FACULTY OF PSYCHOLOGY
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COMPLEMENTARITY OF FACE-SELECTIVE REGIONS IN LEFT- AND RIGHT-HANDERS

Does including dynamics make a difference in asymmetry patterns?

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Abstract – English

The human ability to process faces is critical for social interactions and is supported by a distributed neural network whose core regions include the fusiform face area (FFA), occipital face area (OFA), and superior temporal sulcus (STS). The right-hemispheric dominance of the overall network is well-established, but it is not known how consistent these asymmetries are in the different core-regions. The degree and direction of lateralization across the core-regions have not been investigated within individuals. The distinction between static and dynamic face processing has also been overlooked, even though we primarily encounter moving faces in daily life. Therefore, this study examined asymmetries in static and dynamic face processing across face-selective regions. Furthermore, this study investigated whether lateralization patterns differ between right- and left-handers and whether they are related to face recognition performance. 124 participants (*n left-handed = 62, n right-handed = 62*) performed static and dynamic face processing tasks while undergoing fMRI scans and completed Benton-Facial-Recognition-Task. Approximately 40% showed a right-hemispheric lateralization for all subregions, indicating that the majority was left lateralized for at least one subregion. No difference in lateralization patterns was found between left- and right-handers, and dynamic and static processing. Complementarity patterns significantly influenced the BFRT-c performance in interaction with handedness. These findings provide a more in-depth understanding of face processing lateralization within individuals. They highlight the importance of considering subregions of the face-network to capture interindividual variability of laterality. Future studies should explore the mechanisms underlying the variability in lateralization that affect individuals' face processing abilities.

Keywords: *cerebral dominance, hemispheric specialization, face processing, handedness*

Samenvatting – Nederlands

De menselijke vaardigheid om gezichten te verwerken en herkennen is cruciaal voor sociale interacties en wordt ondersteund door een uitgebreid neuraal netwerk waarvan de kernregio's worden gevormd door de fusiforme gyrus (FFA), occipitale gezichtsgebieden (OFA), en superieure temporale sulcus (STS). Hoewel hemisferische dominantie goed begrepen is voor bepaalde 'links hemisferische' cognitieve functies, is dit niet het geval voor gezichtsverwerking. Momenteel ontbreekt het in de literatuur aan onderzoek op twee cruciale gebieden. Ten eerste zijn de mate en richting van lateralisatie binnen verschillende subregio's van het 'gezichtsnetwerk' nog niet op individueel niveau onderzocht. Ten tweede hebben studies tot nu toe geen onderscheid gemaakt tussen statische en dynamische gezichtsverwerking bij het onderzoeken van lateralisatie. Daarom heeft deze thesis zich gericht op het onderzoeken van de lateralisatie van zowel statische als dynamische gezichtsverwerking in de gezichts-selectieve regio's. Bovendien heeft deze studie onderzocht of er verschillen zijn in lateralisatiepatronen tussen linkshandigen en rechtshandigen, en of deze patronen geassocieerd zijn met prestaties in gezichtsherkenning. In totaal hebben 124 participanten (*n linkshandig = 62, n rechtshandig = 62*) statische en dynamische gezichtsverwerkingstaken uitgevoerd in de fMRI-scanner en hebben zij de Benton Facial Recognition Task (BFRT-c) voltooid op de computer. Ongeveer 40% van de deelnemers vertoonde een rechts-hemisferische dominantie voor alle regio's, wat impliceert dat voor de meerderheid minstens één regio links-hemisferisch dominant was. Er werd geen verschil gevonden in de lateralisatie patronen van linkshandige en rechtshandige individuen, en complementariteitspatronen hadden een significant effect op de prestaties in gezichtsherkenning. Deze bevindingen dragen bij aan een gedetailleerder en diepgaander begrip van lateralisatie in gezichtsverwerking op individueel niveau en ze benadrukken het belang van het in overweging nemen van subregio's van het gezichtsnetwerk om interindividuele variabiliteit te vatten. Toekomstig onderzoek is aangewezen om de mechanismen te verkennen die ten grondslag liggen aan de variabiliteit in lateralisatiepatronen die de gezichtsverwerkingsvaardigheden van individuen beïnvloeden.

Sleutelwoorden: cerebrale dominantie, hemisferische specialisatie, gezichtsprocessing, linkshandigen en rechtshandigen

Preface

I would like to start by thanking my incredible promotor, dr. Emma Karlsson. Thank you for always making time to answer any questions I had, proofreading my thesis, and providing constructive feedback. I have learned so much from you! Your guidance and support over the past two years made my learning experience so much more enjoyable.

I would also like to thank prof. dr. Guy Vingerhoets for teaching me the behavioral testing protocol and for giving me the amazing opportunity to test participants on my own later on. This thesis would not have been possible without all the individuals that committed to participate in this study. Their time and energy allowed us to further investigate the amazingly interesting brain, so a big thank you to everyone that participated!

Last, but not least, I would like to thank my friends and family for being there for me throughout this thesis process and during the past five years of studying. Thank you for embracing my stress and less pleasant moments; without your unconditional love and support, I would not be standing where I am today. And a special shout-out to those of you who took the time to proofread my thesis – your help was invaluable. I know it was probably quite a task, but your unfiltered feedback was really appreciated. Thank you, thank you, thank you! I cannot wait to see what the future holds!

Hopefully, while reading this thesis, you will be just as fascinated as I was to discover the complex and extremely interesting workings of our brain!

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Functional human brain organization

The brain is one of the most complex and fascinating organs in the human body. The structural and functional organization of our brain has been a topic of interest and debate among researchers for decades, with implications for understanding cognitive processing and behavior. Functional specialization and functional integration are the two primary and complemenary principles that appear to guide the functional organization of the brain (Friston, 2002; Hugdahl, 2000). Functional specialization refers to the organization and modular distribution of specialized functions within distinct regions of the brain (Fox & Friston, 2012; Yu et al., 2013). Functional integration refers to how populations of neurons collaborate to process information and generate responses, depending on cognitive and sensorimotor attributes; for example, neuronal populations that code for sensory input in the hands differ from those that code for a cognitive process such as attention (Friston, 2004). According to Hohwy (2007), functional integration implies that it is necessary to investigate different interconnected brain areas and integrated cognitive functions simultaneously to understand the mind and cognition.

The functional human brain organization can be described along two different axes (Hugdahl, 2000). First, the human brain is organized along the longitudinal axis, which divides the brain into four lobes with different functions. Research shows that the frontal lobe is mainly responsible for executive functions (e.g., planning, self-monitoring of actions), and motor control (Chayer & Freedman, 2001; Stuss & Benson, 1984). The temporal lobe is typically related to learning, memory, and face recognition (Pitcher & Ungerleider, 2021; Wong & Gallate, 2012), and the parietal lobe is involved in visuospatial processes and attention, with lesions often resulting in neglect or ideomotor apraxia (Posner & Driver, 1992; Vuilleumier, 2013; Wheaton & Hallett, 2007). The occipital lobe, also referred to as the ‘visual cortex’, is predominantly responsible for visual processes (Brewer et al., 2005; Tohid et al., 2015).

Second, the human brain exhibits organization along the lateral axis (i.e., left and right hemisphere), with both lateral symmetry and lateral asymmetry. Lateral symmetry refers to homologue regions in the left and right hemisphere that perform functions equally well (Hugdahl, 2000). This can be seen, for example, in the primary motor and visual cortex, which show a functional cross-over from the left side of the body to the right hemisphere and vice versa (i.e., contralateral organization), with equivalent processing of certain sensory functions in left and right hemispheric counterparts (Banihani, 2010). Contrary, lateral asymmetry refers to homologue regions in the left and right hemisphere who perform different functions or differ in importance for certain cognitive processes (Hugdahl, 2000). The inferior parietal lobe can serve as an example of this organizing principle. Lesions in the right inferior parietal lobe are likely to result in neglect of the left visual field, whereas neglect symptoms are rare when the homologous left inferior parietal lobe is affected (Stone et al., 1993). Even when neglect symptoms do occur as a consequence of left hemispheric lesions, they are generally less severe compared to when the right hemisphere is lesioned in this particular region, which indicates that the right hemisphere is especially important for visuospatial processing (Stone et al., 1993).

Asymmetries of the brain

Thus, even though the human brain structurally seems to be organized as two symmetrical cerebral halves, both structural and functional hemispheric asymmetries are present in these so-called 'mirror images' (Hugdahl, 2005). Structural asymmetries are established early on in life, driven by genetic factors, and lead to differences in topographic organization of both cerebral hemispheres, which are repeated across the majority of the population (Behrmann & Plaut, 2015; Dubois et al., 2009; Hervé et al., 2013). The topographic organization of the brain means that spatially adjacent sensory receptors are represented in adjacent positions of the cortex, which divides the brain in distinct cortical areas (Eickhoff et al., 2018; Patel et al., 2014).

Functional asymmetries develop progressively, and can emerge from cortical dynamics and the different network structures of the hemispheres (Behrmann & Plaut, 2015; Hervé et al., 2013). Functional asymmetries of the brain are also referred to as hemispheric specialization or functional lateralization/specialization, meaning that one hemisphere is specialized for a certain cognitive function (Hugdahl, 2005; Hervé et al., 2013). This specialization is expressed by more activity in one hemisphere (i.e., the dominant hemisphere), compared to the other hemisphere (i.e., the non-dominant hemisphere) during a specific cognitive process (Güntürkün et al., 2020). Studies investigating the functional lateralization of hemispheres are embedded within the broader research field concerning the localization of functions in the human brain. Since the discoveries by Marc Dax, Paul Broca, and Carl Wernicke on language localization in the 19th century, extensive research has been carried out to investigate functional cerebral asymmetries (Hugdahl, 2005).

Prior to the use of modern, neuroimaging techniques, research on hemispheric specialization relied on case studies and post-mortem examinations to explore lateralization (Broca, 1863; 1865; Hugdahl, 2000; Manning & Thomas-Antérion, 2011). In lesion studies, patients with brain damage are examined to establish a connection between the location of the lesion and the observed symptoms or cognitive impairments, thereby indicating that the affected region is involved in that particular cognitive function (Güntürkün et al., 2020; Hutsler & Galuske, 2003). For example, Marc Dax and Paul Broca independently discovered patterns of language dominance towards the left hemisphere (Broca, 1863; 1865; Güntürkün et al., 2020; Manning & Thomas-Antérion, 2011). They observed that patients with aphasia (i.e., inability to communicate or produce speech properly) all presented with lesions in the left inferior frontal lobe. The left hemisphere is traditionally linked with specialization for arithmetic functions, praxis, and language processing (Behrmann & Plaut, 2015; Rossion & Lochy, 2021). Contrary, the right hemisphere is linked to specialization for non-verbal abilities, such as visuospatial processing, object, face and body recognition, and emotional processing (Gerrits et al., 2020a; Karlsson, 2019).

Nowadays, non-invasive neuroimaging techniques can be used to determine dedicated areas responsible for certain functions or tasks and the functional lateralization of these processes. The number of studies utilizing functional magnetic resonance imaging (fMRI) to investigate hemispheric specialization has increased significantly in the last decades (Seghier, 2008). fMRI, a hemodynamic imaging method, allows to localize changes in blood flow as a response to specific cognitive stimuli (Hugdahl, 2005). Hemispheric dominance is defined by relatively more activated voxels and larger blood oxygen level-dependent (BOLD) signal amplitude in the dominant hemisphere compared to the non-dominant hemisphere (Behrmann & Plaut, 2015). The most common way to express hemispheric specialization in fMRI research is by calculating a laterality index (LI; Seghier, 2008). LI's quantify the relative contribution of one hemisphere compared to the other (Cai et al., 2013; Hunter & Brysbaert, 2008). LI's typically range from negative to positive values (e.g., [-1;+1]), with negative values indicating right hemispheric dominance and positive values indicating left hemispheric dominance (Karlsson, 2019; Seghier, 2008). Thus, these imaging techniques enable a comprehensive characterization of the functional organization of the human brain, at rest or while engaged in cognitive processes (Hervé et al., 2013).

Why does the brain exhibit asymmetries?

Hemispheric specialization is often seen as advantageous due to its ability to reduce cognitive redundancy, and increase neural efficiency and cognitive capacity through increased parallel processing (Güntürkün et al., 2020; Rogers, 2000). Despite limited evidence supporting these advantages, the occurrence of lateralization across various species suggests that it should have some benefit, both at the individual and populational level, to have survived natural selection over time (Güntürkün et al., 2020).

Lateralized functions tend to show strong 'prototypical' directional biases within the population (i.e., typical lateralization), but it should be noted that a minority of individuals deviate from these patterns (i.e., atypical lateralization; Badzakova-Trajkov et al., 2015; Gerrits et al., 2020b; Karlsson et al., 2021). Consequently, it is often thought that the typical lateralization pattern is beneficial for human functioning. Hence, some researchers have explored the potential cognitive dysfunctions associated with atypical lateralization patterns or more broadly, whether deviating from the typical lateralization pattern has any consequences. According to Mundorf and colleagues (2021), various neurodevelopmental and psychiatric disorders are associated with atypical functional (or structural) cerebral asymmetries. For example, evidence for atypical lateralization patterns are reported in schizophrenia, autism spectrum disorder, attention deficit hyperactivity disorder, and dyslexia (Alperin et al., 2019; Floris & Howells, 2018; Mundorf et al., 2021; Ocklenburg et al., 2013). Furthermore, Gerrits and colleagues (2020b) found that healthy individuals who deviated from the typical segregation pattern exhibited lower cognitive performance on a neuropsychological test battery (RBANS; Randolph et al., 1998).

Interindividual variability in hemispheric specialization

Factors associated with the variability in hemispheric specialization

Five main domains (involving both genetics and the environment) have been identified as possible mechanisms underlying interindividual variability in hemispheric specialization. It is proposed that anatomical factors (e.g., brain volume), developmental events, biological factors (e.g., testosterone levels), gender, and hand preference (handedness) may play a role in the interindividual variability of lateralization patterns (Bryden et al., 1994; Grimshaw et al., 1995; Hervé et al., 2013; Hirnstein et al., 2019; Toga & Thompson, 2003; Whitehouse & Bishop, 2009; Witelson & Nowakowski, 1991).

Empirical evidence suggests some sort of relationship between functional asymmetries and handedness (Hécaen et a1 1981; Hervé et al., 2013). For example, according to a study conducted by Szaflarski and colleagues (2012), left hemispheric dominance for language processing was observed in 93% of right-handed individuals and 85% of left-handed individuals. Similar results were reported by Rasmussen and Milner (1977). In their sample, 96% of right-handers and 70% of left-handers had speech predominantly lateralized to the left hemisphere. Moreover, a meta-analysis conducted by Carey and Johnstone (2014) suggested that left-handed individuals are more susceptible to aphasia after right hemisphere damage, whereas right-handed individuals show a bias towards developing aphasia following damage to the left hemisphere. In addition, they showed across different neuroimaging studies that on average 91% of right-handers and 76% of left-handers are left hemisphere dominant for language.

Although the lateralization patterns of language processing in relation to handedness within the population are well-established, for other cognitive processes this relationship has not yet been examined extensively (Johnstone et al., 2020). One of these processes is face processing. It has been shown that most individuals are right hemispheric dominant for face processing, but little is known about the association of this asymmetry to, for instance, handedness and language lateralization (e.g., Badzakova-Trajkov et al., 2010; Duchaine & Yovel, 2015; Rossion & Lochy, 2021). An exception is the study by Bukowski and colleagues (2013) who investigated face processing in relation to handedness. These authors observed that the fusiform face area (FFA) is lateralized towards the left hemisphere in left-handers, whereas it is most common for other face processing areas (in both left- and right-handers) to lateralize towards the right hemisphere, suggesting a relation between the lateralization of the FFA and handedness.

