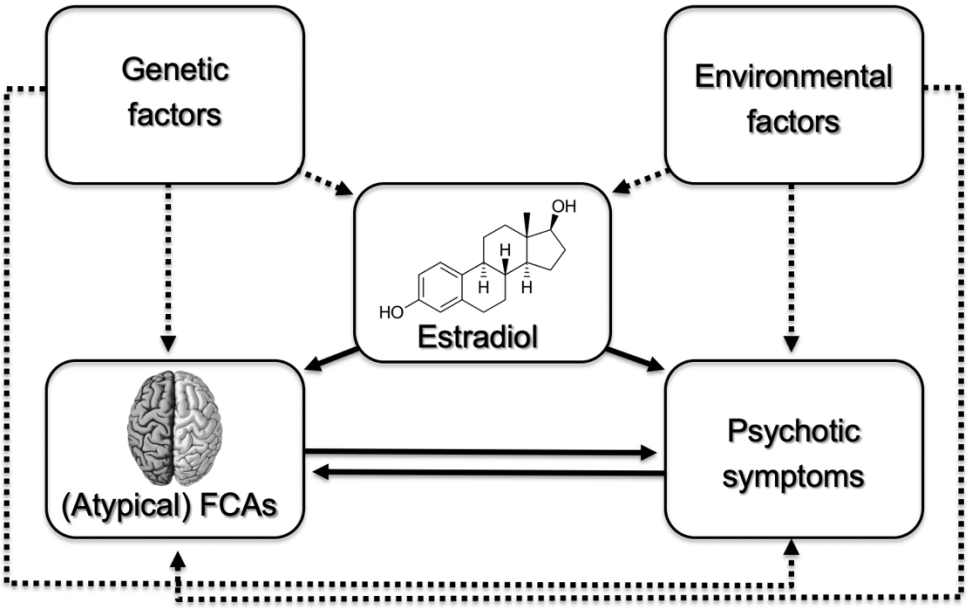

Fig. 1. The influence of estradiol on functional cerebral asymmetries (FCAs) and psychotic symptoms in schizophrenia and other mental disorders such as major depression, bipolar disorder, anxiety and neurodevelopmental disorders. Estradiol can affect functional asymmetries and cognitive control and can reduce psychotic symptoms. The causality of the relationship between atypical asymmetries and psychotic symptoms is still unclear. There is empirical evidence for both atypical asymmetries as a trait marker of the disorder and as a neuro-compensatory mechanism. The relationships considered in this chapter are indicated by the solid arrows. Reprint from Cortex, 127, S. Hodgetts & M. Hausmann, Antipsychotic effects of sex hormones and atypical hemispheric asymmetries, p. 317, Copyright (2020), with permission from Elsevier.

3.5. The case for a biopsychosocial approach

Although the evidence presented above demonstrates that sex hormones can significantly influence both lateralisation and connectivity, it is incorrect to assume that they underpin all of the demonstrated sex/gender differences in the brain (Cahill, 2006; Hausmann, 2020). Indeed, studies have revealed that environmental factors associated with sex/gender, such as gender roles and stereotypes, can also influence sex/gender differences such as those seen for lateralisation and connectivity (Jäncke 2018; Hodgetts and Hausmann 2020b).

It has been suggested that a relationship exists between socially derived gender roles (i.e., masculinity, femininity) and brain structure (Belfi et al. 2014). In this study, 108 children (56 boys and 52 girls), aged 7–17 years, completed a gender role questionnaire and underwent structural MRI. The results showed that masculinity positively correlated with WM volumes in the frontal lobe, while femininity positively correlated with GM volumes in the temporal lobe, even after biological sex was controlled for. Although the causality of this relationship is not clear, the authors suggested that this effect may represent an environmental influence on sex/gender differences in the brain (see Bourne and Maxwell 2010). Similar results have been found for sex/gender differences in cognition, with several studies suggesting that gender roles (Hoffman et al. 2011; Reilly et al. 2016; Compère et al. 2018; Pletzer et al. 2019) and gender stereotypes (Hausmann, 2014; Hausmann et al., 2009, Hirnstein et al., 2014) underlie differences in sex/gender-sensitive (some of them lateralised) cognitive tasks such as mental rotation and verbal fluency.

In light of the evidence presented above, an increasing number of studies have begun to consider the interactive effects of biological and environmental factors concerning sex/gender differences in the brain and behaviour (Hausmann 2020; Hodgetts and Hausmann 2020b). The biopsychosocial approach (Halpern and Tan 2001; Miller and Halpern 2014) suggests that environmental factors, including gender roles and stereotypes, can interact with biological factors, including sex hormones, to influence sex/gender differences in the brain and behaviour (Halpern and Tan 2001; Wraga et al. 2006; Krendl et al. 2008; Haier et al. 2009; Hausmann et al. 2009; Smith et al. 2013; Dunst et al. 2013; Pletzer et al. 2019). Using fMRI, Wraga et al. (2006) investigated the effects of gender stereotyping on the neural underpinnings of visuospatial performance in 54 women. As expected, significantly poorer performance was found in women exposed to a negative gender stereotype, when compared

to women given a positive gender stereotype. Additionally, poorer performance in the negative stereotype group was characterised by greater activation in brain regions associated with emotional processing, including the orbital and medial frontal gyri, and the anterior cingulate cortex. These results suggest that gender stereotypes can influence the efficiency of neural activity in sex/gender-sensitive tasks. Hausmann et al. (2009) investigated the effect of gender stereotypes in both men and women using a battery of sex/gender-sensitive cognitive tasks (incl. mental rotation and verbal fluency) and determined testosterone levels in all participants. To prime gender, one-half of the entire sample completed a questionnaire concerning gender stereotypes, while the other half completed a gender-neutral version of the same questionnaire. Overall, the expected sex/gender differences favouring men and women were found for mental rotation and verbal fluency, respectively. However, the sex/gender difference in mental rotation was significantly driven by the gender-primed group. Moreover, testosterone levels in the gender stereotype group were 60% higher than those in the control group. These results suggest that the effect of gender priming on cognitive performance can be mediated by the accompanying changes in sex hormone levels, probably depending on whether participants interpreted the testing situation after priming as challenging or threatening. Similar results were recently reported by Pletzer et al. (2019), who showed that high levels of testosterone in conjunction with high levels of self-reported masculinity yielded highly accurate mental rotation scores regardless of biological sex.

4. Conclusion

Research to date supports the notion that sex/gender differences in brain and behaviour exist at many levels, including lateralisation and connectivity. However, the notion that the brain is “sexually dimorphic” is incorrect, and referring to an oversimplified binary (e.g. “male brain”, “female brain”) is misleading and should be avoided in future research. Although many

of these sex/gender differences are characterised by small effect sizes, some of these differences are reliably found and should not be considered trivial. Indeed, there are various reasons for inconsistencies in the literature. Some of them arise from (i) different methodological approaches and reference measures, (ii) small and/or heterogeneous sample composition, (iii) the specific tasks/paradigm used, and (iv) the limited consideration of sex/gender-related factors that can explain inter-and interindividual differences in brain and behaviour better than sex/gender *per se*. Sex/gender differences in laterality and connectivity are no exceptions to this. Sex/gender-related factors include biological factors such as levels of sex hormones and sex-linked genes and environmental factors such as gender roles and stereotypes. These and related factors should be acknowledged routinely within a biopsychosocial approach when studying sex/gender differences in brain and behaviour.

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