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Cerebral asymmetries: handedness and the right hemisphere

Karlsson, Emma

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Cerebral asymmetries: Handedness and the right hemisphere

Emma M. Karlsson

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Summary

There are well-known, but poorly understood, links between left cerebral language dominance and hand preference. Approximately 95% of right-handers and 70% of non-right-handers have language lateralised to the left hemisphere. In contrast, virtually nothing is known about handedness and cerebral dominance for a number of different specialisations linked with the right cerebral hemisphere. This thesis examines several of these asymmetries, including face, emotional, attentional, and body processing, in right-handed and non-right-handed groups using both behavioural and neuroimaging techniques. The main aims of these investigations were to quantify the frequencies of these biases, and to examine possible links between each of these asymmetries and speech/language, to see if they 'anti-localise' in the two hemispheres in a complementary fashion. To do this, a large pool of language 'atypicals' (individuals with right hemisphere dominance for language) were identified for inclusion in the neuroimaging experiments. An important foundation of this work advocates the use of proportional and individual level analyses, rather than the usual exclusive reliance on typical inferential statistics that focus on measures of central tendency.

First, a large-scale battery of perceptual tests, which included measures of language, emotional, attentional, and face-related asymmetry, was administered to a large sample of right-handers and non-right-handers (Chapter 2). These efforts were coupled with a large-scale functional neuroimaging series, quantifying cerebral asymmetries for emotional prosody, emotional vocalisations, bodies, neutral and emotional faces, as well as for language (Chapter 3). The final empirical chapter attempts to predict the neuroimaging asymmetry groups from behavioural measures of asymmetry (Chapter 4).

The results from this thesis confirms the links of the 'target specialisations' to the right hemisphere for the majority of individuals. Intriguingly, it also suggests that there are moderating effects of handedness, with non-right-handers having a more varied laterality profile whilst right-handed participants were largely complementary for all functions measured. The atypically lateralised individuals had the most varied asymmetry profiles, in spite of remarkably similar asymmetry for language with the right-handed and non-right-handed language typical groups. These results are discussed in terms of models of hemispheric specialisation, the use of perceptual tests to aid in the identification of individuals with rare laterality patterns, and future studies important for a full appreciation of cerebral dominance and human handedness.

Table of contents

List of figures and tables

Figures

Tables

CHAPTER 1

General introduction

1.1 The relationship between handedness and functional cerebral asymmetries for language

At a first glance, humans beings appear remarkably symmetrical. Apart perhaps from a crooked smile or a slightly raised eyebrow, each side of the body appears to be a near perfect mirror image of the other. As this thesis will reveal, this is quite the deceptive impression, as the human experience is full of a multitude of asymmetries. Perhaps most noticeable of these asymmetries, in behaviour if not in form, is human handedness. Most humans are incredibly one-sided for skilled activities such as writing or throwing. The magnitude of this asymmetry is remarkable: 90% of any random sample of individuals will have a preference to use their right hand for these skills (Annett, 2002; Coren & Porac, 1977; Gilbert & Wysocki, 1992; Seddon & McManus, 1991). Why this distribution of hand preference is so skewed is unknown. Obviously, if hand preference was determined by chance, then the proportions of left- and right-handers in the world would be roughly equal. If handwriting direction was a serious determinant, then left-handedness would prevail in cultures who use right to left writing systems, which is not the case (Fagard & Dahmen, 2003; Silverberg, Obler, & Gordon, 1979). Whatever the precise determinants, a lack of population-level biases is seen in most of the non-human species (Cashmore, Uomini, & Chapelain, 2008).

One, now, largely disregarded claim regarding this skewed hand preference is that the high rates of right-handedness result from anti-sinistral biases (Blau, 1946; Ashton, 1982; Watson & Watson, 1921). The historical societal pressures against left-handedness are undeniable. However, there is evidence that this bias is largely disappearing, and is not near a sufficient explanation for Homo sapiens' right-handedness (McManus, 2002). Figure 1.1 shows incidence of left-hand preference over many hundreds of studies as a function of birth year. If the low incidence of left handedness was driven exclusively by anti-sinistral bias, these functions should continue rising towards 50%. Even though the anti-sinistral bias has been in steady decline, the rates of left-handedness remain relative stable for individuals born after

1940, suggesting they are unlikely to account for this skewed population-level hand preference.

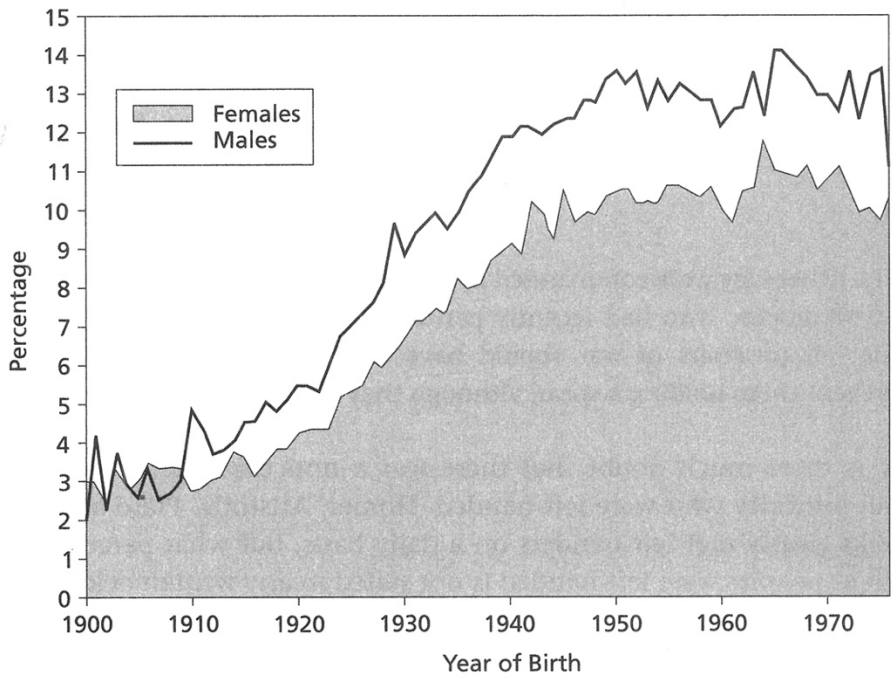


Figure 1.1. Incidence of left-handedness as a function of birth year. Data from Gilbert and Wysocki (1992), reproduced from McManus (2002). Note how the functions for both females and males plateau from 1940s birth cohorts. See also Hugdahl, Satz, Mitrushina, and Miller (1993).

One noticeable detail in Figure 1.1 is that left-handedness[1] seems to be more prevalent in males as compared to females. Indeed, increased rates of male non-right-handedness are often reported (Papadatou-Pastou, Martin, Munafò, & Jones, 2008; Sommer, 2010). This sex difference is perhaps indicative of a biological component to handedness, and has been linked to differential effects of perinatal testosterone on left hemisphere growth in utero (Geschwind, & Galaburda, 1985a,b,c). Biological underpinnings of handedness are also suggested by the unusual relationship that exists between handedness and cerebral organisation of speech and language.