More generally, it is currently assumed that left-handed individuals tend to have more atypically lateralized functions regardless of whether they are left or right hemispheric dominant for language (Willems et al., 2014). Hence, it is important to include left-handers in lateralization samples as they will include the necessary variation present within the population, which is needed to inform us about the lateralization of different cognitive functions. However, in early research regarding lateralization, left-handed individuals were often excluded from the samples, since left-handers showed reduced asymmetries in behavioral studies or because it was thought they would cause more noise to the data (Johnstone et al., 2021).

Complementarity of multiple lateralized functions

Early research regarding lateralization mainly studied cognitive functions in isolation. To examine the complementarity of lateralization (i.e., the relationship between the lateralization of different functions), more recent studies investigated different lateralizing functions within the same sample (Badzakova-Trajkov et al., 2010; Gerrits et al., 2019; Karlsson et al., 2019; Vingerhoets, 2019). Bryden (1990) proposed two hypotheses regarding the relationship between different lateralizing functions. The causal hypothesis suggests that dependent biases underlie lateralizations, hence the lateralization of one function depends on the lateralization of another function (Bryden et al., 1983; Whitehouse & Bishop, 2009). According to this causal hypothesis, the functional specialization of the right hemisphere is due to the fact that the left hemisphere by default needs to process language. In this view, functional asymmetries other than language processing are seen as secondary consequences of language lateralization (Karlsson et al., 2019). This hypothesis further predicts that individuals with right hemisphere language dominance will have non-verbal, 'right hemispheric dominant' functions lateralized to the left hemisphere.

The statistical hypothesis assumes that all functions have independent probabilistic biases to lateralize towards the left or right hemisphere (Bryden, 1990). According to this view, distinct mechanisms lead to the lateralization of different functions towards different cerebral hemispheres, meaning that different functions do not lateralize in relation to each other, even though population-level biases to one hemisphere are observed. Moreover, following the statistical hypothesis, no association is expected between verbal and non-verbal lateralization tasks, whereas the causal hypothesis predicts a negative association between verbal and non-verbal lateralization tasks (Bryden, 1990; Bryden et al., 1983).

To assess the relationship between different functions, Badzakova-Trajkov and colleagues (2010) used fMRI to measure cerebral asymmetries during three different tasks: word generation, landmark, and face perception tasks. They found evidence for a correlation between speech production and spatial attention, and between speech production and face processing. Nonetheless, they did not observe correlations between spatial attention and handedness, and between spatial attention and face processing. In contrast, Karlsson and colleagues (2021) found that, when including both language typical and atypical individuals, face processing did not always lateralize towards the non-language dominant hemisphere. The results of Karlsson and colleagues (2021) contradict earlier research, in which a link between the lateralization of face and language processing was suggested (Behrmann & Plaut, 2015; Centanni et al., 2018; Dehaene et al., 2010). In addition, Bryden and colleagues (1983) found that aphasia is more common after left hemisphere damage and visuospatial disorders are more common after right hemisphere damage, but they observed no association between language and visuospatial processing, which is evidence for independent biases.

In conclusion, despite mixed results, a review by Badzakova-Trajkov and colleagues (2015) found that most empirical evidence supports the statistical pattern rather than the causal pattern of complementarity. To date, there is no consensus on the underlying mechanisms of different lateralizing functions (Gerrits et al., 2020b; Vingerhoets, 2019).

Phenotypic lateralization patterns within the population

In contrast to the complementarity of functions, there is increased empirical evidence (and consensus) on the phenotypic lateralization patterns prevalent within the population. When individuals (both healthy and brain damaged) are recruited at random and tested on at least two cognitive functions, it is typically found that a majority exhibits the typical lateralization pattern (Vingerhoets, 2019). Additionally, two atypical lateralization patterns have been identified: the crowded type where functions share a hemisphere while they would typically lateralize towards opposite hemispheres, and the reversed type in which segregation is retained, but following a mirror-image of the typical pattern. Even though these atypical patterns occur in a minority of the individuals, they are not extremely rare and are observed in several cognitive functions (e.g., language, spatial processing, attention; Flöel et al., 2005; McNeely & Parlow, 2001; Rosch et al., 2012; Whitehouse & Bishop, 2009). Studies that tested individuals with atypical language dominance on other cognitive functions generally find that these language atypical individuals (which are almost exclusively left-handers) show a reversed typical lateralization pattern (Mazoyer et al., 2014; Vingerhoets, 2019). For example, Cai and colleagues (2013) and Vingerhoets and colleagues (2013) observed that all individuals with atypical language dominance showed additional atypical lateralizations (e.g., visuospatial processing, praxis). Gerrits and colleagues (2019) found that individuals with atypical language dominance exhibited a reversed lateralization pattern for face and word recognition. However, an exception is the study by Karlsson and colleagues (2021), in which the atypical lateralization of language was not always accompanied by an atypical lateralization for face and body processing.

To summarize, three main phenotypic lateralization patterns are prevalent within the population (Gerrits et al., 2020b; Vingerhoets, 2019). First, there is the typical segregation pattern, which is most commonly observed (e.g., language and praxis dominant in left hemisphere; spatial processing dominant in right hemisphere). Second, a reversed typical segregation pattern is observed in which the segregation of functions is maintained, however they switched sides (i.e., left-right reversal). Third, some individuals show an atypical segregation pattern, which indicates that they have at least one atypically lateralized function while other functions remain typically lateralized (i.e., crowding of functions). Thus, it is clear that, albeit population biases exist, lots of variability in cerebral asymmetries is present within humankind. Due to the initial neglect of right hemisphere functions within hemispheric dominance research, there is a need for further research on the variability of these functions within the population and the association to factors such as handedness. This study focusses on the right hemispheric function of face processing

Face processing in the brain

What is face processing?

In daily life, humans constantly encounter faces of other people, both in real life or on social media, in newspapers, on television, etc. Face processing includes (amongst other things) interpreting emotional facial expressions, which makes it important for social interactions (Badzakova-Trajkov et al., 2015; Kanwisher & Yovel, 2006; Levy et al., 1983). A few aspects are different between face processing and (non-facial) object processing (Hoehl & Peykarjou, 2012). First, face processing requires to identify the face at an individual level (e.g., identify a person as “Jan”), whereas processing other visual stimuli often occurs at a category-level (e.g., identify what you see on the table as “a plate”; Hoehl & Peykarjou, 2012; Richler & Gauthier, 2014). Second, from the moment babies are born, they acquire extensive expertise to distinguish between faces. Moreover, our ability to process and recognize faces develops incidentally without any explicit instructions or training, i.e., it is a naturally developed skill (Behrmann & Plaut, 2020; Rossion & Lochy, 2021). Combining information on shapes and pigmentation of facial features (feature information) with information on the spatial relationship between different features (configurational information) enables us to encode and recognize faces (Hoehl & Peykarjou, 2012). Additionally, face processing includes (amongst other things) interpreting emotional facial expressions (Levy et al., 1983). Therefore, face processing is important for social interactions (Badzakova-Trajkov et al., 2015; Kanwisher & Yovel, 2006).

According to Kanwisher and Yovel (2006), all facial stimuli consist of three main features: the frontal face configuration, the presence of specific face parts and a bounding contour with hair around an oval-like shape. Despite the similarities in facial configurations and features among most individuals, humans are still able to quickly and accurately distinguish between individual faces, indicating that face processing is a highly developed skill (Le Grand et al., 2006; Zhen et al., 2015). One look at a face provides plenty of information about the individuals’ identity, gender, age, mood, affect, and expressions. This extensive range of information enables humans to finely discriminate between highly similar stimuli (Davies-Thompson et al., 2016).

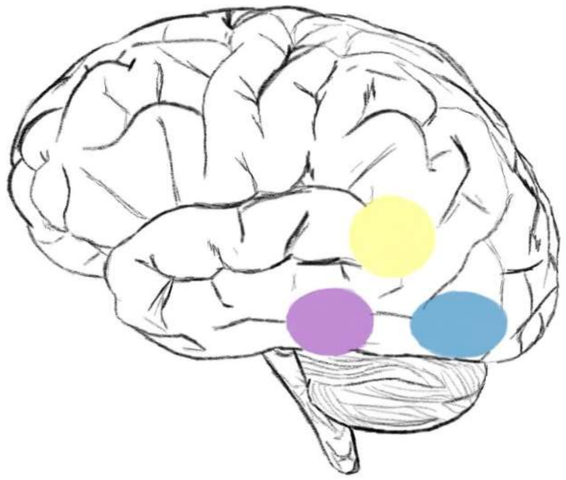
Where does face processing happen in the brain?

A distributed neural network in both hemispheres is assumed to underlie our face processing ability (Thome et al., 2022). Neuroimaging research, and fMRI studies in particular, have identified multiple face-selective cortical regions, often referred to as the face processing network, which can be further divided into two systems (Pitcher et al., 2011b; Thome et al., 2022; Zimmermann et al., 2019).

In one system, parts of the inferior temporal cortex and the occipital-temporal cortex form the core system of our face processing network (Figure 1; Davies-Thompson et al., 2016; Thome et al., 2022; Zhen et al, 2015). The first region in this core system is the occipital face area (OFA). The second important region is the fusiform face area (FFA), which can be divided into a medial and posterior part (Gobbo et al., 2024). Lastly, the superior temporal sulcus (STS) is seen as a major region in the core system, which consists of a posterior part (pSTS) and an anterior part (aSTS; O'Toole & Roark, 2010). The regions of the core system are seen as face selective, meaning that they respond more to facial stimuli than non-facial stimuli (Davies-Thompson et al., 2016). Moreover, according to Weiner and Grill-Spector (2012), these face selective regions exhibit a periodic pattern, with each face selective region covering approximately 10 mm diameter and between those regions around 10-15 mm of cortex. The areas of cortex between these face-selective regions are typically sensitive to non-facial stimuli. In addition to the core system, the extended system comprises face-sensitive areas, including parts of the limbic system, such as the amygdala and insula, as well as parietal and prefrontal regions (Thome et al., 2022; Weiner et al., 2014; Weiner & Grill-Spector, 2012).

Figure 1

Core system of the face processing network



Note: This figure illustrates the location of the main three regions in the core face processing system, i.e., FFA (purple), OFA (blue), and STS (yellow). The locations are based on coordinates provided by Davies-Thompson and Andrews (2011), Kawakami and colleagues (2017), and Pitcher and Ungerleider (2021).

How does the brain process faces?

Different aspects of face perception are processed within the face processing network, which consists of different areas that show relative functional specialization (de Gelder & Van den Stock, 2010). The OFA is responsible for early processing of low level facial features, which allows to distinguish between individual faces (Davies-Thompson et al., 2016; Thome et al., 2022). During the perception of these low level features, the OFA is only sensitive to face parts and the more physical aspects of faces. In contrast, the FFA responds to all facial features, i.e. both face parts and face configurations. The FFA processes high level visual features and social information of faces in order to determine face identity (Kanwisher & Yovel, 2006). Face perception in the FFA is invariant to image transformations (i.e., changes in e.g., position, size and spatial scale), as supported by fMRI adaptation of the FFA (i.e., a decreased response) to identically repeated faces compared to new ones (Davies-Thompson et al., 2016; Thome et al., 2022). However, the responses of the FFA are not invariant to changes in viewpoint or lighting as opposed to the responses of the STS. The STS processes all changeable features of faces, such as expressions, gaze direction and head rotation (Gobbo et al., 2024). Additionally, the extended system of the face processing network extracts further information from faces, such as emotions and attractiveness (Thome et al., 2022; Zimmermann et al., 2019). The extended system also retrieves knowledge about the person and processes non-visual information (such as biographic information).

In addition, a distinction can be made between static and dynamic face processing. Static face processing refers to the processing of facial form, whereas dynamic face processing refers to the processing of facial motion (Berstein et al., 2018). De Winter and colleagues (2015) argue dynamic faces are more naturalistic and that they include more information than static faces. It is also proposed that the temporal information of dynamic faces give additional recognition cues and, therefore, dynamic faces might be easier to decode (de Gelder & Van den Stock, 2010; Van den Stock et al., 2015). Thus, recognizing static facial expressions requires more effort from the brain, because it has to account for the missing temporal dynamic information. For example, Steede and colleagues (2007) reported a prosopagnosic patient who experienced impaired static face recognition, whereas dynamic face recognition was intact. However, these findings are not compatible with a similar study by Lander and colleagues (2004), in which they examined a prosopagnosic patient who was unable to use dynamic face information to explicitly recognize faces, even though the ability to process motion was intact. Nevertheless, it is important to note that there is no consensus on whether dynamic and static face processing involve qualitative rather than quantitative differences.

In contrast, the evidence regarding which regions are involved in both types of face processing is unambiguous. Duchaine and Yovel (2015) propose a neural framework in which the ventral face pathway (i.e., OFA and FFA) processes static face information, while the dorsal stream (i.e., STS) extracts the constantly changing information from moving faces required for ongoing social interactions. Indeed, it is consistently found that the STS has higher activations for dynamic faces than static faces (Dien, 2009; Kanwisher & Yovel, 2006; Pitcher et al., 2011a; Pitcher et al., 2019). Moreover, evidence supports the idea that the STS is selectively responsive to dynamic facial information rather than being sensitive to processing dynamic stimuli in general. Contrary, the OFA and FFA are selectively engaged in processing static faces (Dien, 2009; Kanwisher & Yovel, 2006).

Lateralization of face processing

Although it is established that generally the right hemisphere is involved during face processing, the specifics of lateralized face processing are not that well researched yet. Three main research methods provide evidence for the lateralization of face processing, namely lesion studies, behavioral experiments, and neuroimaging methods. The earliest indications that face processing is a lateralized function came from patients with prosopagnosia, about 150 years ago (Rossion, 2018). Individuals with prosopagnosia experience impaired identity recognition from faces, but they retain their ability to process facial expressions (de Gelder & Van den Stock, 2010; Duchaine & Yovel, 2015). According to Rossion (2018) and Rossion and Lochy (2021), lesions in the right ventral occipital-temporal cortex result in prosopagnosia. Interestingly, even though right hemispheric lesions are necessary (and sufficient) to cause face recognition deficits, bilateral lesions are sometimes observed (Rossion, 2018; Rossion & Lochy, 2021). Moreover, de Gelder and Van den Stock (2010) found that intact functioning of the FFA and OFA are necessary (but not sufficient) for successful face recognition.

Visual half field paradigms consistently report that individuals show a behavioral bias to remember and perceive faces better when they are presented shortly to the left visual field, and thus mainly processed in the right hemisphere (Dundas et al., 2015; Harrison & Strother, 2019; Voyer et al., 2012). Studies using the typical chimeric faces paradigm (i.e., faces consisting of one emotional hemi-face and one neutral hemi-face; Figure 2) consistently indicate preferences for emotional faces shown in the left visual field (e.g., Karlsson et al., 2019; Levy et al., 1983; Roszkowski & Snelbecker, 1982). Individuals moreover show a stronger bias to remember the left visual part of chimeric faces when there are more voxels activated in the right FFA (Yovel et al., 2008). Similarly, Megreya and Havard (2011) showed a clear left-side bias when participants needed to match the identity of a target face to another one presented in a line-up of ten faces. In conclusion, these behavioral experiments all show a superior face recognition performance for faces presented in the left hemi-field (Duchaine & Yovel, 2015). Additionally, behavioral face recognition tasks (e.g., the Benton Facial Recognition Task (BFRT); Benton & Van Allen, 1968) have been widely used to assess human face processing abilities in various populations (including those with neurological or psychological conditions; Murray et al., 2021; Rossion & Michel, 2018). These behavioral face recognition tasks have been able to inform us on the asymmetry of face processing, as differences in performance may indicate deficits in face processing linked to asymmetrical brain functions. For example, Tranel and colleagues (2009) reported that impairments on the BFRT were strongly associated with lesions in the right posterior parietal and right fusiform gyrus regions.

Figure 2

Example of stimuli in chimeric faces paradigm

Note. This figure illustrates stimuli from the typical chimeric faces paradigm. Half of the chimeric face contains an emotional expression, whereas the other half is a neutral face. All four faces shown are identical except that they are mirrored (i.e., the emotional half either on the left or right side of the chimeric face). For example, when participants are instructed to indicate the 'angry face' and panel A is presented, participants are likely to choose the face on the top, since the left side contains the emotional expression. In contrast, when panel B is presented, participants are likely to choose the face at the bottom.

Image source. Karlsson and colleagues (2019)

Different neuroimaging techniques have provided evidence regarding the lateralization of face processing. For example, electro-encephalography (EEG) studies show that the N170 component, related to face processing, exhibits a larger amplitude over the right hemisphere and thus, indicates a right hemisphere processing advantage, whereas fMRI research yields more ambiguous results (Rossion & Lochy, 2021). Review papers indicate that there is plenty of evidence for bilateral occipital-temporal activations during face processing (Badzakova-Trajkov et al., 2015; Rossion & Lochy, 2021). However, even though the whole face processing network is generally bilaterally activated, the right hemisphere is often still dominant with more extensive and increased activations (i.e., larger bold amplitudes and more active voxels). For example, some fMRI studies, contrasting non-facial objects and faces, found that face recognition is dominant in the right hemisphere, whereas word recognition is dominant in the left hemisphere (e.g., Dehaene & Cohen 2011; Ishai et al., 2005; Prete & Tommasi, 2018; Rossion et al., 2012). Although right hemispheric dominance might be present at group level, not all individuals will be right lateralized for face processing, as plenty interindividual variability is observed (Rossion & Lochy, 2021; Thome et al., 2022). Importantly, despite the differences between static and dynamic face processing and although we primarily encounter moving faces in daily life, most of these neuroimaging studies focused on static faces only (de Gelder & Van den Stock, 2010; De Winter et al., 2015).

Consequently, different theories have been proposed to explain the lateralization of face processing. One of those theories is the neural competition or recycling hypothesis, stating that the lateralization of face processing is a result of competition for neural space (Canário et al., 2020; Rossion & Lochy, 2021). According to this hypothesis, lateralization of face processing is the mere consequence of language lateralization, an idea supported by comparing the neural activity in the fusiform face area (FFA) and visual word form area (VWFA). Both the FFA and VWFA activate similar networks and show some overlap due to partial lateralization, which causes a neural competition between face representations and visual representations of words and letters, that are more dominant in the left hemisphere, since they prefer to be in close proximity to other language functions (Rossion & Lochy, 2021). The VWFA collateralized with the language dominant hemisphere, since these visual representations of words and letters prefer to be close in proximity to other language functions. Therefore, the FFA gradually needs to rely more on the non-language dominant hemisphere, as the neural space of the language dominant hemisphere gets completely occupied by these language-related processes (Canário et al., 2020; Rossion & Lochy, 2021).

Another theory, the distributed theory of lateralization, is proposed by Behrmann and Plaut (2015; 2020). They argue that there is no strict separation for face and word representations, but that there is a weighted asymmetry for both processes. According to these authors, there is no clear distinction between faces and words, which is supported by the consistent finding of bilateral activations for faces and words. In their hypothesis of graded and overlapping functional specialization, they claim that, even though faces and words are bilaterally active on average, there is a gradient with slightly more activation for faces to the right and for words to the left hemisphere.

Albeit the complexity of the face processing network, only a few studies have investigated the lateralization of the different subregions. The results of these studies imply that there are both functional and structural interhemispheric differences regarding the face processing network. First, Thome and colleagues (2022) found that all subregions in the face processing network exhibited a similar degree of lateralization, however, a strong rightward asymmetry at the group level was not found due to large interindividual variability. They additionally found an interaction with handedness and gender, i.e., left-handed males were less lateralized towards the right hemisphere for the FFA compared to right-handed males, right- and left-handed females.

Second, Zhen and colleagues (2015) also investigated the lateralization patterns of the subregions in the core system. In their sample the dorsal face-selective region (i.e., STS) exhibited a greater rightward asymmetry, on average, than the ventral face-selective regions (i.e., OFA and FFA). Furthermore, they found that the posterior parts of the face processing network show a higher face selectivity magnitude (i.e., indicating these regions are more specific for face processing) compared to anterior parts. The face-selective regions in the right hemisphere were also larger in volume and exhibited less variation of their anatomical location than their homologue regions in the left hemisphere. Zhen and colleagues (2015) assessed to which degree the face-selective subregions were, on average, lateralized between individuals. However, the degree and direction of lateralization patterns of these subregions at an intra-individual level, have not yet been investigated. Moreover, given the differential sensitivity to dynamic face-related information between the ventral and dorsal pathways, the distinction between static and dynamic processing should be considered in future, as this difference in sensitivity may imply different lateralization patterns of these pathways.

Current research

Previous literature demonstrated that the lateralization of cognitive functions is organized in a complex manner and susceptible to variation. Within the face processing literature, there is some evidence suggesting that the different subregions of the face network may differ in their lateralization (Duchaine & Yovel, 2015; Pitcher et al., 2011a; 2019; Thome et al., 2022; Zhen et al., 2015). However, to date, little is known about the relationship between the asymmetries of the core face-selective regions within individuals (i.e., the issue of complementarity applied to the face processing network), and whether (and how) this relationship is associated with factors such as handedness and type of face processing. Combining the knowledge of the relationship between lateralized functions and the complexity within the face-processing network, the question can be raised as to how complementarity of specialization applies within the face-processing network at an individual level during both static and dynamic face processing tasks. Therefore, the current study aimed to capture the complexity of static and dynamic face processing asymmetries of three face-selective regions within individuals. Additionally, the current study aimed to compare whether left- and right-handers differ in the way they express these complex lateralization patterns.

The primary research question of this study was to assess how the core face-selective regions (FFA, OFA, and STS) lateralize within an individual, during static and dynamic face-processing tasks, and whether these lateralization patterns differ between left- and right-handers. The first hypothesis was that the FFA and OFA would lateralize to the same hemisphere within an individual, whereas the STS might lateralize to the opposite hemisphere within an individual. This hypothesis was based on the fact that the different subregions are responsible for different subfunctions of face processing (i.e., FFA and OFA are relatively more involved in static face processing, while the STS is relatively more involved in dynamic face processing). The second hypothesis expected different lateralization patterns between dynamic and static face processing, as it was hypothesized that the different subregions predominantly involved in either types of face processing would drive the lateralization of the entire face network (i.e., STS as driving force during dynamic face processing, and FFA and OFA during static face processing). The third hypothesis posited that left-handed individuals would show more variability in their lateralization patterns of the regions of interest than right-handed individuals. This would be expressed by an increased proportion of left-handers showing partial complementarity patterns in comparison to the proportion of right-handers. Moreover, it was expected that face processing in left-handers would be more frequently lateralized towards the left hemisphere compared to right-handers.

The secondary research question was whether these lateralization patterns are associated with the performance of individuals on a behavioral face-matching task. A previous study reported that individuals with atypical lateralization patterns, performed worse on a neurocognitive test battery (Gerrits et al., 2020b). Since it is established that generally the right hemisphere is involved during face processing (Rossion & Lochy, 2021; Thome et al., 2022), it was hypothesized that right hemispheric lateralization of face-selective subregions would be beneficial for face recognition performance. Additionally, it was expected that the lateralization pattern, in which all face-selective subregions are lateralized in the same hemisphere, would be associated with an improved performance on the behavioral face-matching task.

Methods

The research of this dissertations falls within a larger research project conducted at Ghent University. Within this project, the goal is to assess the neurodiversity of hemispheric specialization in the population (i.e., investigate the interindividual variability). This study included behavioral data and data from two fMRI scans, related to face processing, from this larger project.

Participants

For this study, 124 participants were recruited via word of mouth, as well as posters and flyers distributed on social media and around Ghent, using a convenience sampling method. To obtain a sample representative of the Flemish population, all age categories ranging from 20 to 65 years old were included for both sexes and all educational levels. Details of the demographic information for the sample are reported in Table 1. One subject was more difficult to classify as either left- or right-handed (i.e., ambidextrous). For the readability purposes of the current study, this individual was labeled as left-handed (i.e., to avoid the use of non-right-handed individuals), which may be justified as the results remained unchanged when this subject was excluded for analysis.

All individuals that took part in this study had Dutch as their native language. Additionally, eligibility of participants for inclusion required meeting the MRI safety criteria (e.g., no metal or electrical devices implanted in their body). In return for their participation in the 3-hour experiment, subjects received 50 euros, and parking or public transport costs were reimbursed. The present study was carried out in accordance with the ethical rules for human subjects as described in the Declaration of Helsinki ("World Medical Association Declaration of Helsinki", 2013). Additionally, the study was approved by the Medical Ethics Committee at Ghent University Hospital. All participants signed informed consent forms, before commencing any part of the study.

Table 1

Summary of demographic information of final sample (n = 124)

Handedness Group	*EHI* (mean score (sd))	*Age* (mean years (sd))	*Higher education* (mean years (sd))	*Sex* (% F/M)
LH (*n = 62*)	-69.37 (35.68)	36.58 (11.99)	14.27 (2.07)	58/42
RH (*n = 62*)	89.35 (23.88)	42.56 (13.22)	14.42 (2.53)	44/56

Abbreviations. LH = left-handed, RH = right-handed, EHI = Edinburgh Handedness Inventory (Oldfield, 1971) used to assess handedness, with scores that range from -100 to +100.

Stimuli, Materials, and Procedures

Behavioral measures

Edinburgh Handedness Inventory. During the behavioral testing, participants completed a Dutch version of the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). In this questionnaire, individuals are presented with ten different daily actions that are related to hand preference use, such as writing, drawing, using cutlery, and hand sewing. They are then asked to indicate whether they ‘always’ or ‘usually’ perform these actions with their left or right hand, or whether they are ambidextrous. Based on these responses, a hand preference score is calculated that can range from -100 (i.e., completely left-handed) to +100 (i.e., completely right-handed; Edlin et al., 2015). In this study, individuals with values larger than zero were classified as right-handed and individuals obtaining EHI scores smaller than zero as left-handed.

Benton Facial Recognition Task. Participants performed a computerized version of the Benton Facial Recognition Test (BFRT-c; Rossion & Michel, 2018). The Benton Facial Recognition Test is a behavioral test measuring the ability to recognize faces (Benton & Van Allen, 1968; Levin et al., 1975). It is one of the oldest measures of facial recognition, but remains widely used as an assessment to evaluate how individuals identify and interpret facial features. The aim of the BFRT is to match grayscale photographs of individual faces to one identity (Murray et al., 2021; Rossion & Michel, 2018).

Performance of the BFRT-c consisted of two different phases (see Figure 3). First, subjects were asked to match one target face, with a neutral facial expression and in a front view at the top of the screen, to one of six faces that were simultaneously presented at the bottom of the screen. During this first phase, the response face at the bottom was identical to the target face shown at the top of the screen. Second, subjects were once again shown a target face and instructed to match it to three of the six faces at the bottom (i.e., three different items of the same identity must be found among the six faces). These six faces would vary in either head orientation or lighting of the image, making it harder to match the identities. At the start of each task phase, participants received instructions on how many faces they had to find, and that once they clicked on a face, they could not undo this decision.

All items used were greyscale images of Caucasian faces with neutral facial expressions. The overall shape of the faces was retained, but hair, clothing, or any other cues (such as earrings, beards, makeup) were removed from the images (Rossion & Michel, 2018). Participants performed six trials (half of them male faces) during the first phase and sixteen trials (half of them male faces) during the second phase, which included eight items with changes in head orientation and eight items with changes in lighting. A maximum score of 54 points could be obtained, by receiving one point for each correct response (i.e., 1 x 6 for matching single faces in the first phase, 3 x 8 for matching three correct faces with different orientations in phase two, and 3 x 8 for matching three correct faces with different lighting in phase two).

Figure 3

Example items of the BFRT-c

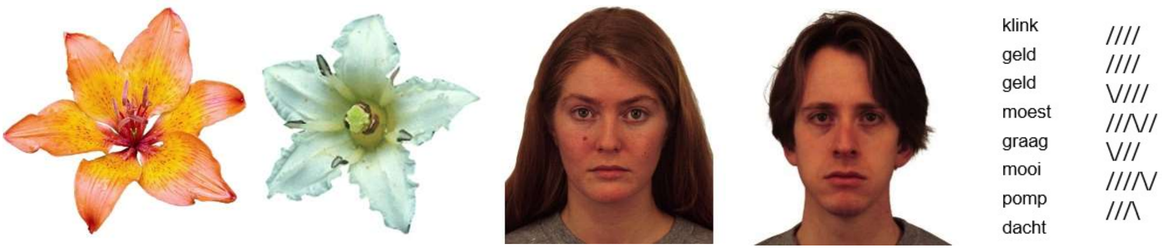
Note. The target face (i.e., an unfamiliar face with a neutral facial expression) was presented at the top of the screen in a frontal view. This target had to be found amongst the six other faces that were simultaneously shown at the bottom of the screen. Panel A represents the first phase in which the target face had to be matched to one (almost identical) face. Panel B and C represent the second phase in which the target face had to be matched to three of the six faces, which varied in head orientation (B) and lighting (C) (stimuli adapted from Rossion & Michel, 2018).

fMRI paradigms

Static face localizer. A four-condition visual localizer task was performed to obtain brain activation related to static face perception. In the blocks of this task, participants were presented with images from four different stimulus categories: faces, flowers, words and symbol-strings (see Figure 4). The contrast of interest for this localize was faces > flowers, i.e., the pictures of the faces were contrasted with the pictures of the flowers to retain face-specific activation only. A total of 20 stimuli per category were used. Moreover, the words were matched in length and for the face stimuli half of the faces were male, half of them female. The task consisted of 4 active blocks for each stimulus category (i.e. 16 active blocks in total) interspersed with 5 rest blocks, which lasted 16 seconds each and in which a central fixation cross was presented on screen. In every block 16 images were displayed for 600 ms, each followed by a blank screen for 400 ms, thus each block lasted for 16 seconds. While the stimuli were shown on screen, participants performed a one-back task in which they had to press a button with both hand when they saw a consecutive, repeated image. The stimuli used for the flower category were acquired from Karlsson and colleagues (2021), and the neutral faces were adopted from the Karolinska Directed Emotional Faces database (KDEF; Lundqvist et al., 1998). The static face localizer task was run in PsychoPy version 2022.2.4 (Peirce et al., 2019). All backgrounds were gray and any text was presented in black, using the Courier New font.