Functional hemispheric asymmetries and its relationship to handedness have been a topic of neuropsychological interest since the pioneering work of Paul Broca and Marc Dax in the early to mid-1800s (for an overview of the controversy over the discovery of the role of the

[1] Left-handedness will be referred to as non-right-handedness throughout the rest of this thesis, encompassing both left-handed individuals and those forced to switch and use their right hand

left hemisphere in speech, see e.g. Cubelli & Montagna, 1994; Finger & Roe, 1996; Finger & Roe, 1999). Broca (1863; 1865) described a series of right-handed aphasic patients with lesions located in the posterior part of the inferior frontal gyrus (IFG; see Figure 1.2). Most importantly, he noted that all of these individuals had unilateral damage to the left hemisphere. Broca's discovery was pivotal in establishing the important connection between speech and the IFG, and the link to the left cerebral hemisphere in *right-handed* individuals. Since Broca's time, the approximate region has become known as Broca's area and is now typically defined in terms of the pars opercularis and pars triangularis of the IFG.

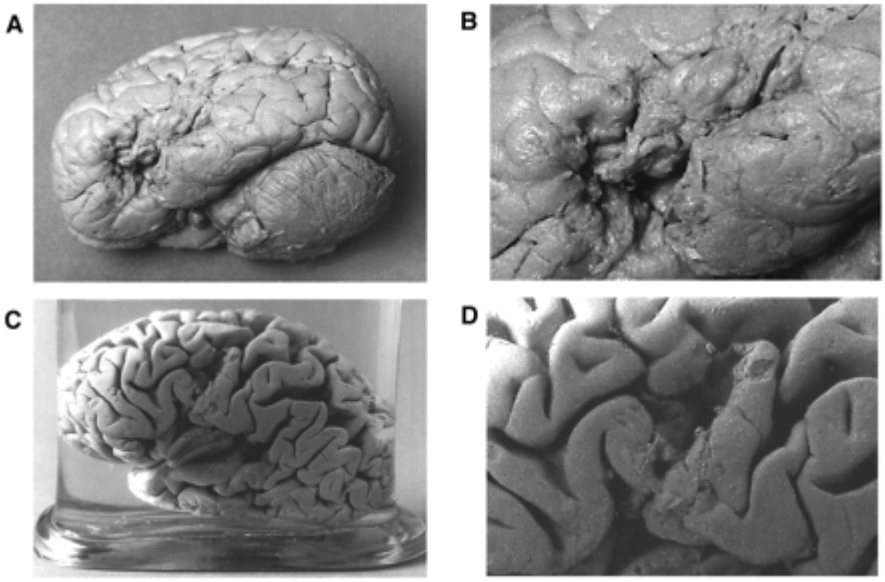


Figure 1.2. Photographs of the post-mortem brains of Paul Boca's first aphasic patients, Leborgne and Lelong. (A) shows a lateral view of the brain of Leborgne. A lesion in the inferior frontal lobe is clearly visible and is shown close up in (B). (C) shows a lateral view of the brain of Lelong. Here, only the posterior parts of what now is referred to as Broca's area is infarcted and can be seen in close-up in (D). Image reprinted from Dronkers, Plaisant, Iba-Zizen, and Cabanis (2007).

In 1866, British neurologist John Hughlings-Jackson was one of the first to describe a non-right-handed aphasic patient with considerable speech defects. This patient had, in fact, a lesion to the right hemisphere. Hughlings-Jackson (1880) subsequently proposed one of earliest theories linking functional cerebral asymmetries to handedness. He postulated that the dominant speech hemisphere would be contralateral to an individual's preferred hand, suggesting that language dominance and handedness were related. This concept became known as Broca's 'rule' (Hecaen & Sauguet, 1971), although it should be noted that Paul Broca never explicitly made such claims (Eling, 1984; Harris, 1991). Nonetheless, some

reports of ‘crossed aphasia’, where the lesion was located ipsilateral to the preferred hand, appeared in this literature very early on (e.g. Bramwell, 1899). However, despite the gradual accumulation of cases of patients with crossed aphasia, Broca’s rule was never particularly challenged until increased cases of non-right-handed patients with unilateral lesions and speech defects appeared after World War II. It became clear that crossed aphasia was a more frequently occurring phenomenon in non-right-handers than inverted (i.e. right hemispheric) dominance (e.g. Brown & Somonson, 1957; Conrad, 1949; Goodglass & Quadfasel 1954; Russel & Espir, 1961).

More evidence against Broca’s rule came with neurosurgical advances such as the development of the Wada test (Wada, 1948), which is a technique used to uncover an individual’s language lateralisation. In this test procedure, sodium amytal is injected into the left or right internal carotid artery, temporarily anesthetizing the associated hemisphere, whilst simple speech tasks are being performed with in the patient (e.g. Branch, Milner & Rasmussen, 1964; Milner, 1974; Milner, Branch & Rasmussen, 1964). Rasmussen and Milner (1977) presented data from 140 right-handed and 122 non-right-handed epilepsy patents without any clinical evidence of early left hemisphere injury. Of the right-handed individuals, only 6 (4%) were found to be right hemisphere dominant, whilst the remaining 96% were found to be left hemisphere dominant. For non-right-handers, 70% of the patients were found to be left hemisphere dominant, 15% to be right hemisphere dominant and the remaining 15% bilateral (i.e. the patient could either still speak or not speak at all when each of the two hemispheres were anesthetized), a category not found in the right-handed sample.

Some researchers have suggested that estimates taken from patients with epilepsy does perhaps not reflect proportions seen in healthy individuals, as abnormal lateralisation of functions may result from early brain damage (e.g. Kimura, 1983). There is at least some evidence that perinatal brain damage changes the frequencies of language dominance (Geschwind & Galaburda, 1985a). Nevertheless, evidence from a meta-analysis by Carey and Johnstone (2014) of frequency data using a variety of techniques including behaviour, Wada, electroconvulsive therapy, transcranial magnetic stimulation, and functional magnetic resonance imaging (fMRI), all point to a similar 15-25% reduction in left-sided speech and language dominance in non-right-handers relative to right-handers. It is also crucial to note that for all of these estimates, left hemisphere dominance remains for the majority of non-right-handers, despite the reduction in frequency relative to right-handers.

A core, critical suggestion from Carey and Johnstone (2014) has important implications for this thesis. They argue that the emphasis in psychology and neuroscience on measures of central tendency has resulted in people failing to report the proportion in any sample who

show either directional bias. In fact, reduced asymmetries for language, on average, in non-right-handers were reported so frequently in the literature of the 1970s-2000s that people rarely measure them anymore. It is important to note that these reduced asymmetries could be a consequence of two different underlying data structures. Weakened asymmetries in *most* non-right-handed participants (relative to the right-handed) would have quite a different interpretation than if the reduction is accounted for by a *small subgroup of non-right-handers with reversed* asymmetries. Instead, although often implicitly, authors tend to link any obtained difference in asymmetry to the known proportion of non-right-handers with reversed language dominance (i.e. the latter of the two alternative structures).

This kind of logic is also frequently extended to asymmetries which instead tend to favour the right hemisphere, in right-handed individuals at least. For example, Levy, Heller, Banich, and Burton (1983), examined face perception biases in a large number of right-handers (n = 111) and non-right-handers (n = 111), with non-right-handers being less asymmetrical, *on average*. Even in these early papers, average asymmetry reductions for non-right-handers were assumed to parallel the relatively well-established proportions for speech and language. These ideas are, in effect, assuming *complementarity* of hemispheric specialisations. The veracity of such arguments for other asymmetries could be tested using this proportional approach advocated here.

1.2 Asymmetries and the right hemisphere: neuropsychological evidence

Speech and language-related enquires have dominated the field of laterality and questions related to hemispheric specialisations. For many years, the right hemisphere was considered 'the minor hemisphere', as an analogy to its limited or non-existent role in speech and language processing (Benton, 1972; Butler & Norrsell, 1968; Gainotti, 1972; Gooddy, 1969; Zangwill, 1967). However, there were several early reports of disorders that now might be labelled as visuospatial or visuoperceptual, that followed lesions of this 'minor' hemisphere in single case reports in the neurological literature. For example, what we would now call prosopagnosia, after a right hemisphere lesion, was described in 1867 by Quaglino (translated by Della Sala & Young, 2003). Yet, the idea of a right hemispheric specialisation for processing faces remained controversial well into the 20th century (De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994; Landis, Cummings, Christen, Bogen, & Imhof, 1986). It is now known that the right hemisphere plays an important role in variety of non-verbal abilities, including spatial abilities (Corbetta & Shulman, 2011), face perception (Duchaine & Yovel, 2015), body perception (Downing, Jiang, Shuman, & Kanwisher, 2001), and emotional processing (Witteman, van IJzendoorn, van de Velde, van Heuven, & Schiller, 2011). However, these

functions are profoundly neglected, from a handedness/cerebral asymmetries perspective, in comparison to the vast focus on language dominance.

Visuospatial attention is one class of asymmetry well known as depending more on the right cerebral hemisphere, deduced primarily from neuropsychological studies of hemispatial neglect. Hemispatial neglect refers to deficits in awareness including detecting, acting on or sometimes even imagining information from/in the contralesional space. The patients most often have lesions to the inferior parietal lobule (Bisiach & Vallar, 2000; Heilman, Watson, & Valenstein, 1994; Mesulam, 1990; Vallar, 1998) and the occurrence is more frequent after right, than left, hemisphere lesions in right-handed individuals (Bowen, McKenna, & Tallis, 1999; Stone, Halligan, & Greenwood, 1993; Stone, Patel, Greenwood, & Halligan, 1992).

Unfortunately, neglect is infrequently studied in non-right-handers (a few case reports excepted, e.g. Dronkers & Knight, 1989; Padovani et al., 1992). One of the rare studies which tested non-right-handed patients with unilateral lesions found that 6 out of 28 patients (21%) with left hemisphere lesions were diagnosed with neglect (Goldenberg, 2013). Neglect was more frequently seen after right hemisphere lesions, with 10 out of 22 (46%) non-right-handed patients diagnosed. The same study also included right-handed patients with right hemisphere lesions (72% of patients had neglect), but were sadly not able to provide data from right-handed patients with left hemisphere damage (G. Goldenberg, personal communication, September 30, 2017).

The lack of information for incidence rates of hemispheric specialisation in non-right-handed samples does not only apply to neglect, but also for most types of specialisations linked predominantly with the right hemisphere. One such class is face processing. The first evidence that suggested that face perception may rely on specialised ‘mechanisms’, distinct from object recognition, came from the syndrome of acquired prosopagnosia. Acquired prosopagnosia leaves the individual with a selective inability to recognise faces after brain damage, but able to recognise people based on other features, such as voice and descriptive information (Della Sala & Young, 2003; Hécaen & Angelergues, 1962; Wigan, 1844).

Prosopagnosia was initially reported to occur after damage to ventral occipital and temporal cortical areas of the right hemisphere (Benton & Van Allen, 1968; Hécaen & Angelergues, 1962), but some controversy arose as some reported that bilateral damage was necessary to cause the deficit (Cohn, Neumann, & Wood, 1977; Damasio, Damasio & van Hoesen, 1982; Meadows, 1974; Nardelli et al., 1982). Despite these cases, the preponderance of evidence from clinical case reports, autopsy data, and clinical and cognitive neuropsychological investigations indicates that the right hemisphere, rather than the left, is primarily responsible for the perceptual processing and recognition of faces in right-handed

individuals (Benton, 1990; De Renzi, 1986; De Renzi, et al., 1994; Landis et al., 1986; Sergent & Villemure, 1989; Takahashi, Kawamura, Hirayama, Shiota, & Isono, 1995; Wada & Yamamoto, 2001).

Only a handful of reports have challenged the view that unilateral damage to the *right* hemisphere is necessary to cause prosopagnosia, and some case studies after unilateral lesions to the left hemisphere do exist. Interestingly, all of these, bar one (Wright, Wardlaw, Young, & Zeman, 2006), are from non-right-handed patients (Barton, 2008; Eimer & McCarthy, 1999; Mattson, Levin, & Grafman, 2000; Tzavaras, Merienne, & Masure, 1973). Unfortunately, prosopagnosia is a rare condition which makes this data hard to come by. Moreover, there are no standardised tests of face recognition ability with agreed cut-offs, which further limits the possibility of large case series datasets reporting prosopagnosia incidence. Without standardised tests and cut-offs applied to large, unselected datasets where handedness and lesion side are recorded, little can be deduced about *incidence* of face processing asymmetry in these groups. The appearance of so-called developmental prosopagnosia in the 1980s led to more serious discussions of defining prosopagnosia (as compared to poor but non-pathological face recognition), but much of this came rather late in neuropsychological history (Duchaine, 2011; Susilo & Duchaine, 2013).

It is not just processing of faces per se that may depend more on the right cerebral hemisphere. Faces, in fact, are an easy source by which to access the emotional state of a conspecific, or to communicate emotional states. Mills (1912a,b), for example, noted that some patients with right hemisphere lesions showed decreased emotional facial expressions. Patients with right hemisphere lesions have also been found to have deficits in recognising emotional facial expressions. For example, DeKosky, Heilman, Bowers, and Valenstein (1980) tested individuals with right brain damage (RBD), left brain damage (LBD), and controls on different emotion recognition and discrimination tasks. Although both groups were impaired compared to controls, the RBD group did worse in all tasks as compared with the LBD group.

Of course, emotions are not only perceived and communicated through facial expressions. Another crucial medium is through the speech stream. Emotional speech prosody refers to the way emotional states are communicated through tone of voice, and is, at a perceptual level, characterised by modulation of loudness (sound intensity), pitch (variation in fundamental frequency), speech rhythm (duration of syllables and pauses) and voice quality or timbre (distribution of spectral energy) across the utterance (Banse & Scherer, 1996; Lehiste, 1970; Scherer, Johnstone, & Klasmeyer, 2003). The interest in hemispheric specialisation of emotional speech can be traced back to Hughlings-Jackson (1879) who described cases where individuals with extensive left hemisphere damage could utter

emotional words and sentences, despite difficulties with non-emotional words and sentences. Later work also suggested that right hemisphere lesions can affect the production of the 'prosodic contour', resulting in flat and monotone speech production (e.g. Gandour, Larsen, Dechongkit, Ponglorpisit, & Khunadorn, 1995; Gorelick & Ross 1987; Ross 1981; Ross & Mesulam 1979; Tucker, Watson, & Heilman, 1977).