Figure 4

Example stimuli four-condition localizer



Note. This figure illustrates the different stimuli categories used during the four-condition localizer task, on which participants had to perform a one-back task. From left to right: flowers, faces (all neutral expressions), words and symbol strings. The contrast of interest for this localizer was faces > flowers.

Dynamic face localizer. The laterality of dynamic face processing was determined using a one-back task, in which participants viewed 2-second video blocks of faces or inanimate moving objects. Similarly to the four-condition localizer, participants were instructed to press a button with both hands every time that they saw a video which was an identical repetition of the previously viewed video. The dynamic faces one-back procedure is based on research by Fox and colleagues (2009) and their stimuli were used. A total of 16 active blocks, half of which were faces and the other half were inanimate objects, were presented with 16 rest blocks interspersed. Both active and rest blocks lasted for 12 seconds each. During the active blocks 6 clips were presented, 5 of which were novel clips with 1 repetition. On the one hand, participants performed a face block, in which dynamic changes of facial expressions were displayed. These facial expressions changed from neutral to happy or from neutral to sad. On the other hand, participants viewed inanimate moving objects during the control blocks. In these control blocks, only object videos with little positional translations were presented, to make the dynamic changes of the objects comparable to the dynamic facial changes. The 8 experimental (face) blocks and 8 control (object) blocks were counterbalanced. The contrast of interest was dynamic face perception > dynamic object perception. The dynamic face localizer task was run in PsychoPy version 2022.2.4 (Peirce et al., 2019). All backgrounds were gray and any text was presented in black, using the Courier New font.

fMRI data acquisition

The scans were acquired in a Siemens 3 Tesla Prisma magnetic resonance (MR) scanner at the University Hospital in Ghent using a 64-channel head coil. Functional images were acquired with a T2-weighted gradient-echo EPI sequence, multiband factor: 4, field of view (FOV) = 210, 60 slices; acquired voxel size (mm) = 2.5 x 2.5 x 2.5 (reconstructed voxel size (mm) = 2.53), repetition time (TR) = 1070 ms, echo time (TE) = 31 ms, flip angle (FA) = 52°, acquisition volumes for each task: four-conditions = 450 and dynamic faces = 362. The first 5 scans of each functional run were discarded before image acquisition to establish steady-state magnetization. T1-weighted structural images were obtained with the following parameters: T1-weighted image acquisition using a MPRAGE sequence, TR = 2250 ms, TE = 4.18 ms, inversion time [TI], 900 ms, acquisition time = 314 seconds, FA = 9°, FOV (mm) = 256 x 256 x 176, voxel size (mm) = 1 x 1 x 1 (reconstructed voxel size = $1mm^3$).

Statistical analyses

fMRI preprocessing

Results included in this manuscript come from preprocessing performed using fMRIPrep 21.0.2 (Esteban et al., 2019; RRID:SCR_016216), which is based on Nipype 1.6.1 (Gorgolewski et al., 2011; RRID:SCR_002502).

Anatomical data preprocessing. The T1-weighted (T1w) image was corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection (Tustison et al., 2010), distributed with ANTs 2.3.3 (Avants et al., 2008; RRID:SCR_004757), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast (FSL 6.0.5.1:57b01774, RRID:SCR_002823, Zhang et al., 2001). Volume-based spatial normalization to standard space (MNI152NLin6Asym) was performed through nonlinear registration with antsRegistration (ANTs 2.3.3), using brain-extracted versions of both T1w reference and the T1w template. The following template was selected for spatial normalization: FSL's MNI ICBM 152 non-linear 6th Generation Asymmetric Average Brain Stereotaxic Registration Model [Evans et al. (2012), RRID:SCR_002823; TemplateFlow ID: MNI152NLin6Asym].

Functional data preprocessing. For each of the 2 BOLD runs, the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL 6.0.5.1:57b01774, Jenkinson et al., 2002). The BOLD time-series (including slice-timing correction when applied) were resampled onto their original, native space by applying the transforms to correct for head-motion. The BOLD reference was then co-registered to the T1w reference using mri_coreg (FreeSurfer) followed by flirt (FSL 6.0.5.1:57b01774, Jenkinson and Smith, 2001) with the boundary-based registration (Greve and Fischl, 2009) cost-function. Co-registration was configured with six degrees of freedom.

The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (CompCor, Behzadi et al., 2007). Principal components are estimated after high-pass filtering the preprocessed BOLD time-series (using a discrete cosine filter with

128s cut-off) for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 2% variable voxels within the brain mask. For aCompCor, three probabilistic masks (CSF, WM and combined CSF+WM) are generated in anatomical space. The implementation differs from that of Behzadi and colleagues (2007) in that instead of eroding the masks by 2 pixels on BOLD space, the aCompCor masks are subtracted a mask of pixels that likely contain a volume fraction of GM. This mask is obtained by thresholding the corresponding partial volume map at 0.05, and it ensures components are not extracted from voxels containing a minimal fraction of GM.

Finally, these masks are resampled into BOLD space and binarized by thresholding at 0.99 (as in the original implementation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. Automatic removal of motion artifacts using independent component analysis (ICA-AROMA, Pruim et al., 2015) was performed on the preprocessed BOLD on MNI space time-series after removal of non-steady state volumes and spatial smoothing with an isotropic, Gaussian kernel of 6mm FWHM (full-width half-maximum). Corresponding "non-aggressively" denoised runs were produced after such smoothing. Gridded (volumetric) re-samplings were performed using antsApplyTransforms (ANTs), configured with Lanczos interpolation to minimize the smoothing effects of other kernels (Lanczos 1964). Non-gridded (surface) re-samplings were performed using mri_vol2surf (FreeSurfer).

fMRI analysis

Following fMRI preprocessing, the analysis of the fMRI data was conducted in SPM12, executed in MATLAB_R2023A (Penny et al., 2007; The MathWorks Inc., 2022). The general linear model (GLM), utilizing boxcar regressors, was employed to map the hemodynamic response function onto each experimental condition. Subsequently, the boxcar function was fitted to the time series at each voxel, yielding a weighted beta-image. The fitted model was then transformed into a t-statistic image, constituting the statistical parametric map.

Region of interest analysis

The experimental data obtained by the four-condition localizer and the dynamic face localizer was separately used to localize the regions of interest (ROIs; i.e., FFA, OFA, and STS) in the current sample. The center ROI coordinates of the current study were based on data reported in two previous studies. Zhen and colleagues (2015) reported coordinates of these

ROIs based on their dynamic facial localizer. Additionally, Thome and colleagues (2022) reported a range of MNI coordinates based on previous studies and a meta-analysis of the Neurosynth platform. Each region of interest was created by adding a sphere with 10 mm diameter around the central coordinates in MNI coordinate space. The FFA mask was built around the center of X = ± 41, Y = – 45, Z = – 19. The center of the OFA mask was X = ± 41, Y = – 80, Z = – 10. The STS mask was defined around the center of X = ± 55, Y = – 47, Z = 7. Once the masks were created, they were realigned with the voxel dimensions of the fMRI images in our sample using SPM.

The MARSBAR toolbox, running in SPM12, was used to create the ROIs (Brett et al., 2002). ROIs were constructed for the left and right hemisphere separately. However, it was ensured that the coordinates in both hemispheres were symmetrical, to ensure that identical areas were investigated in the left and right hemisphere. Afterwards, the left and right counterparts of the ROIs were combined into one ROI mask constituting both hemispheres.

Laterality analysis within the regions of interest

Next, the LI-toolbox plugin for SPM12 was used to evaluate the hemispheric contribution to processing the static and dynamic face localizer tasks (Wilke & Lidzba, 2007; Wilke & Schmithorst, 2006). The LI-toolbox allows to compare right and left hemispheric activations, mitigating common challenges such as complications arising from statistical outliers, threshold-dependent comparisons, or data sparsity (Wilke & Lidzba, 2007).

The LI-toolbox utilizes a bootstrapping method, wherein 20 equally sized thresholds are computed between zero and the maximum t-value in the dataset. One hundred bootstrapped samples (with a resampling ratio of k = 0.25) are obtained in each hemisphere at each threshold. The 10,000 LI combinations are then calculated from these samples for all surviving voxels on the left and right hemisphere, using the standard LI formula (i.e., LI = (L-R)/(L+R)). If the resulting score is positive, this indicates more left hemispheric activity; whereas a resulting negative score indicates more right hemispheric activity. Only the central 50% of the data are retained, to avoid the effects of statistical outliers. A final LI is calculated from all the LIs, weighted to their corresponding threshold. This LI score provides an estimate of how lateralized a participant is for a given contrast. In the current study, six LI scores were obtained per subject, i.e., one for static face processing via the faces > flowers contrast, and one for dynamic face processing via the faces > objects contrast, for each ROI (FFA, OFA, and STS).

To translate these LI scores into a categorical decision regarding the direction of lateralization, a cutoff score is needed (Wilke et al., 2010). This decision is made arbitrarily, but in language research the recommended cutoff value is ± 0.2 (Wegrzyn et al., 2019).

However, even though previous studies on face processing also used ± 0.2 as the LI cutoff value, LI scores in face selective regions may have smaller LI scores than regions associated with language (e.g., Bradshaw et al., 2017; Thome et al., 2022). Therefore, the cut-off value of 0 was used in the current study, in line with previous research of Gerrits and colleagues (2020b) investigating complementarity of different functions. By setting the LI threshold to 0, the need to create a third group with bilateral lateralization was avoided. Thus, for both dynamic and static face processing for the three ROIs, participants were classified as left lateralized when their overall LI exceeded the zero-threshold and classified as right lateralized when their overall LI was smaller than zero. For one left-handed subject, no LI could be calculated in the OFA during dynamic face processing due to the absence of significant voxel activity within the ROI mask.

Main statistical analyses

Lateralization of the face-selective regions at an intra-individual level. To investigate how the face-selective regions are lateralized within individuals (cf. primary research question), the lateralization pattern of the ROIs (i.e., segregation and complementarity types) was computed for each individual, in the first step of the analysis. Within-subject correlations were used to statistically assess the association between the LIs of the face-selective regions at an intra-individual level. Next, the proportions of the different lateralization patterns were calculated for each handedness group (i.e., left-handed and right-handed individuals) and for each type of face processing (i.e., static and dynamic). To evaluate whether left- and right-handers expressed their lateralization patterns differently, the proportions of segregation and complementarity types were compared between both handedness groups by means of a Pearson's Chi-squared test. Similarly, to investigate whether the lateralization patterns differed during static and dynamic face processing, a Pearson's Chi-squared test was performed on the proportion of lateralization patterns between both types of face processing.

Given that each region of interest can lateralize towards the left or right hemisphere, there are 8 possible hemispheric segregation patterns (2^3) that can occur within individuals. Firstly, it is possible that all regions of interest are lateralized towards the same hemisphere. In that case individuals either exhibit a typical lateralization pattern with all ROIs in the right hemisphere (RRR), or a reversed typical pattern with all ROIs dominant in the left hemisphere (LLL). Secondly, the ventral face processing regions (FFA and OFA) might lateralize towards the same hemisphere, whereas the dorsal face processing region (STS) might lateralize towards the opposite hemisphere. Considering the hypothesis that regions associated in function are more likely to lateralize towards the same hemisphere, these lateralization patterns can be described as an 'expected' deviation from the typical pattern when the FFA and OFA lateralize towards the right and the STS towards the left hemisphere (RRL). When the FFA and OFA are dominantly represented in the left hemisphere and the STS in the right hemisphere, this may be seen as an 'expected' deviation from the reversed typical pattern (LLR). In contrast, if the ventral regions lateralize towards opposite hemispheres (i.e., FFA and OFA not dominant in the same hemisphere), another four lateralization patterns may occur. There could be an 'unexpected' deviation from the typical pattern when either the FFA or the OFA are lateralized towards the left hemisphere, which results in a LRR or RLR pattern respectively. Similarly, individuals might exhibit an 'unexpected' deviation from the reversed typical pattern, with either the FFA or OFA lateralizing towards the right hemisphere, leading to a RLL or LRL pattern respectively.

Regarding the complementarity of lateralization within the face processing network, three different complementarity types can be distinguished. Complete complementarity is observed when the three regions of interest are lateralized towards the same hemisphere. Partial complementarity occurs if one of the regions is lateralized towards the opposite hemisphere. This situation arises when the FFA and OFA lateralize towards the same hemisphere while the STS lateralizes towards the opposite hemisphere; or, alternatively, when the FFA and OFA are segregated by lateralizing towards different hemispheres.

Lateralization of the face-selective regions at an inter-individual level. Some group-level analyses were performed to examine how the face-selective regions were lateralized, on average, during static and dynamic face processing in left- and right-handed individuals. Non-parametric statistical tests were used, since LI scores are typically not normally distributed (i.e., they are concentrated around the extremes instead of around zero; Sainani, 2012). First, a Wilcoxon signed rank test compared the mean LI of each ROI to zero, within each handedness group, which indicated whether the ROI was, on average, lateralized towards one hemisphere in that handedness group. Second, a Mann-Whitney U test was performed to compare the mean LI of each ROI between the left- and right-handed group to examine whether the handedness groups, on average, differed in how strongly they were lateralized for the face processing network.

Association cerebral asymmetries and face-recognition skills. The secondary research question aimed to assess whether performance differences on the Benton Facial Recognition Task (BFRT-c) were associated with the observed lateralization patterns. To this end, two multiple linear regression models were used to predict the performance scores on the BFRT-c by means of the different lateralization patterns (i.e., one model for the segregation patterns, and one model including the complementarity types as a predictor), handedness, and age. Age was included as a predictor in the models, since previous research report worse performances on face recognition an matching tasks in elderly populations compared to (younger) adults (Lamont et al., 2005; Ochi & Midorikawa, 2021).

Results

Variability in hemispheric lateralization patterns across subjects

Different segregation patterns

All eight possible segregation patterns were present in the current sample (see Table 2). The typical (RRR) segregation pattern was most frequently observed, ranging from 30.6% to 41.9% in the different subgroups, followed by both the expected and unexpected deviations of the typical pattern, ranging from 6.5% to 21.3%. Finally, the reversed typical pattern as well as the expected and unexpected deviations of the reversed typical pattern were least frequently observed, ranging from 1.6% to 11.5%. As a validity check of the created ROIs, one large ROI that included the three defined subregions was considered. Based on this ROI for the entire core network, 77.4% of the right-handers and 69.4% of the left-handers could be classified as right-hemispheric dominant.

Table 2

Observed segregation patterns (FFA-OFA-STS) during static and dynamic face processing, for right-handers (RH) and left-handers (LH).

		Segregation patterns *(n (%))*							
		Typical	Reversed typical	Expected deviation		Unexpected deviation			
Type of face processing	Handedness group	*RRR*	*LLL*	*RRL*	*LLR*	*LRR*	*RLR*	*RLL*	*LRL*
Static	LH *(n = 62)*	19 (30.6)	3 (4.8)	8 (12.9)	4 (6.5)	7 (11.3)	12 (19.3)	5 (8.1)	4 (6.5)
	RH *(n = 62)*	26 (41.9)	2 (3.2)	7 (11.3)	4 (6.5)	4 (6.5)	10 (16.1)	7 (11.3)	2 (3.2)
Dynamic	LH *(n = 61)*	20 (32.8)	7 (11.5)	13 (21.3)	3 (4.9)	9 (14.8)	6 (9.8)	2 (3.3)	1 (1.6)
	RH *(n = 62)*	23 (37.1)	3 (4.8)	8 (12.9)	4 (6.5)	6 (9.7)	12 (19.3)	5 (8.1)	1 (1.6)

Note. During the dynamic face processing task an LI for the OFA could not be calculated for one left-handed individual. Therefore, the percentages in the dynamic-LH row are based on 61 individuals.

Different complementarity types of lateralization within individuals

The distribution of complementarity types of lateralization was examined in both left-handed and right-handed participants, for both static and dynamic face processing (Table 3). The data show that less than half of the participants (i.e., ranging from 35.5% to 45.2%) showed complete complementarity with the three ROIs lateralized to the same hemisphere. Partial complementarity where the FFA and OFA are separated by lateralizing towards different hemispheres occurred in 28.7% to 45.2% of the participants. Partial complementarity where the STS lateralizes towards the opposite hemisphere compared to the FFA and OFA occurred least frequently in the current sample (i.e., ranging from 17.7% to 27.9%). These complementarity data are presented for both static and dynamic face processing, and show a similar distribution across complementarity types in both face processing conditions. Figure 5 visualizes the complementarity patterns for each individual in the left-handed and right-handed subsamples, during static and dynamic face processing.

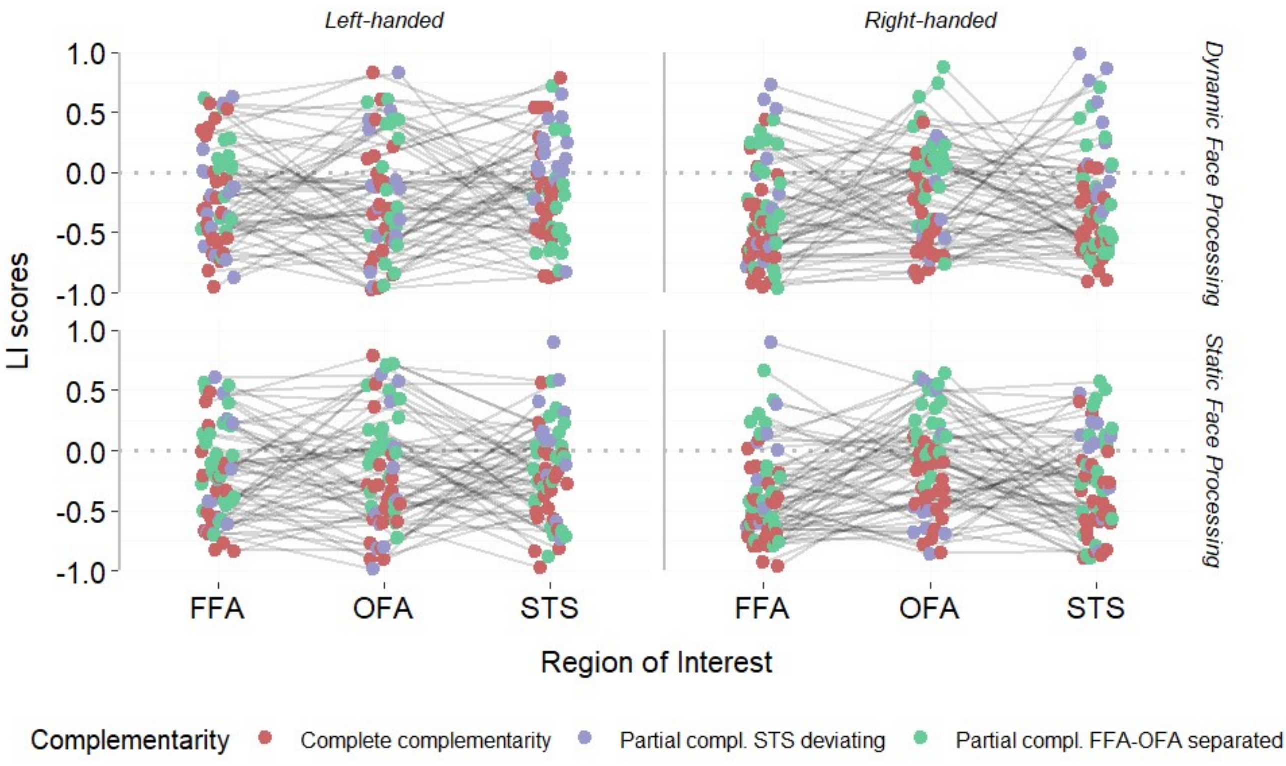
Table 3

Observed complementarity types (i.e., complete, partial complementarity with STS deviating, and partial complementarity with FFA and OFA separated) during static and dynamic face processing, for right-handers (RH) and left-handers (LH).

		Complementarity *(n(%))*		
Type of face processing	Handedness	Complete	Partial STS	Partial FFA/OFA
Static	LH *(n = 62)*	22 (35.5)	12 (19.3)	28 (45.2)
	RH *(n = 62)*	28 (45.2)	11 (17.7)	23 (37.1)
Dynamic	LH *(n = 61)*	26 (42.6)	17 (27.9)	18 (29.5)
	RH *(n = 62)*	26 (41.9)	12 (19.4)	24 (28.7)

Figure 5

Individual complementarity patterns plotted for left-handed and right-handed subsamples, during dynamic and static face processing.



Note. Dots represent individual LI scores and lines connect LI scores obtained from the same individual. The color-coding of the LI scores indicates the complementarity type for this individual (i.e., red = complete complementarity, purple = partial complementarity with the STS deviating, and green = partial complementarity where the FFA and OFA are separated).

To further explore the lateralization patters, bivariate Pearson's correlations (i.e., within-subject correlations) were computed for the laterality indices of the FFA, OFA, and STS (see Table 4). The results show that, during both static and dynamic face processing, the laterality scores of the FFA and OFA were significantly correlated (r_{static} = .26 [CI = .09, .42], *p-value* = .003**; and $r_{dynamic}$ = .27 [CI = .10, .43], *p-value* = .002**). These results indicate that there was a significant relationship between the LI score of the FFA and the OFA at the interindividual level. However, neither the FFA nor the OFA were significantly correlated with the STS (from r_{static} = .04 [CI = -.13, .22], *p-value* = .68 (ns) to r_{static} = .07 [CI = -.11, .24], *p-value* = .50 (ns); and from $r_{dynamic}$ = .06 [CI = -.11, .24], *p-value* = .49 (ns) to $r_{dynamic}$ = .13 [CI = -.05, .30], *p-value* = .16 (ns)). This indicates that there was no relationship between the LI values of the ventral (i.e., FFA and OFA) and the dorsal (i.e., STS) face-selective regions within subjects.

These correlations were also computed within each handedness group separately. During static face processing, the significant correlation between the FFA and the OFA was found in both right-handers (r_{RH} = .26 [CI = .01, .48], *p-value* = .037*) and left-handers (r_{LH} = .29 [CI = .05, .5], *p-value* = .023*). During dynamic face processing, the significant correlation between the FFA and the OFA present in the left-handed individuals (r_{LH} = .36 [CI = .12, .56], *p-value* = .009**), whereas there was no significant correlation in the right-handed individuals (r_{RH} = .20 [CI = -.05, .43], *p-value* = .21 (ns)).

Table 4

Means, standard deviations (SD), and correlations with confidence intervals for the laterality indices (LI) of each region of interest.

Type of face processing	Sample	Region of interest	LI score *(Mean (SD))*	Correlation with LI-FFA	Correlation with LI-OFA
Static	Entire sample	FFA	-0.27 (0.40)		
		OFA	-0.13 (0.45)	**.26**** [.09, .42]	
		STS	-0.22 (0.40)	.07 [-.11, .24]	.04 [-.13, .22]
	LH	FFA	-0.19 (0.39)		
		OFA	-0.15 (0.50)	**.29*** [.05, .50]	
		STS	-0.16 (0.40)	.02 [-.23, .27]	.04 [-.21, .28]
	RH	FFA	-0.36 (0.40)		
		OFA	-0.12 (0.40)	**.26*** [.01, .48]	
		STS	-0.28 (0.40)	.06 [-.19, .31]	.06 [-.19, .30]
Dynamic	Entire sample	FFA	-0.26 (0.44)		
		OFA	-0.20 (0.46)	**.27**** [.10, .43]	
		STS	-0.19 (0.44)	.06 [-.11, .24]	.13 [-.05, .30]
	LH	FFA	-0.18 (0.42)		
		OFA	-0.21 (0.50)	**.36**** [.12, .56]	
		STS	-0.15 (0.43)	.08 [-.17, .32]	.21 [-.05, .43]
	RH	FFA	-0.34 (0.44)		
		OFA	-0.19 (0.42)	.20 [-.05, .43]	
		STS	-0.24 (0.46)	.02 [-.23, .27]	.05 [-.20, .30]

Note. Values in square brackets indicate the 95% confidence interval for each correlation, which indicates a plausible range of population correlations that could have resulted in the observed sample correlation. * indicates $p < .05$ and ** indicates $p < .01$.

Effects of handedness and type of face processing on hemispheric lateralization

Figure 6 visualizes the proportion of right-hemispheric dominance for each ROI, conditioned on the type of face processing, complementarity types, and handedness groups. For complete complementarity, there was a larger proportion of individuals showing right-hemispheric dominance during static ($\hat{p}$ = .90) compared to dynamic face processing ($\hat{p}$ = .82). Additionally, within the complete complementarity, there was a larger proportion of right-handed individuals ($\hat{p}$ = .90) that exhibited right-hemispheric dominance for all ROIs compared to the proportion of left-handed individuals ($\hat{p}$ = .80).

Figure 6

Proportion of right-hemispheric dominance conditioned on the type of face processing, handedness group (LH – RH), and complementarity type.

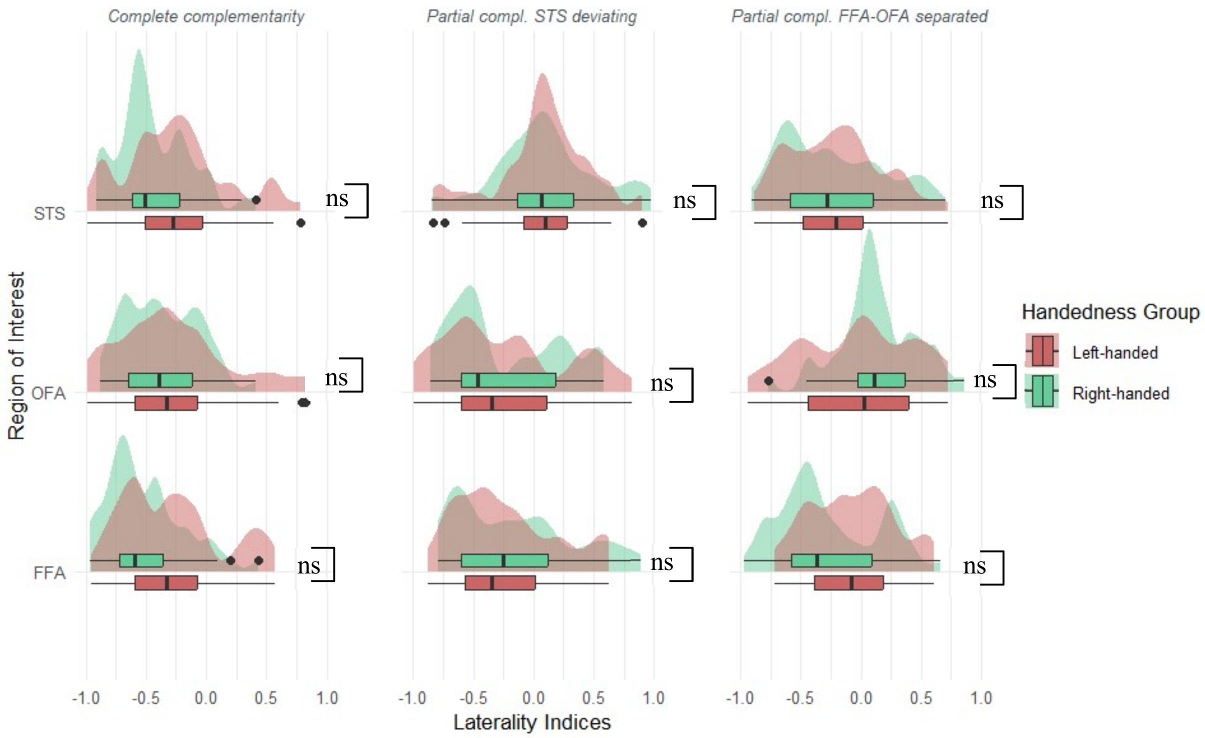
For partial complementarity where the STS deviates, there was a larger proportion of right-hemispheric dominance for the FFA and OFA during dynamic ($\hat{p}_{FFA}$ = .72; $\hat{p}_{OFA}$ = .72) compared to static ($\hat{p}_{FFA}$ = .65; $\hat{p}_{OFA}$ = .61) face processing, and for the STS during static ($\hat{p}_{STS}$ = .35) compared to dynamic ($\hat{p}_{STS}$ = .28) face processing. In contrast, for partial complementarity where the FFA and OFA lateralize to different hemispheres, there was a larger proportion of right-hemispheric dominance for the STS and OFA during dynamic ($\hat{p}_{STS}$ = .79; $\hat{p}_{OFA}$ = .40) compared to static ($\hat{p}_{STS}$ = .65; $\hat{p}_{OFA}$ = .33) face processing, and for the FFA during static ($\hat{p}_{FFA}$ = .67) compared to dynamic ($\hat{p}_{FFA}$ = .59) face processing. There was also a larger proportion of right-handers (with partial complementarity where the FFA and OFA are separated) that was right-hemispheric dominant for the FFA ($\hat{p}_{RH}$ = .72; $\hat{p}_{LH}$ = .54), while the proportion of right-hemispheric dominance for the OFA ($\hat{p}_{RH}$ = .28; $\hat{p}_{LH}$ = .45) and STS ($\hat{p}_{RH}$ = .68; $\hat{p}_{LH}$ = .74) was larger in left-handers.

To evaluate whether there was an association between handedness and the lateralization of face processing, two Pearson's chi-squared tests were conducted. The first Pearson's chi-squared statistical test was conducted on the proportion table of segregation patterns, which detailed the proportion of individuals exhibiting each of the segregation patterns (i.e., RRR, LLL, RRL, LLR, RLR, LRR, LRL, RLL) for each handedness group (i.e., LH and RH) separately. These tests did not reveal a significant association between the proportion of segregation patterns observed in the left- and right-handed groups, for either static ($\chi^2(7)$ = 3.36, *p-value* = .85 (ns)), or dynamic ($\chi^2(7)$ = 7.02, *p-value* = .43 (ns)) face processing.

The second Pearson's chi-squared test was performed on the proportion table of the complementarity types, which detailed the proportion of individuals exhibiting each of the complementarity types (i.e., complete, partial with STS deviating, and partial with FFA-OFA separated) in left- and right-handed individuals. This test evaluated whether there was an association between handedness and the distribution of our sample over the three complementarity types (see Figure 7). Similar to the results of the segregation patterns, there was no significant association between handedness and the proportion of observed complementarity types, during static ($\chi^2(2)$ = 1.25, *p-value* = .53 (ns)) and dynamic ($\chi^2(2)$ = 1.71, *p-value* = .42 (ns)) face processing.

Figure 7

Visualization of the density distributions and boxplots on the LI scores for each ROI, within each complementarity type, comparing left- and right-handed individuals.