Additional evidence for the role of the right hemisphere in the processing of emotional prosody comes from studies of the perception and recognition of these attributes in speech. For example, Heilman, Scholes, and Watson (1975) presented right-handed patients who had left or right temporoparietal lesions with sentences, and asked them to either report back the content of sentences or the emotional tone of the speaker. All patients were able to report back on the content of the sentence, but the RBD group performed at chance level when asked to report back the emotional tone.

Although several subsequent neuropsychological studies support right hemisphere specialisation for emotional prosody in right-handed patients as compared to right-handed controls (Blonder, Bowers, & Heilman, 1991; Bowers, Coslett, Bauer, Speedie, & Heilman, 1987; Ehlers & Dalby, 1987; Lalande, Braun, Charlebois, & Whitaker, 1992; Ross & Monnot, 2008; Rymarczyk & Grabowska, 2007), some clinical data questions the unique role of the right hemisphere in emotional prosody processing all together (Breitenstein, Daum, & Ackermann, 1998; Darby, 1993; Pell, 1998; Schlanger, Schlanger, & Gerstman, 1976; Starkstein, Federoff, Price, Leiguarda, & Robinson, 1994). For instance, Breitenstein and colleagues (1998) examined right-handed patients with either RBD, LBD or subcortical dysregulation of the basal ganglia (Parkinson's disease), together with two control groups. They found no difference in the severity of prosody impairments depending on lesion site, and those in advanced stages of Parkinson's disease showed the same impairments as those with cortical lesions (in fact, subcortical brain structures have also been found to play a critical role in processing emotional prosody; e.g. Brådvik et al., 1991; Ross & Mesulam, 1979; Starkstein et al., 1994). Of course, it is worth noting that these studies all report central tendency measures, and not the number of patients with deficits compared with relevant controls.

The results from clinical studies of prosody processing imply a broad network of both cortical and subcortical brain regions, that appear to be more right lateralised. This conclusion was supported in a meta-analysis by Witteman et al. (2011). Their meta-analysis suggests that both left and right hemisphere damage compromise performance in emotional perceptual tasks. However, when comparing RBD and LBD patients directly, damage to the right hemisphere results in more severely impaired prosody perception (mean weighted effect size [g] = -0.47, 95% CI's -0.74, -0.20).

In conclusion, there is evidence from lesion studies to suggest that the right hemisphere, on average, plays a more important role in attention, face, and emotional perception in right-handed individuals. In parallel, there are complications of interpreting evidence from clinical patients. Divergences in subject characteristics such as differences in patients lesion sites and location, time post-onset, presence of associated deficits, and experimental paradigms can heavily impact on findings. Furthermore, the lack of large datasets from non-right-handed patients for these non-language functions means that inferences regarding the impact of handedness are particularly challenging.

1.3 Behavioural asymmetries: perceptual asymmetries relating to cerebral asymmetries

One way to examine brain asymmetries and how they might be affected by handedness is by examining perceptual biases, as these may be, at least, indirectly related to underlying functional organisation. These investigations are predominantly carried out by utilising visual half field and dichotic listening techniques.

Dichotic listening is a technique in which two different stimuli are presented simultaneously, one to each of the ears. This task was originally developed by Broadbent (1952) for studying attention switching, but was later used by Kimura (1961a,b) to examine hemispheric asymmetries in the perception of speech. Kimura (1961a) observed that left hemisphere language-dominant individuals as assessed with Wada, on average, had a right ear advantage (REA). This means that they were more likely to report the speech-related information presented to the right ear. The assumption is that the REA is an indication of left-hemispheric specialisation for language processes (see Bryden, 1988, for historic review).

The structural model by Kimura (1967) proposes that the ear advantage is the result of the anatomy of auditory projections from the cochlear nuclear in the ear to primary auditory cortex. The model proposes that the projections from the cochlea are anatomically stronger to the contralateral hemisphere compared to the ipsilateral projections. Thus, even though the auditory signals from each ear reaches both auditory cortices, the contralateral projections are stronger and more preponderant which means that auditory information from ipsilateral pathway is supressed or blocked by contralateral information under dichotic conditions (Kimura, 1967; Milner, Taylor, & Sperry, 1968; Sparks & Geschwind, 1968). This stronger contralateral representation, combined with left hemisphere specialisation of language and the fact that information presented to the ipsilateral right hemisphere has to be transferred across the corpus callosum to the language specialised areas of the left hemisphere, is thought to be the reason for the predominant REA found in the task.

When non-right-handers are tested, it is sometimes found that they have a weaker REA, as compared to right-handed groups (e.g. Bryden, 1965; Bryden, 1970; Curry, 1967; Curry & Rutherford, 1967; Satz, Achenbach, & Fennel, 1967). However, this is not always the case as some studies report comparable ear advantages (e.g. Briggs & Nebes, 1976; Hugdahl et al., 2009; Kimura, 1961a; Sequeira et al., 2006). It is important to note that most of these dichotic listening papers only report differences in central tendency measures. An exception to this norm is from older papers in the literature where it was more commonplace to include frequency measure as part of the results section, or at the very least in tables describing the data. Nevertheless, the weaker ear advantage for non-right-handers in the verbal dichotic listening tasks has been attributed to the increased number of individuals with *atypical* (i.e. right hemisphere) language dominance.

One concern with dichotic listening tests, at least with language-related perceptual asymmetries, is that they underestimate the proportions of typical hemispheric asymmetry that the Wada and aphasia literatures suggest (e.g. Carey & Johnstone, 2014). Some have therefore questioned the ability of dichotic listening tasks to predict hemispheric specialisation. This concern is based on the fact that the prevalence of left ear advantage (LEA) or no ear advantage (NEA) is significantly greater (approximately 20%) than the prevalence of right or bilaterally represented speech *in the right-handed population*. For example, validation procedures in both epileptic patients and normal subjects using fMRI or Wada have found that although a REA in predicative of left hemisphere dominance for language, an LEA does not always predict right hemisphere dominance (e.g. Bethmann, Tempelmann, De Bleser, Scheich, & Brechmann, 2007; Fernandes, Smith, Logan, Crawley, & McAndrews, 2006; Fontoura, Branco, Anés, Costa, & Portuguez, 2008; Hugdahl, Carlsson, Uvebrant, & Lundervold, 1997; Strauss, Gaddes, & Wada, 1987; Van Ettinger-Veenstra et al., 2010; Zatorre, 1989). Surprisingly, most of these studies are carried out with right-handed participants where rates of right hemisphere dominance for language are low. This LEA misclassification is therefore perhaps not surprising considering that most individuals are left hemisphere dominant for speech-related material, and most of the noise in the measure will therefore most likely be to misclassify someone who is left hemispheric as having a LEA.