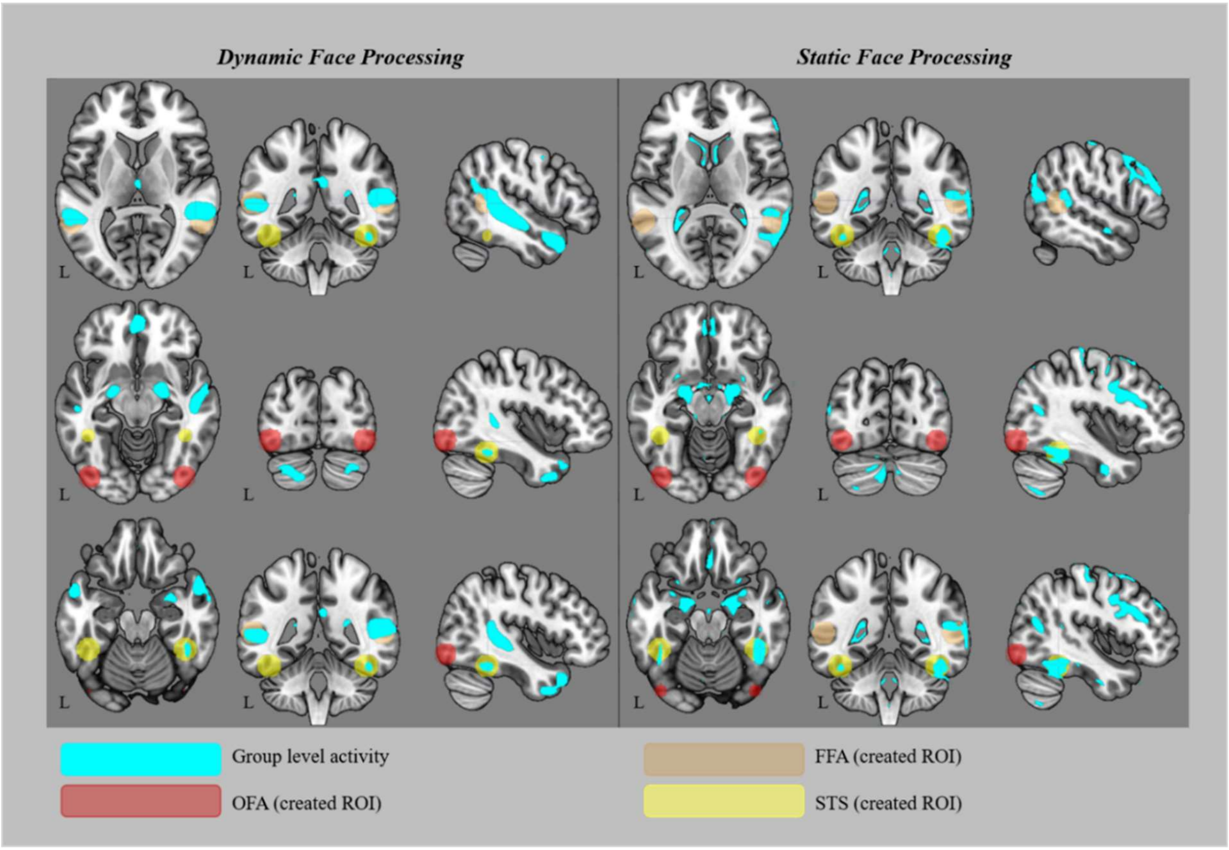
A Pearson's chi-squared test was additionally performed to assess whether the lateralization patterns in the entire sample were associated with the type of face processing (i.e., static or dynamic face processing). The results of the chi-squared test of independence on both the segregation patterns ($\chi^2(7) = 7.11$, *p-value* = .42 (ns)) and the complementarity types ($\chi^2(2) = 1.60$, *p-value* = .45 (ns)) indicated that the observed proportions of the different lateralization patterns were not associated with the type of face processing (i.e., equivalent distributions for both types of face processing).

Group level analysis of lateralization in the regions of interest

The aim of the group level analysis was to assess how the regions of interest are lateralized on average in both right-handers and left-handers (group level activations of the entire sample are visualized in Figure 8). Right-handed individuals showed, on average, the strongest LI scores for the FFA, followed by the LI scores for the STS, and the weakest LI scores for the OFA, during both static and dynamic face processing (see Table 5). The LI scores for the FFA and the STS were, on average, the strongest in left-handed individuals during static face processing, followed by the weakest LI scores for the OFA. In contrast, left-handed individuals showed, on average, the strongest LI scores for the OFA, followed by the FFA, and the STS during dynamic face processing.

Figure 8

Visualization of group level activations in the regions of interest.



Note. This figure represents the averaged brain activity (blue) of the entire sample (both right- and left-handers) during the static and dynamic face processing task. Each region of interest is added as an overlay to visualize where the activity is located. The FFA (beige) and STS (yellow) are clearly active during static and dynamic face processing, with the FFA predominantly active in the right hemisphere and the STS more bilaterally lateralized. However, there was no averaged brain activity in the OFA region (red).

Table 5

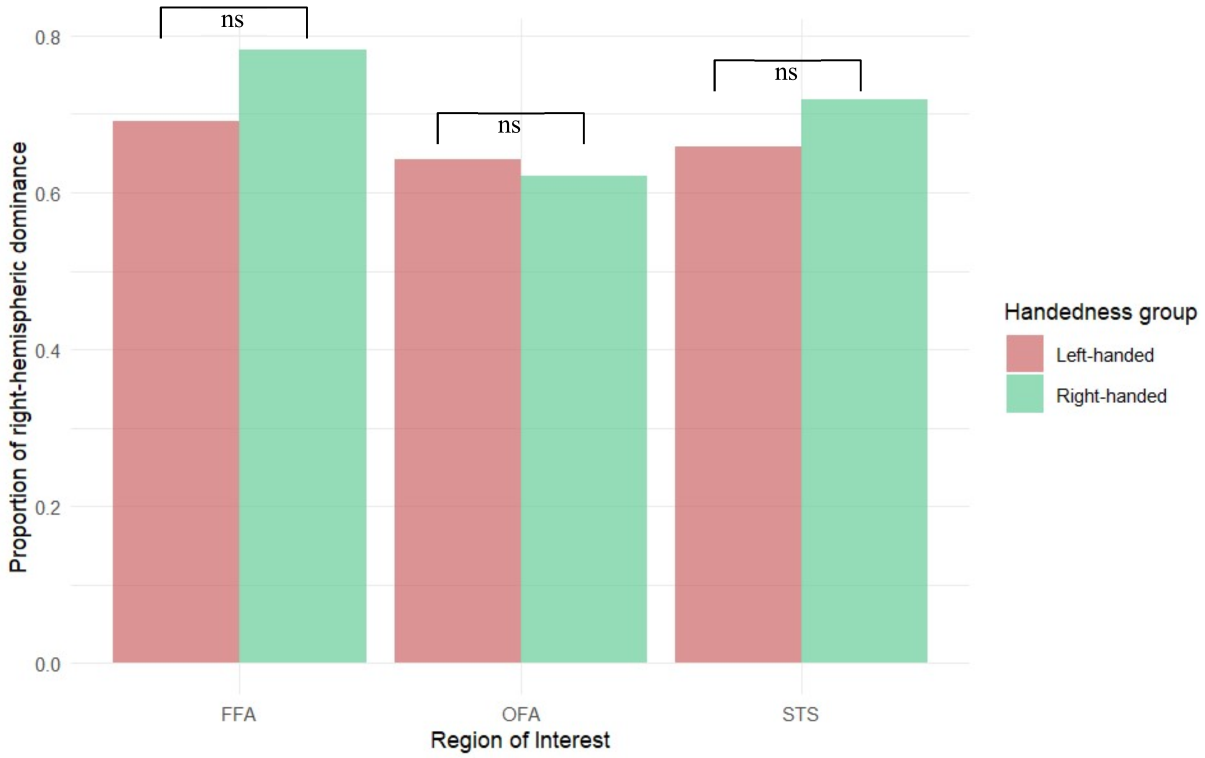
Mean LI scores for each region of interest, conditioned on the type of face processing and handedness; together with the statistical results of the Wilcoxon signed-rank test.

		Region of Interest (ROI)								
		FFA			**OFA**			**STS**		
Type of face processing	Handedness	LI score *(Mean (SD))*	*V-statistic*	*p-value*	LI score *(Mean (SD))*	*V-statistic*	*p-value*	LI score *(Mean (SD))*	*V-statistic*	*p-value*
Static	LH	-0.19 (0.40)	491.0	<.001***	-0.15 (0.48)	598.5	.02*	-0.19 (0.40)	552.5	.003**
	RH	-0.36 (0.40)	222.5	<.001***	-0.12 (0.41)	679.0	.037*	-0.28 (0.41)	335.0	<.001***
Dynamic	LH	-0.18 (0.42)	539.5	.002**	-0.20 (0.49)	525.0	.004**	-0.15 (0.43)	552.5	.003**
	RH	-0.33 (0.44)	281.5	<.001***	-0.19 (0.42)	528.5	.002**	-0.23 (0.45)	450.5	<.001***

Wilcoxon signed rank tests revealed that each region of interest was significantly lateralized towards one hemisphere at a group level, during both static and dynamic face processing (see Table 5 for the statistical results). More specifically, the data indicated that each region of interest was significantly lateralized towards the right hemisphere. This is visually supported by Figure 9, which shows that the majority of participants in the current sample exhibited right-hemispheric dominance during face processing (i.e., the proportion of right-hemispheric dominance in left-handers was $\hat{p}_{FFA}$ = .69, $\hat{p}_{OFA}$ = .64, $\hat{p}_{STS}$ = .66; and right-handers was $\hat{p}_{FFA}$ = .78, $\hat{p}_{OFA}$ = .62, $\hat{p}_{STS}$ = .72). Additionally, the results of Pearson's chi-squared tests with Yates' continuity corrections indicated that the direction of hemispheric dominance of the regions of interest was not associated with handedness ($\chi^2_{direction\ FFA}(1)$ = 2.67, *p-value* = .10 (ns); $\chi^2_{direction\ OFA}(1)$ = 0.23, *p-value* = .63 (ns); $\chi^2_{direction\ STS}(1)$ = 1.00, *p-value* = .32 (ns)), indicating once more that both handedness groups were equivalent in their lateralization direction during face processing.

Figure 9

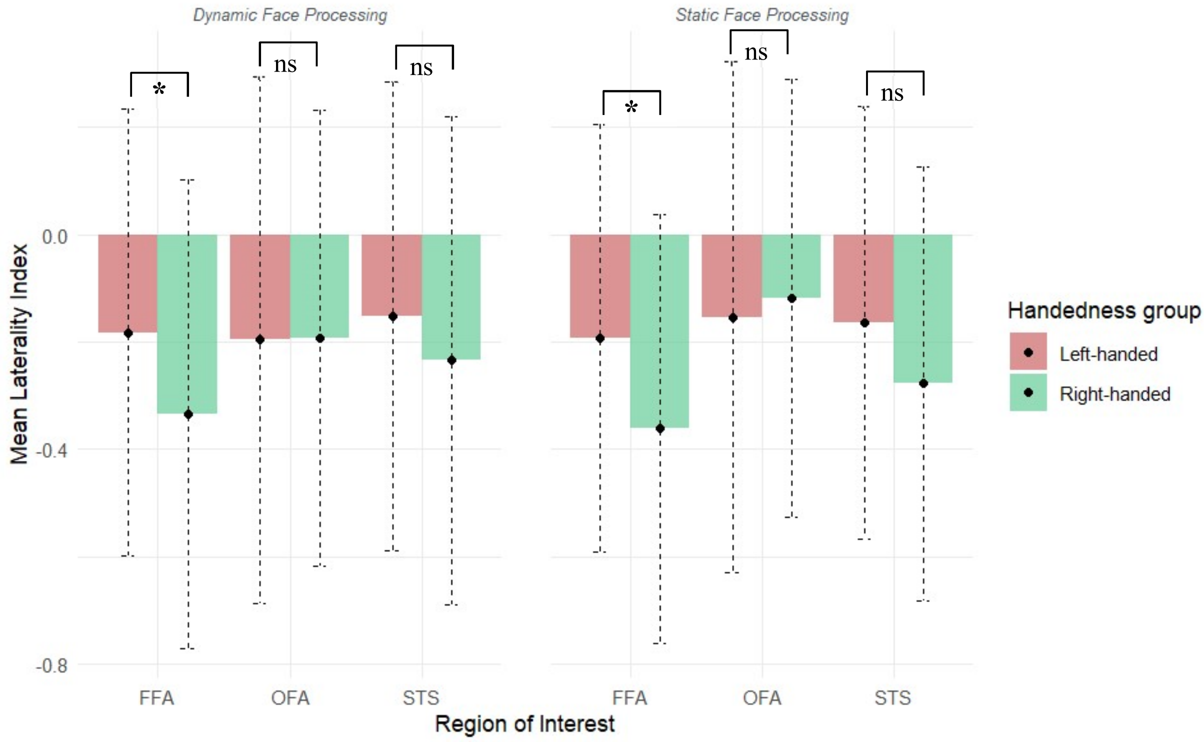
The proportion of right-hemispheric dominance for each ROI, collapsed over static and dynamic processing, for each handedness group separately.



Furthermore, a Mann-Whitney-U test (with continuity correction) comparing the laterality index scores of each region of interest (i.e., indicating the strength of the lateralization) between both handedness groups found a significant difference for the FFA, during static (W = 2430, *p-value* = .011*) and dynamic (W = 2390, *p-value* = .019*) face processing. As seen in Figure 10, the FFA is on average stronger lateralized towards the right hemisphere in right-handed individuals ($M_{FFA-stati} = -0.36$; $M_{FFA-dynamic} = -0.33$) compared to left-handed individuals ($M_{FFA-static} = -0.19$; $M_{FFA-dynami} = -0.18$). The strength of the lateralization of the OFA (and STS was not significantly different between both handedness groups during neither static ($M_{OFA(LH/RH)} = -0.15/-0.12$, W_{OFA}= 1816, *p-value* = .6 (ns); $M_{STS(LH/RH)} = -0.19/-0.28$, W_{STS}= 2240, *p-value* = .11 (ns)), nor dynamic face processing ($M_{OFA(LH/RH)} = -0.20/-0.19$, W_{OFA}= 1822, *p-value* = .73 (ns); $M_{STS(LH/RH)} = -0.15/-0.23$, W_{STS}= 2203, *p-value* = .16 (ns)).

Figure 10

Mean LI scores (SD error bars) for each ROI and handedness group.