Some have also argued that the reliability of dichotic listening measures is poor (Berlin & Cullen, 1977; Blumstein, Goodglass, & Tartter, 1975; Geffen & Caudrey, 1981). Some of this unreliability may be attributed to the fact that participants are able to selectively attend to one ear during the testing procedure. For example, some participants may notice that they have an initial bias towards one ear and therefore try to counteract this bias, as they are told to

attend to both ears, by focusing more on the other ear. However, other researchers have found good test-retest reliability, estimated at $r = .90$ (Speaks, Niccum, & Carney, 1982), or $r = .85$ (Hugdahl, 2011) when also controlling for attentional effects by specifically asking participants to selectively attend to one ear. Both Bryden (1988) and Voyer and Rodgers (2002) have argued that it is only realistic to expect some measurement error for a perceptual non-invasive procedure. Even so, Hund-Georgiadis and colleagues (2002) found that dichotic listening estimates could correctly classify 88% of their participants as right or left language dominant, as classified with fMRI, in 17 right-handed and 17 non-right-handed participants. All of the four incorrectly classified participants were non-right-handers. Two of these had no ear advantage on the DL task even though one was strongly left lateralised and one weakly right lateralised according to the fMRI task. One participant had a REA for DL, but was bilateral for language processing, and one participant had a LEA, but was left lateralised. The remaining 7 right hemisphere dominant, and 23 left hemisphere dominant participants were correctly identified. These results suggest that dichotic listening serves as a suitable technique for questions related to language asymmetries, at least.

The dichotic listening technique has also been used to study other auditory stimuli. One of these is emotional prosody. In the typical paradigm, participants are presented with words spoken in two different (or one neutral) emotional tone(s), and are asked to indicate if a target emotional tone is present in each of the trials. In this kind of experiment, group responses tend to favour the left ear, which is assumed to indicate the greater role of the right hemisphere to process auditory emotional stimuli (Ley & Bryden, 1982). In fact, some researchers have even used the exact same stimuli, and depending on the characteristic participants are asked to focus on (the word or the emotional tone), obtain ear advantages favouring the different ears (Bryden, Free, Gagné, & Groff, 1991; Bryden & MacRae, 1989). A left ear advantage, on average, in right-handed individuals has also been obtained with non-verbal emotional expressions presented dichotically, such as cries, growls, and laughter (Harms & Elias, 2014; King & Kimura, 1972).

In comparison to language, handedness investigations in emotional dichotic listening paradigms are much rarer, and the evidence is more mixed. For example, Bryden et al. (1991) found that the proportion of individuals with a left ear advantage was *increased* in non-right-handed participants compared to the right-handed sample. Grimshaw (1998) instead found that a larger proportion of non-right-handers, in fact, were more biased towards the right ear, showing reversed ear asymmetries as compared to the right-handed sample. The discrepancy between these two studies points to likely heterogeneity in any small sample of non-right-

handers, and it would be attractive to make use of meta-analysis to combine the small samples of non-right-handers that currently exists, in order to obtain a more precise estimate of the likely biases in these samples.

Another paradigm often used for assessing perceptual asymmetries is the visual half field (VHF) task. This technique capitalises on the organisation of the visual system, where information is initially processed in the contralateral hemisphere (Horton & Hoyt, 1991). In these paradigms, stimuli are presented for a brief period of time to the left or right visual hemifields and task performance is usually measured as reaction time or accuracy, as a function of presentation location. Therefore, using stimuli that have been associated with a specialised function may reveal something about the underlying hemispheric processing within individuals.

There are a few theories of how VHF tasks work. The callosal relay model postulates that the laterality effects obtained are because of the non-dominant hemisphere's inability to process the stimuli, thus, information has to be 'relayed' over from the dominant hemisphere, resulting in increased reaction times (Geffen, Bradshaw, & Wallace, 1971; Moscovitch, 1970). These reaction times may be additionally affected if the information is degraded in the process. The direct access model instead proposes that the initial hemisphere 'takes control' of the processing of that stimuli, and that the differences in processing times reflect the proficiency of that hemisphere to process specific stimuli (Geffen et al., 1971).

Perhaps not surprisingly so, language-related asymmetry has also been the focus of VHF studies comparing right-handers and non-right-handers (Hugdahl & Franzon, 1985; Isaacs, Barr, Nelson, & Devinsky, 2006), where it is often found, similar to DL tasks, that non-right-handers have weaker asymmetries in tachistoscopic presentation of language-related stimuli (e.g. Bryden, 1965; Orbach, 1967; Zurif & Bryden, 1969). VHF tasks have also been used with face stimuli to investigate face asymmetry, and consistently find a left visual field (LVF) superiority for faces (Geffen et al., 1971; Marcel & Rajan, 1975). The VHF task has been utilized to examine a wide array of other biases, but many of these have fallen out of fashion, as visual field advantages have not always been obtained. For example, spatial dot localisation was found to be superior in the LVF, consistent with other evidence for right hemispheric specialisation of attentional processes. Although this advantage is often cited, the effect is fairly small and not reliably obtained (Bryden, 1973, 1976; Kimura, 1969; Pohl, Butters, & Goodglass, 1972).

Perceptual experiments utilising other methods, such as free-viewing techniques, have also been used to investigate asymmetries. One such task is the greyscales task, developed by Mattingley, Bradshaw, Nettleton, and Bradshaw (1994). It requires individuals to choose which of two vertically-arranged horizontal bars with a black to white gradient is darker. The bars are in fact mirror-images of one another, such that participants should chose the bar with the left side darkest and the right side darkest approximately an equal number of times. Mattingley et al. (1994) found a small but significant mean bias to select the bar with the darker end on the left, and this effect has been replicated in several laboratories (Friedrich & Elias, 2014; Nicholls, Bradshaw, & Mattingley, 1999; Tant, Kuks, Kooijman, Cornelissen, & Brouwer, 2002; Tomer et al., 2012). Although this is a potentially useful measure of some form of attentional asymmetry, unfortunately, biases from this task are yet to be reported in non-right-handed groups.

Another free-viewing task is the chimeric face task. The chimeric face task gives, potentially, the most convincing evidence from behavioural paradigms in that at least some non-language asymmetries seem to be reduced in non-right-handed samples. In a typical paradigm, participants are presented with two face stimulus that are chimeras, comprising of one emotive hemiface and one neutral hemiface, shown on reversed sides in the two faces. This task is consistently found to produce preferences for emotions shown on the left half of the face that are reduced in the non-right-handed group (e.g. Gilbert & Bakan, 1973; Heller & Levy, 1981; Levy, Heller, Banich, & Burton, 1983; Roszkowski & Snelbecker, 1982). These experiments, despite power issues in some of them, had considerable face validity, given the reduced left sided bias, paralleling known reduction in leftward asymmetry for speech and language, in the non-right-handed participants.