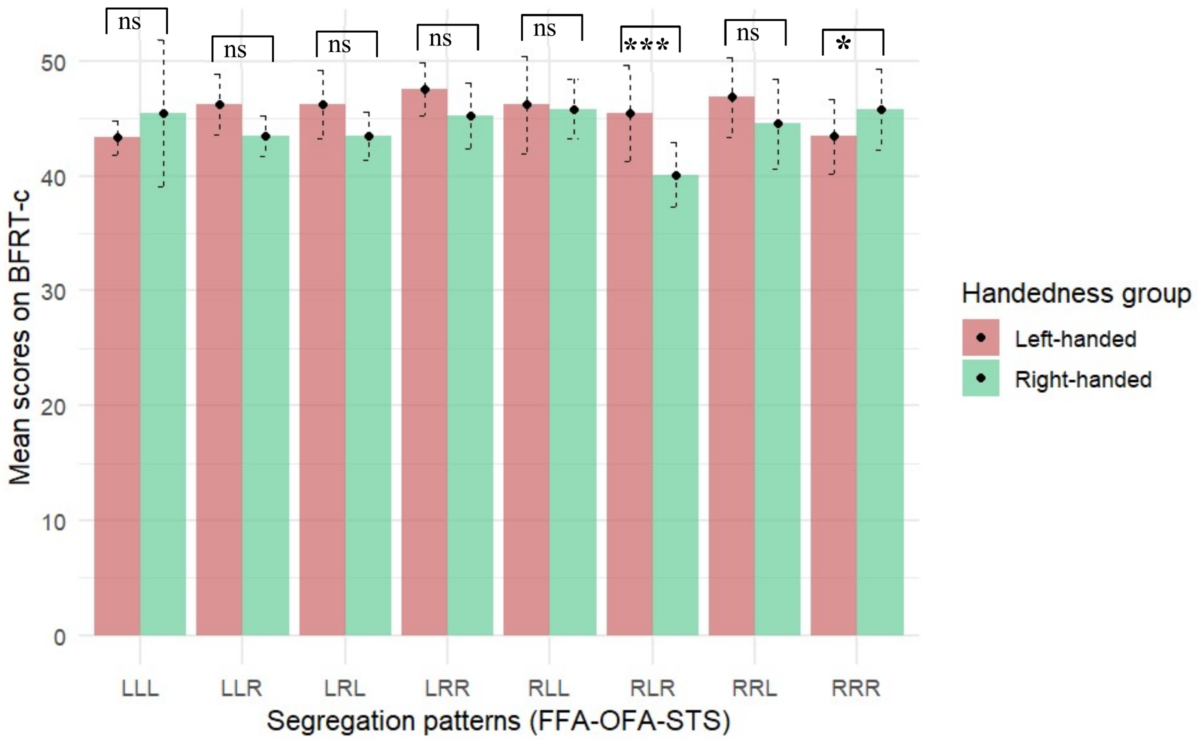
Association lateralization patterns and behavioral performance face matching task

The aim of the secondary research question was to investigate whether the performance on the BFRT-c could be predicted by the observed lateralization patterns of the face network. Before obtaining any p-values, some basic model diagnostics were checked for the multiple linear regression models predicting the BFRT-c performance (i.e., *BFRT-c score ~ segregation pattern + handedness + age + handedness * segregation pattern*; and *BRFT-c score ~ complementarity type + handedness + age + handedness * complementarity type*). These models showed no abnormalities regarding autocorrelation of residuals, outliers, homoscedasticity, and fitted versus observed values. Since two linear models were fitted on the BFRT-c data, Bonferroni corrections for multiple comparisons were applied on these results.

The first linear regression model including the segregation patterns of the face processing network did not yield any main effects of segregation patterns ($F(7,105) = 1.75$, *p-value* = .10 (ns)), individuals their handedness ($F(1,105) = 0.47$, *p-value* = .49 (ns)), and their age ($F(1,105) = 0.21$, *p-value* = .65 (ns)). These results indicated that scores obtained on the BFRT-c could not be predicted by individuals' segregation pattern, handedness, or age. However, the interaction between the segregation patterns and handedness was significant ($F(7,105) = 3.18$, *p-value* = .0043**). Post-hoc analysis (with Tukey's method for p-value adjustments) using the estimated marginal means method revealed that this significant interaction effect was driven by two segregation patterns (Figure 11). More specifically, left-handed individuals (*n = 12*) with the RLR pattern scored significantly higher on the BFRT-c than the right-handed individuals (*n = 10*) with the RLR pattern (*t*(105) = 3.62, *p-value* <.001***). Additionally, left-handed individuals (*n = 19*) exhibiting a RRR segregation pattern performed significantly worse on the BFRT-c compared to the right-handed sample (*n = 26*) with the RRR pattern (*t*(105) = -2.13, *p-value* = .035*).

Figure 11

Mean scores on the Benton Facial Recognition Task for each segregation pattern



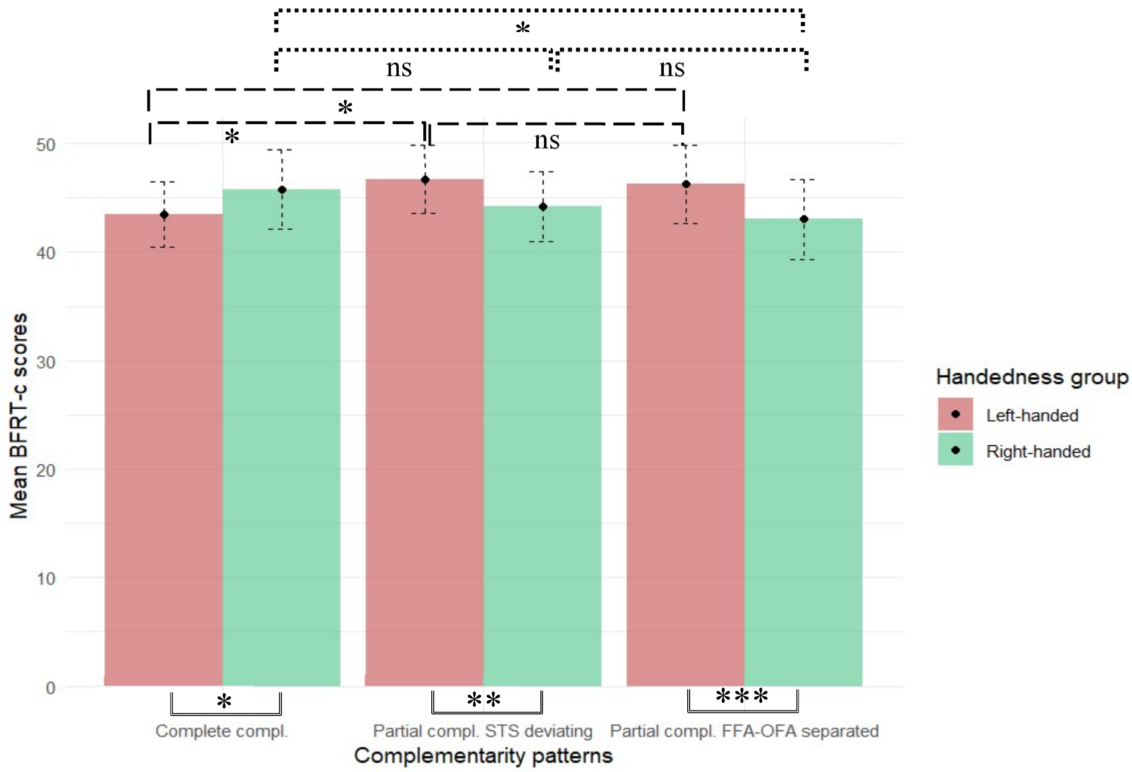
Note. All eight segregation patterns are represented on the x-axis. The coding of the segregation patterns must be interpreted as follows. For example, LRL indicates a left-hemispheric dominance for the FFA, a right-hemispheric dominance for the OFA, and a left-hemispheric lateralization for the STS.

The second linear regression model including the complementarity types as a predictor of the BFRT-c scores yielded a main effect of complementarity type (*F*(2,115) = 5.16, *p-value* = .0071**) and handedness (*F*(1,115) = 5.4, *p-value* = .022*); but no significant main effect of age (*F*(1,115) = 0.0073, *p-value* = .93 (ns)). Individuals exhibiting partial complementarity with the STS deviating (*β-estimate* = 3.21) or with the FFA and OFA separated (*β-estimate* = 2.8) scored higher on the BFRT-c than individuals with complete complementarity. Within the reference complementarity type (i.e., complete complementarity) right-handed individuals also performed significantly better compared to left-handed individuals (*β-estimate* = 2.31).

Furthermore, a significant interaction of the complementarity patterns and handedness was found ($F(2,115) = 8.56$, *p-value* < .0001***; Figure 12). Unlike right-handed individuals with complete complementarity, right-handers exhibiting partial complementarity performed significantly worse than the left-handers exhibiting these partial complementarity patterns ($t(115) = -2.75$, *p-value* = .007**, *β-estimate* = -4.78 for partial complementarity with STS deviating; and $t(115) = -3.93$, *p-value* < .001***, *β-estimate* = -5.49 for partial complementarity with FFA and OFA separated). More specifically, post-hoc analysis (with Tukey's method for p-value adjustments) showed that within the left-handed subsample, individuals with complete complementarity scored significantly lower than those with partial complementarity patterns ($t(115) = -2.60$, *p-value* = .03*, *β-estimate* = -3.21 for partial complementarity with STS deviating; and $t(115) = -2.85$, *p-value* = .014*, *β-estimate* = -2.80 for partial complementarity with FFA and OFA separated). The difference between the BFRT-c scores of individuals with both partial complementarity types did not reach significance ($t(115) = 0.35$, *p-value* = .93 (ns), *β-estimate* = 0.42). Contrary, in the right-handed subsample, scores of complete complementarity were only significantly different from scores of partial complementarity in which the FFA and OFA were separated, with higher scores for complete complementarity ($t(115) = 2.7$, *p-value* = .021*, *β-estimate* = 2.7). Scores with complete complementarity did not differ significantly from those of partial complementarity with STS deviating ($t(115) = 1.28$, *p-value* = .41 (ns), *β-estimate* = 1.57) and scores of both partial complementarity types were also not significantly different ($t(115) = 0.88$, *p-value* = .66 (ns), *β-estimate* = 1.13).

Figure 12

Mean scores on Benton Facial Recognition Task conditioned on the type of complementarity patterns and handedness groups.



Note. This figure visualizes the mean BFRT-c scores obtained in the current sample. The full lines indicate the main effect of handedness and its interaction effect with complementarity type. The post-hoc results comparing the scores for each complementarity type within each handedness group are represented by the long-striped lines for the left-handed subsample and by the dotted line for the right-handed subsample.

Discussion

The present study aimed to determine the interindividual variability of hemispheric specialization during face processing in a sample including both left- and right-handed individuals. Specifically, the aim was to examine the number of individuals who could be classified as left- or right-hemispheric dominant for the three main face-selective regions of the core face network (i.e., FFA, OFA, and STS) and how these regions lateralized in relation to each other. In addition, the study sought to determine whether factors, such as handedness and type of face processing (i.e., static or dynamic), influenced the observed lateralization patterns and whether these lateralization patterns had an effect on how individuals performed during a behavioral face recognition task. Little comparative data are available as previously few to no studies have investigated how these face-selective regions exhibit hemispheric lateralization at the intra-individual level (i.e., how are the ROIs lateralized in relation to each other within an individual), while including both static and dynamic face processing tasks.

Large interindividual variability in hemispheric specialization of face processing

Lateralization of the face network within individuals

The primary research question aimed to investigate how the face-selective regions (i.e., FFA, OFA, and STS) lateralized at the intra-individual level. Some variability in the hemispheric specialization of the ROIs was expected. However, the first hypothesis posited that the FFA and OFA are likely to lateralize towards the same hemisphere, whereas the STS might deviate and lateralize towards the opposite hemisphere. Thus, segregation patterns in which the FFA and OFA are lateralized in the same hemisphere (i.e., RRR, LLL, RRL, LLR) were expected to occur more frequently compared to segregation patterns where the FFA and OFA lateralized towards opposite hemispheres (i.e., RLR, LRL, RLL, LRR).

Segregation patterns. All eight possible segregation patterns where observed within the left- and right-handed subsamples. Two findings regarding these individual segregation patterns are noteworthy. First, the literature often reports a clear right-hemispheric lateralization of the entire core face network at a group level (e.g., Badzakova- Trajkov et al., 2010; Behrmann & Plaut, 2015). However, the intra-individual-level data in the current study clearly show that less than half of the participants was fully right-hemispheric dominant for all three face selective regions (i.e., RRR segregation). Thus, a majority in the current sample (58%) showed left-hemispheric dominance for at least one face-selective region. Previous fMRI studies that have examined the lateralization of different subregions individually, rather than investigating the entire core system, have also reported high levels of interindividual variability (e.g., Canário et al., 2020; Davies-Thompson et al., 2016; De Winter et al., 2015; Johnstone et al., 2020; Thome et al., 2022). In their samples, the face-selective regions were not lateralized towards the right hemisphere in up to 45% of the participants. However, it is important to note that these previous studies only focused on how many individuals were left or right lateralized for each subregion. Thus, they do not inform us about the within-individual lateralization patterns across different subregions.

Complementarity types. The data of the distribution of complementarity types in the current sample showed that complete complementarity (39%) and partial complementarity where the FFA and OFA lateralize towards opposite hemispheres (39%) occurred most frequently. In contrast, partial complementarity where the STS deviates towards the opposite hemisphere (22%) was least frequently observed. These percentages are in contrast to the first hypothesis that expected to observe complete complementarity and partial complementarity where the STS deviates most frequently. This hypothesis was based on the different relative contribution of the face-selective subregions to either static or dynamic face processing (e.g., Dien, 2009; Pitcher et al., 2019). Despite the close structural and functional relationship between the FFA and OFA, and the structural separation from the functionally-distinct STS (e.g., Duchaine & Yovel, 2015; Pitcher et al., 2014; Pyles et al., 2013), the current study observed that the FFA and OFA lateralized to opposite hemispheres in approximately 39% of the sample. This counterintuitive finding seems to indicate that the specific functions are not driving the lateralization direction of these face-selective regions. Rather, the lateralization of these face-selective regions is likely influenced by complex interactions of genetic, developmental, and environmental factors, causing the high amount of interindividual variability.

The within-subject correlational analysis revealed a significant relationship between the LI scores of the FFA and OFA. This significant correlation indicates that there was a tendency for these regions to show similar degrees of left- or right-hemispheric dominance within individuals, suggesting a coordinated functional organization. This coordinated functional organization can be reconciled with the close structural and functional connectivity observed between the FFA and OFA (e.g., Duchaine & Yovel, 2015; Pitcher et al., 2014; Pyles et al., 2013). Interestingly, during dynamic face processing, the significant correlation between the FFA and OFA was only present for the left-handed individuals, which suggests that the correlation found in the entire sample was driven by this significant correlation in left-handers. These correlational results are inconsistent with the findings of Thome and colleagues (2022). These authors did not find any significant correlations between the LI scores of the FFA, OFA, and STS, suggesting that there was no consistent lateralization pattern of these regions within their sample ($N_{LH} = 23, N_{RH} = 85$). Three main differences in research design may explain these inconsistent results. First, Thome and colleagues (2022) also used the LI-toolbox in SPM, but they used a tripartite division of laterality (i.e., left-, right-, or bilateral-lateralized), whereas the current study used a bipartite division. Second, the subsample of left-handed individuals of Thome and colleagues (2022) was limited in numbers. Since the correlation in the entire sample of the current study was likely driven by the correlation in the left-handed subsample, their limited amount of left-handers may have caused the lack of significant correlation in their entire sample. Third, these researchers calculated the center coordinates for each ROI mask individually for each participant, while the current study used the same ROI mask for all individuals. It is possible that Thome and colleagues (2022) captured more variability in the anatomical location of the face-selective regions. Future replications should implement this individualized ROI-mask approach and examine whether equivalent significant correlations between the FFA and OFA are obtained.