Unfortunately, chimeric face tasks are not routinely paired with language tasks in order to examine hemispheric processing for both tasks within individuals. In fact, apart from the small number of DL tasks comparing language stimuli and emotional stimuli, or attempts to compare relationships between DL and VHF language tasks, examining multiple perceptual biases in the same individuals is relatively rare. One potential reason this is the case for VHF studies, at least, is that it has been claimed that a large number of trials are needed in order to obtain stable visual field advantages for language-related tasks (Brysbaert, & d'Ydewalle, 1990a; Hunter & Brysbaert, 2008). This limitation, coupled with difficulties in reliably monitoring fixation, may have affected the use of such tasks for assessing several asymmetries in the same participants. Shorter tasks, however, might be worth pursuing in the context of a

multiple-asymmetries battery in order to characterise several perceptual biases within the same individuals (see Chapter 2).

1.4 Functional magnetic resonance imaging as a measure of functional asymmetries

Whilst neuropsychological methods significantly advanced the understanding of brain function, they are limited in the inferences that can be made regarding the relative contribution of the two hemispheres[2]. Contemporary neuroimaging methods, such as functional magnetic resonance imaging (fMRI), allow for the examination of these asymmetries by functionally localising them in vivo, using non-invasive approaches.

fMRI is a non-invasive neuroimaging technique which infers brain activity by measuring changes in blood flow. Blood oxygenation level dependent (BOLD) is a contrast method which exploits differences in the magnetic susceptibility of oxyhaemoglobin and deoxyhaemoglobin in the vascular system of the brain (Buxton & Frank, 1997; Logothetis, 2003). The BOLD signal is thought to reflect an increase in neural activity, as metabolic demand leads to an increase of oxygenated blood to a given brain structure, which changes the ratio of oxyhaemoglobin and deoxyhaemoglobin in that area. A decrease in the level of deoxyhaemoglobin results in an increase in MR signal, or BOLD, and is therefore an *indirect* measure of neural activity.

Task-based fMRI methods can localise regions that are more active for different categories of stimuli by contrasting BOLD signal in an experimental condition with a control condition, by subtracting activation in the latter from the former. For example, in neuroimaging studies of visual perception, Nancy Kanwisher and her colleagues used this subtractive methodology to localise areas in posterior occipitotemporal cortex that were particular responsive or selective to particular visual stimulus categories such as scenes (Epstein & Kanwisher, 1998), bodies (Downing, Jiang, Shuman, & Kanwisher, 2001), and faces (Kanwisher, McDermott, & Chun, 1997). These studies all tend to compare BOLD signal in a condition where participants are viewing exemplars of a specific category minus a control, selected to match the target category in terms of general image properties, semantic complexity etc. In these tasks, participants are typically required to respond to the presence of a repeated stimulus presentation, as the activation patterns have been found to be more reliable if the task is more attentionally demanding (Berman et al., 2010).

fMRI approaches to localising speech and language functions in the brain have tended to use a more diverse neuroimaging toolkit. Many of these experiments (unfortunately from the

[2] When right or left lateralised, or, hemispheric dominance is referred to, it does not mean that is the indicated hemisphere is solely doing all of the work. It refers to the fact that the relevant hemisphere is doing more or most of the work.

perspective of this thesis) were designed to examine questions unrelated to the left hemispheric dominance for language in most people. In terms of asymmetry, a number of language tasks have been used to examine hemispheric dominance of language-related material using fMRI: passive speech listening tasks, text reading, phonetic judgment, semantic judgment, sentence comprehension, naming, verbal fluency, and sentence generation tasks. However, the classification and/or degree of hemispheric processing derived from these tasks can vary hugely depending on the task that is used, the specifics of the task, the subtraction condition that is used, and the region of interest(s; ROI) used to examine hemispheric dominance (a more in-depth review can be found in Bradshaw, Thompson, Wilson, Bishop, & Woodhead, 2017).

Verbal fluency tasks, where participants are asked to generate words that meet certain criteria (e.g. starting with a single letter), consistently yields some of the strongest laterality indices (LI – a measure of the relative contribution of the hemispheres, most often measured on a scale from a negative value, indicating more right hemisphere contribution, to a positive value, meaning more left hemisphere contribution; Baciu et al., 2005; Cai, Van der Haegen, & Brysbaert, 2013; Harrington, Buonocore, & Farias, 2006; Hunter & Brysbaert, 2008; Niskanen et al., 2012; Ocklenburg, Hugdahl, & Westerhausen, 2013; Van der Haegen et al., 2011; Vikingstad, George, Johnson, & Cao, 2000; Zaca, Jarso, & Pillai, 2013). However, the subtraction task also plays a role, as active subtraction tasks (e.g. silent word repetition) have found to produce stronger LIs compared to using passive (e.g. fixation) ones (Dodoo-Schittko, Rosengarth, Doenitz, & Greenlee, 2012).

Other tasks in which strong LIs are reported include sentence generation tasks (e.g. Mazoyer et al., 2014; Partovi et al., 2012b), and phonological decision tasks (Morrison et al., 2016; Pillai & Zaca, 2011). More variable average LIs have been reported from semantic decision tasks, naming tasks, and text reading tasks (Bradshaw et al., 2017). Passive listening often produces near-zero average LIs and seems to be one of the weakest lateralised language tasks (Binder, Swanson, Hammeke, & Sabsevitz, 2008; Harrington, Buonocore, & Farias, 2006; Miró et al., 2014; Ocklenburg et al., 2013).

One difficulty is selecting a task for measuring speech and language laterality is posed by models which suggest that different components are more or less asymmetrical. Contemporary models of language processing predict different patterns of lateralisation depending on the language process that is being measured (e.g. Hickok & Poeppel, 2007; Peelle, 2012; Poeppel, 2014; Price, 2012). Although these models vary slightly, most agree that the initial acoustic processing of speech is considered to be a more bilateral process, whilst the comprehension and generation/production of meaningful language is considered to

be more lateralised. These models are, of course, derived from group-average data in right-handed individuals (e.g. Liebenthal, Binder, Spitzer, Possing, & Medler, 2005; Vouloumanos, Kiehl, Werker, & Liddle, 2001).

In fact, virtually all language-related neuroimaging investigations exclude non-right-handed participants. The most likely reasons for doing so (often unstated) is that scientists are concerned about adding any other source of heterogeneity to their datasets. Some authors even seem to assume (incorrectly) that most non-right-handers would be right hemispheric for language. However, approximately 10% of any random sample would be non-right-handed, and very few of them would be right hemisphere dominant for language. A few people are now arguing for inclusion of non-right-handers in neuroimaging (Willems, Van der Haegen, Fisher, & Francks, 2014). Indeed, some important questions about the nature of language lateralisation, at least, can be answered by including large numbers of non-right-handers. First, an important possibility for models of innate language dominance might be that they are truly 'bimodal' in nature: genes prescribe either left or right hemispheric dominance for language (or some other related factor that results in language dominance). If this is indeed the case, then non-right-handers who are left lateralised for language should be as left hemispheric in some sense as their right-handed counterparts. A corollary of this idea is that right hemisphere dominant individuals would also be matched in magnitude of their language LIs to *'typically'* (i.e. the most common pattern) lateralised individuals. Such data are collectable, but not routinely gathered or shared, until recently (e.g. Mazoyer et al., 2016).