Effect of type of face processing on the lateralization of the face-network

The second hypothesis expected a difference in the lateralization patterns between static and dynamic face processing, since static and dynamic face processing rely differently on the ventral and dorsal face-selective regions. The current data do not support differences in segregation patterns and complementarity types between static and dynamic face processing. The observed proportions of all lateralization patterns were equivalent for both types of face processing. These results suggest that the differential reliance on either ventral or dorsal face-selective regions during both types of face processing tasks does not influence the lateralization patterns within the face-network. Consistent with earlier reported results on the frequently observed segregation of the FFA and the OFA, this seems to indicate that the specific functions within the face-network do not drive the lateralization direction of these regions.

Although this may indicate that it is not necessary to include both types of face processing when assessing the complex lateralization patterns within individuals, future research should still include both static and dynamic face processing tasks to examine whether equivalent lateralization patterns are consistently found. If this is the case, then previous and future research investigating static faces only, could be generalized to dynamic face processing. This would be advantageous as static face processing tasks are easy to implement and less time-consuming than dynamic tasks. Nonetheless, dynamic face processing is an extremely important skill used in daily life and provides researchers with more information.

Effect of handedness on the lateralization of the face-network

The third hypothesis expected to observe more variability in left-handed individuals compared to right-handed individuals. This would be reflected by an increased proportion of left-handed individuals exhibiting partial complementarity types, and an increased proportion of left-hemispheric dominance of the face-selective regions in left-handed compared to right-handed individuals. The current study found that the proportions of observed segregation patterns and complementarity types were not associated with handedness. All segregation patterns and complementarity types occurred equally often in both handedness groups (i.e., the proportion of left-handers with partial complementarity was not significantly higher than the proportion of right-handers), which is in contrast with the third hypothesis. This result is also inconsistent with research suggesting that left-handed individuals are more variable in their lateralization patterns (e.g., Karlsson, 2019).

If neither handedness, nor type of face processing are influencing factors in the lateralization patterns, the question arises as to what underlies the observed variability in the lateralization patterns of face processing. It seems unlikely that if the majority presents with "atypical" lateralization patterns for face processing, that this observed variation in lateralization patterns reflects a "normal" versus "abnormal" brain organization. An alternative explanation suggests that individuals with different segregation patterns may use different processing strategies, relying more on one hemisphere than the other (Gerrits et al., 2019). For example, some researchers have suggested that face processing in the left FFA is feature-based, whereas the right FFA uses a holistic approach to process faces (e.g., Frässle et al., 2016; Meng et al., 2012). Future research is needed to investigate whether the lateralization patterns do, in fact, reflect different strategies for processing and recognizing faces. Different processing strategies might emphasize the use of one hemisphere over the other. However, lateralization is thought to be relatively stable, with studies reporting stronger LI scores over time, but no observed changes in the direction of lateralization (e.g., Olulade et al., 2020; Szaflarski et al., 2005). Therefore, it is unlikely to expect changes in laterality patterns as a consequence of adopting new processing strategies later on in life. However, Zhen and colleagues (2015) did argue that the large interindividual variability could be explained by functional plasticity in the brain, caused by individual experiences during early development. Therefore future research should investigate the extent to which variability of lateralization in face-selective regions is determined by genetic and environmental factors; for instance, by conducting longitudinal studies examining the intra-individual lateralization of the face-network in both monozygotic and dizygotic twins.

Stronger right-hemispheric lateralization for the FFA in right-handers

Even though plenty of interindividual variability in the lateralization patterns was observed in this study, the face-selective regions were, on average, significantly lateralized towards the right hemisphere at a group level. This result is in line with the general pattern of right-hemispheric dominance of face processing observed within the population (e.g., Behrmann & Plaut, 2015; Gerrits et al., 2020; Karlsson, 2019; Rossion & Lochy, 2021). The proportions of right-hemispheric dominance at the group level for each region of interest were equivalent for both handedness groups (i.e., approximately 66% of the left-handers and 71% of the right-handers). The current study expected to observe more lateralizations of face processing to the left hemisphere in left-handed individuals compared to right-handed individuals (cf. third hypothesis). However, these results indicate that the direction of lateralization of the face-selective regions was not influenced by the handedness of individuals at the group level. This is in contrast to previous research that reported lateralization of the FFA towards the left hemisphere in left-handers, compared to right hemispheric lateralization for other face-selective regions in both left- and right-handed individuals (e.g., Bukowski et al., 2013; Frässle et al., 2016).

The current results showed a significant difference in the strength of lateralization between both handedness groups. More specifically, the FFA was, on average, more strongly lateralized to the right hemisphere in the right-handed subsample compared to the left-handed subsample. This is consistent with a previous study by Johnstone and colleagues (2021) that reported a reduced mean LI score in left-handers compared to right-handers for verbal fluency, scene, body, and face perception. Thome and colleagues (2022) also found a small reduction in the LI scores of the FFA in left-handed individuals compared to right-handed individuals. However, the effect did not reach significance in their sample, possibly due to their small subsample of left-handers included. In contrast, Zhen and colleagues (2015) reported a stronger right hemisphere lateralization in the dorsal face-selective regions (STS) compared to the ventral face-selective regions (FFA and OFA). It is important to note though that these authors do not report on the handedness of their sample, which limits the comparability and interpretability of these results. Moreover, some studies on face processing have reported bilateral lateralization patterns for the FFA at the group level in left-handed individuals (Bukowski et al., 2013; Dundas et al., 2015; Willems et al., 2010). The FFA in the current left-handed subsample still showed right hemisphere lateralization, despite its reduction in lateralization strength compared to right-handers. There were no significant differences in the strength of lateralization for the OFA and STS between left- and right-handed individuals in the current study. This reduction of the lateralization in left-handers of only the FFA, may be caused by a shared circuitry between the VWFA and the FFA within the same hemisphere (e.g., Dehaene et al., 2015; Johnstone et al., 2021). In this view, the weaker observed lateralization of the FFA in left-handers is a result of the shared neural space with reading.

Face recognition performance is differently related to complementarity types in left- and right-handers

The secondary research question aimed to investigate whether the behavioral performance on the Benton Facial Recognition Task-c could be predicted by the different lateralization patterns, handedness, and age. In contrast to the literature claiming that people's ability to recognize faces declines with age, we did not find any age differences in performance on the BFRT-c (Boutet et al., 2015; Lamont et al., 2005; Ochi & Midorikawa, 2021). The current data did not reveal any main effects of segregation patterns or handedness on the

BFRT-c scores, but a significant interaction effect between the segregation patterns and handedness was found. Right-handed individuals exhibiting the 'RLR' segregation pattern performed worse on the BFRT-c than the left-handed individuals with 'RLR' segregation. Similarly, left-handed individuals who exhibited the 'RRR' segregation pattern performed significantly worse than the right-handed individuals with the same segregation pattern. These interaction effects should be interpreted with caution, considering the small amount of individuals in each subgroup. Future research should examine whether these segregation patterns consistently result in decreased BFRT-c scores in interaction with handedness.

The results regarding the second model, which included complementarity types as a predictor of the BFRT-c scores, yielded a significant main effect of complementarity type, handedness, and an interaction effect of complementarity type and handedness. Specifically, within the complete complementarity group, right-handers performed significantly better than left-handers. In contrast, within the partial complementarity groups (i.e., either the FFA and OFA lateralized to opposite hemispheres, or the STS deviating to the opposite hemisphere), right-handed individuals performed significantly worse than left-handers. Thus, in the current study, behavioral face-matching performance was not influenced by the direction of lateralization, but it was influenced by the type of complementarity within the face-network in interaction with handedness. More specifically, left-handed individuals with partial complementarity types performed better than left-handers with complete complementarity. Contrary, right-handed individuals with complete complementarity performed better than right-handers with partial complementarity types.

Consequently, the question can be raised why it would be beneficial for some people to exhibit a segregated face-network across both hemisphere while this implies longer interhemispheric connections instead of short intra-hemispheric connections. The importance of interhemispheric connectivity in face processing has been recently highlighted by Quinn and colleagues (2024). These authors reported a stronger interhemispheric connectivity between corresponding face-regions than intra-hemispheric connectivity of the face network. Even though interhemispheric connectivity is often absent in models of face processing, neuroimaging studies and research on "prosopometamorphopsia" (i.e., a condition in which faces appear distorted) provide support for the importance of interhemispheric connectivity (Almeida et al., 2020; Blom et al., 2021; Herald et al., 2023). It would be interesting to examine whether the interhemispheric connectivity patterns in individuals is related to individual differences in face recognition behavior.

Additionally, Coutanche and colleagues (2023) recently proposed the use of "multivariate Laterality Indices" (mLI) to investigate lateralization as a difference in information instead of activation. They propose that, even when regions show similar levels of activation, they may contain different amounts and forms of information. Therefore, mLI can reveal how each hemisphere contributes uniquely to face processing by examining the richness, diversity, and specific types of information each region processes (Coutanche et al., 2023). As some researchers have suggested that processing in the left hemisphere is feature based and holistic processing occurs in the right hemisphere, involving both hemispheres during a face processing task enables the brain to integrate these different types of processing to achieve more efficient and accurate face recognition (e.g., Frässle et al., 2016; Meng et al., 2012). Additionally, distributing the activation during face processing can prevent overload in one hemisphere, allowing for parallel processing and efficient use of neural resources (e.g., Güntürkün et al., 2020). The use of mLI in future studies might elucidate why some individuals benefit from segregated complementarity patterns. To date it remains unclear why this would be more beneficial for left-handers compared to right-handers. Therefore, mLI should be computed in both left- and right-handers to investigate what specific type of information is processed in each complementarity type and how the information is integrated (e.g., balanced integration versus disruption affecting performance).

Strengths, limitations, and future directions

Finally, some strengths and limitations of the current study can be highlighted. A major strength of the current study was the large sample size available for analyses ($N = 124$). Typically, sample sizes of approximately 30 individuals are used in fMRI research (Poldrack et al., 2017). However, recent research has shown that these small sample sizes are insufficient and reduce the replicability of task-based fMRI studies (Turner et al., 2018). Furthermore, previous studies investigating the lateralization of face processing have often excluded left-handed individuals or focused on only one subregion (e.g., only investigating the FFA; Willems et al., 2010). For example, Thome and colleagues (2022) were, to our knowledge, the first to investigate the hemispheric dominance of the different subregions within the core face network. Their overall sample size was large ($N = 119$), but their sample consisted of 85 right-handed and 23 left-handed individuals. Thus, the equally large left- and right-handed subsamples ($N = 62$) of the current study are unique in research regarding the lateralization of the face-selective subregions. The results presented in the current study are also novel, as the relationship between the lateralization of the face-selective subregions intra-individuals has not been previously investigated.

Despite these strengths, it is important to address certain limitations. There are several methodological issues associated with laterality research using fMRI data. First, the laterality indices obtained can vary depending on various factors, such as the study paradigm (e.g., task instructions, stimuli, difficulty) and the method used to obtain laterality scores (Chlebus et al., 2006; Seghier, 2008). For example, some laterality methods are threshold dependent and influenced by statistical outliers (e.g., subjects with extremely high activity in one hemisphere could distort the mean in group level analysis, causing a greater average lateralization than actually present for most of the individuals). Therefore, a threshold independent bootstrapping method was chosen to compute weighted laterality indices that minimize the effect of these outliers (Wilke & Schmithorst, 2007). There is currently also no consensus on which tasks should be used to quantify the laterality of functions using fMRI, although different tasks may lead to different lateralization estimates within the same individual (Johnstone et al., 2021; Woodhead et al., 2021). Future studies should attempt to replicate the current results using both the same and different face processing tasks, especially since these results are novel with respect to within-individual lateralization patterns of the core face network. These replication attempts will then provide more information about the patterns of segregation and complementarity that exist within the broader population.

Second, the selection and delineation of regions of interest may introduce variability in laterality scores across different studies, thereby affecting the specificity and sensitivity of LI measurements. The results of the performed validity check suggest that the ROIs of the FFA, OFA, and STS – used in the current study – were adequately defined and captured the face processing network well. The proportion of right-hemispheric dominance for the entire network was consistent with the literature that reports approximately 70% to 80% of the population to be right lateralized for the core face-network overall (Bukowski et al., 2013; De Winter et al., 2015; Thome et al., 2022). Third, the current study considered only one cognitive function (i.e., face processing), as the investigation of additional functions was beyond the scope of this thesis. Follow-up studies should include other cognitive functions to investigate how the lateralization of different functions is related to the observed lateralization patterns within the face processing network. Examining multiple cognitive functions could provide a comprehensive understanding of the brain lateralization and inform us on how different cognitive functions interact and influence each other.

A few directions for future research are described in what follows. One possibility is to examine whether the segregation patterns within the face processing network are related to individuals' language lateralization, as there are theoretical accounts that propose that language dominance drives other lateralizations in the brain. For example, Gerrits and colleagues (2019) found a significant correlation between the direction of lateralization between language and face recognition, albeit considering the face network as a whole. Thus, it would be interesting to investigate differences in the segregation and complementarity patterns of the three face-selective regions in language typical (i.e., left-hemispheric dominant) and language atypical (i.e., right-hemispheric dominant) individuals, to assess whether a similar correlation between the direction of language lateralization and the different subregions is found.

In addition, future studies should look at other demographic variables besides handedness that might explain some of the observed (variability in) lateralization patterns. For example, some studies indicate that the strength of hemispheric lateralization is influenced by hormonal factors (such as the menstrual cycle), suggesting that the lateralization patterns may differ between the sexes (Beking, 2018; Beking et al., 2017; Pfannkuche et al., 2009). In the context of face processing, Thome and colleagues (2022) found evidence for an interaction between sex and handedness. Specifically, left-handed males showed bilateral or left-hemispheric dominance for the FFA, whereas right-handed males, and left- and right-handed females were right lateralized for the FFA. Investigating the effect of sex in addition to handedness would have led this thesis too far. However, it is important for future studies to examine the interaction of handedness and sex differences in the complementarity types of the face-selective regions, as the current study found that these types influenced face recognition abilities.

Lastly, future research should investigate which face selective region is the most diagnostic of the overall hemispheric dominance of the face processing network. The current results suggest that the FFA is the most lateralized of the three face-selective regions. However, examining dynamic changes in lateralized connectivity patterns over time would provide insight into which sub-region drives overall lateralization during specific face processing tasks. In addition, the diagnostic power of each face-selective region should be assessed by its ability to predict the overall lateralization of the face processing network (e.g., through regression models). These results would indicate whether one (or more) of the face-selective regions reliably predicts the lateralization observed across the network.

Conclusion

In summary, approximately 40% of our sample showed right-hemispheric dominance for all three face-selective regions. The majority of individuals in our sample exhibited left-hemispheric dominance for at least one face selective region. These results further question whether face processing can be described as “typically right-hemisphere lateralized” based on fMRI data, given the high amount of variability within the population when the face-network is not considered as a whole. Moreover, the data revealed that left-handers do not show more variability in their segregation and complementarity patterns when the face-selective regions are considered separately, rather than the core network overall. At the group level, there were no differences in the direction of lateralization between the left-handed and right-handed subgroups, again highlighting that both handedness groups were equivalent in their lateralization patterns when examining the subregions of the core network separately. However, in the current sample, the FFA was less lateralized in left-handed individuals, whilst still remaining right lateralized. These results provide additional support against an inherent difference in the neural implementation of face recognition in left-handed individuals.

Taken together, the results presented in this thesis provide a more in-depth understanding of the lateralization patterns during face processing within individuals. These findings highlight the importance of considering the subregions of the face processing network when investigating the lateralization of face processing, as much inter-individual variability is not captured when examining the core network as a whole. Future studies should attempt to elucidate the mechanisms underlying the observed variation in lateralization patterns of face processing.

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