Most non-right-handers (~70%) are also unusual in that the speech-dominant hemisphere does not also control their dominant hand. In this sense, language-typical left-handers are similar to language 'atypical' right-handers (about 5% who are right hemispheric for speech). This unusual neurological relationship in most non-right-handers deserves further exploration. Secondly, the increased rates of atypical, right hemisphere, language dominance in non-right-handers makes them a suitable group to study for a number of theoretical questions relating to relationships between cognitive functions, and for questions relating to functional and anatomical underpinnings of language in typically and atypically lateralised individuals. They would be an excellent target group to evaluate different models of language and speech processing. Unfortunately, their rarity makes these individuals difficult to find.

In addition to language asymmetry, fMRI can be used to examine localised responses for a variety of cerebral functions. Some of these functions, in concordance with the neuropsychological evidence presented above, have been reported to be lateralised to the right hemisphere. These include, but are not limited to, visuospatial/attention processes, some emotional processes, emotional prosody processing, body processing, and face processing

(e.g. Beacousin et al., 2006; Cai et al., 2013; Downing et al., 2001; Kanwisher et al., 1997; Zago et al., 2016). There are some arguments that these processes may *'anti-localise'* (i.e. localise in the opposite hemisphere) relative to language in a complementary fashion (see section 1.5 below). However, the majority of studies examining these 'non-language' functions are not interested in asymmetry, per se. Nonetheless, there is a small pool of evidence to suggest that most right-handers, at least, have a rightward asymmetry for these functions.

For example, Kanwisher and colleagues (1997) used fMRI to identify a face-selective region of human extrastriate cortex. The fusiform face area (FFA), a region that responds more strongly to face stimuli than to any other stimulus category, was only activated in the right hemisphere for five out of 10 right-handed participants, whilst the other five had more bilateral patterns. Downing et al. (2001) also located an area in the lateral occipitotemporal cortex that was preferentially activated to human bodies and body parts. This area was activated above threshold in the right hemisphere in all 19 participants, with most of these also showing weaker activation in the left hemisphere.

The perception of emotional prosody has also been linked with the right hemisphere through fMRI. The idea of paralinguistic aspects of speech (i.e. the prosodic contour of emotional speech) being processed in the right hemisphere, and linguistic aspects, such as grammar and syntax, in the left hemisphere, is appealing. However, fMRI of hemispheric differences in emotional prosody is sparser than one might expect, given its importance in neurology and psycholinguistics/paralinguistic aspects of speech (Paulmann, 2017). Much of it casually reports greater right hemisphere activation (e.g. Beacousin et al., 2006; Ethofer, Van De Ville, Scherer, & Vuilleumier, 2009; Grandjean et al., 2005; Mitchell, Elliott, Barry, Cruttenden, & Woodruff, 2003; Wiethoff et al., 2008), but again, non-right-handers are routinely excluded as potential unwanted sources of heterogeneity.

Reporting data from individual people, in fMRI in particular, is rare (Kanai & Rees, 2011). Individual differences are often overlooked in favour of group composite patterns. Averaging data across non-right-handed participants, where the underlying cortical organisation is more variable (for language at least), is a common weakness in research examining laterality effects. For example, a non-right-handed sample including a small proportion of individuals with atypical language dominance may reveal a more bilateral representation, on average, as compared to the more consistently lateralised right-handed group. The conclusion drawn may be that the non-right-handed group is 'less symmetrical' than their right-handed counterparts. However, it is hard to interpret whether non-right-handers, as individuals, are less asymmetrical, or if this effect is an artefact of central tendency measures and actually driven by the small number of individuals with reversed asymmetry. Of course, this is a pitfall with all

group averaged data, but is of particular relevance in neuroimaging, where small sample sizes are the norm (Button et al., 2013). Averaging data may therefore not be representative of individuals in the underlying sample. Using techniques to examine hemispheric patterns on an individual level can give us a better understanding of the variation of these asymmetries in the sample.

Although most neuroimaging studies produce the necessary data needed for assessing laterality effects in individual people, very few apply statistical tests to do so. This absence makes it difficult to draw inferences about lateralised activity from published studies. Nevertheless, recent developments in both technique and practice suggest the situation is improving. Researchers who do assess laterality effects have used a multitude of techniques (for comprehensive reviews in relation to language lateralisation see Bradshaw, Bishop, & Woodhead, 2017; and Seghier, 2008). Most of these techniques calculate the relative difference between activity in each of the two hemispheres, usually using the traditional LI formula: LI = (left hemisphere activation – right hemisphere activation)/(left hemisphere activation + right hemisphere activation). However, these techniques also require a number of arbitrary decisions which will have an impact on the LI value that will be obtained (Jansen et al., 2006; Seghier, 2008).

For example, some techniques include all voxels across the hemispheres; others use a subset of task-dependent ROIs. ROIs can be defined functionally (by patterns of activation, usually derived from a pilot study or previous research), or anatomically, by using structural landmarks. Some argue that ROIs give LI values that are more reliable (Fernandez et al., 2001; Suarez, Whalen, O'Shea, & Golby, 2008). Others find no difference (Hund-Georgiadis et al., 2002), or that whole-brain analyses are more reliable (Wilke & Lidzba, 2007). Furthermore, LIs can either be calculated using the magnitude of the activation (determined by t-values), or the extent of the activation (the number of activated voxels in the region). The majority of studies opt for an extent measure, but magnitude measures are becoming more popular in recent years (Bradshaw et al., 2017). Crucially, obtained LIs are highly influenced by the statistical threshold that is chosen to classify voxels as active (Binder et al., 1996; Deblaere et al., 2004).

Since early fMRI research, the most popular approach when assessing laterality effects has been to compare activated number of voxels in the right hemisphere with those activated in the left hemisphere above a certain threshold. However, this dependence of a statistical threshold is *a major drawback* of this procedure. At low thresholds, the occurrence of false positives typically leads to small differences between the two hemispheres. Using a high threshold will decrease the number of falsely activated voxels, but may instead exclude truly

activated voxels, and create an inflated difference between the two hemispheres. Furthermore, fixed thresholds make intersubject comparisons more difficult, as there are large intersubject variability in activation levels (Jansen et al., 2006).

An awareness of the issues of using a fixed threshold has led to a decline in this practice in favour of different techniques. One approach is to calculate LIs across multiple thresholds. More specifically, threshold-dependent laterality curves (a plot of the LI as a function of the threshold) are created. These can then be used to examine the general tendency towards a pattern of dominance over several thresholds, and often have a transition point where the slope of LI usually start plateau at a certain LI value (see Figure 1.3). However, one criticism of this technique has been that LI curves are not always reproducible within individuals (Jansen et al., 2006; Rutten et al., 2002).

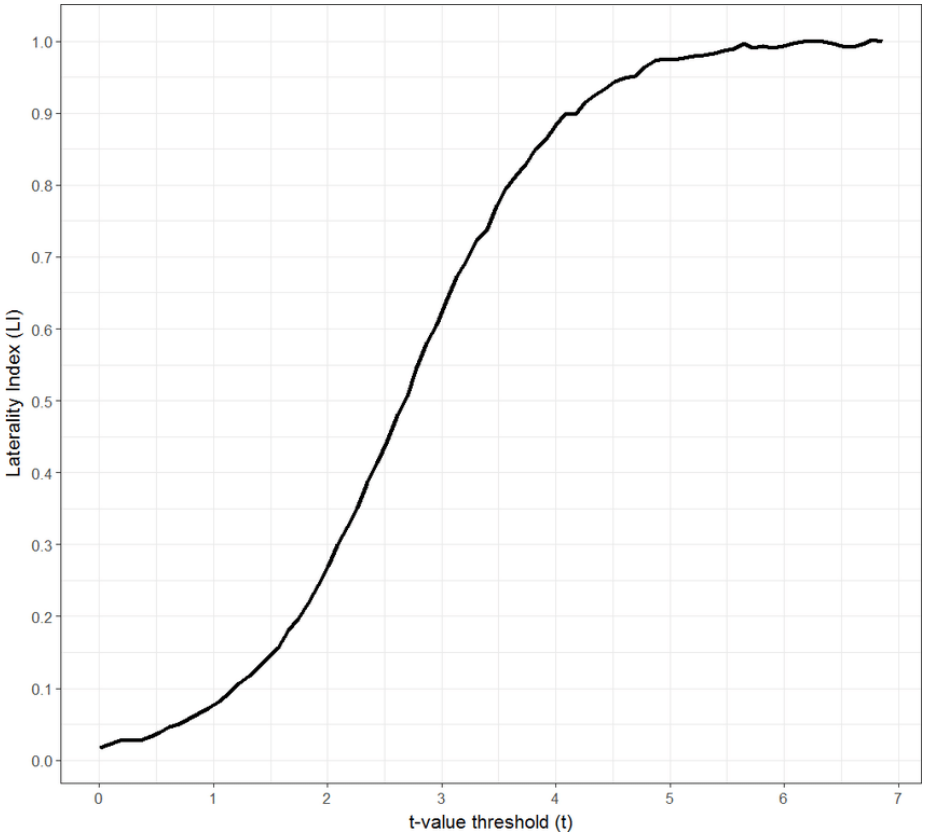


Figure 1.3. Threshold dependent laterality curve. The plot represents the LI value as a function of threshold (t-value) that is applied to the calculation. Reprinted from Bradshaw et al. (2017).

Other studies have shown that individually adapting thresholds are better than fixed thresholds for analysing single subject data, both in order to obtain comparable results across individuals, and to increase intrasubject reliability (Fesl et al., 2010; Klöppel & Büchel, 2005; Specht, Willmes, Shah, & Jäncke, 2003). One of these approached involves setting the threshold at fixed number of activated voxels (Bukowski, Dricot, Hanseeuw, & Rossion, 2013; Jansen et al., 2006; Knecht et al., 2003). However, this method still requires arbitrary decisions on how many voxels 'should' be active. Some have instead utilised methods where the threshold is set in proportion to the maximum or mean intensity of voxels in an image, or area, to get around this issue (Allendorfer et al., 2016; Partovi et al., 2012a; Partovi et al., 2012b; van Veelen et al., 2011; Wilke & Lidzba, 2007).

Alternatively, the issues of using thresholds can be avoided altogether by using a threshold-independent method. One such method was developed by Wilkie and colleagues (Wilke & Lidzba, 2007; Wilke & Schmithorst, 2006), and involves iterative resampling and calculation of LI values across multiple thresholds. It then uses the central 50% of data to make the calculation resistant to outliers, and calculates a weighted mean, as higher weight is given to higher thresholds. This technique is readily available as a plugin for neuroimaging analysis software, and has been widely used in recent laterality research (e.g. Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Berl et al., 2014; Häberling, Badzakova-Trajkov, & Corballis, 2011; Mazoyer et al., 2014; Perlaki et al., 2013; Van der Haegen et al., 2011; Van der Haegen, Cai, & Brysbaert, 2012; Zago et al., 2016).

One last methodological issue that need to be considered is the LI cut-off used to classify individuals as belonging to a certain category or not. In fact, this problem is similar to an issue in handedness research about what cut-off score to use to define a person as right-handed or non-right-handed using performance or preference data (Annett, 2002). In the absence of any agreement on what band around zero constitutes bilateral, there may be an implicit or explicit temptation to define such a group in a data-driven way. In some experiments, the utilised cut-off for bilateral has been fairly large, with LI cut-offs of ± 0.5 or 0.6 in published papers (e.g. Cai et al., 2013; Van der Haegen et al., 2012) In other studies, ± 0.2 have been used (e.g. Springer et al., 1999). This decision could have considerable implications. For example, Cai and colleagues (2013) argue that using an LI threshold of > ± 0.5 distinguishes between, what they refer to as, 'clear' and 'unclear' laterality patterns, and changes data that otherwise supports independent relationships between lateralised function, into patterns that anti-localise with one another. This specific issue will be explored with the data presented in Chapter 3.

Jansen et al. (2006) found that if a bilateral category was used (< ± 0.2) participants who were classified as bilateral by one calculation, were often not by a different calculation of laterality indices, or in a second testing session. They therefore argue that a bilateral category should only be used if there is support from different measures of calculating hemispheric dominance, but also preferably by repeated testing. Furthermore, it is important to keep in mind that the categorisation of participants into lateralised or bilateral from fMRI data is somewhat arbitrary unless independent validation by other measures are used (for language at least).

In summary, fMRI can be used to localise task-related activity in the two hemispheres, in healthy individuals. With the promising concordance with more direct measures of hemispheric dominance, such as Wada and improved and more robust techniques to calculate LI values, fMRI methods have a clear potential to contribute to laterality research.

1.5 Complementarity of hemispheric specialisations

Although several hemispheric specialisations have been documented in many cognitive domains, research investigating the relationship between different (or multiple) functional cerebral asymmetries has been less forthcoming or conclusive. The question remains to whether the localisation of one function to a certain hemisphere predicts the localisation of another function to the opposite hemisphere, or whether they lateralise independently of one another. Complementarity of functions are generally assumed, and seems to be a part of lore of contemporary neuropsychology and neuroscience especially as viewed from popular press (Bryden et al., 1983; Corballis & Häberling, 2017). Yet, cognitive functions are often examined in isolation, with researchers from different fields rarely crossing paths, and with little attention to the relationship of degree or direction of lateralisation within individuals. Nonetheless, theories of relationships between lateralisation of different functions exist and can be divided into causal or statistical theories of complementarity.

In causal pattern of complementarity theories (Bryden, 1990; Bryden et al., 1983), the lateralisation of one function to one hemisphere causes, in some fashion, another function to lateralise to the opposite hemisphere. These functions may have been symmetrically located at an initial point, but growth or development of one system (often deemed to be language-related), have a causal role for the other function to lateralise in the opposite direction (Bradshaw & Nettleton, 1981). For example, contemporary versions of these 'crowding hypotheses' link the acquisition of *reading* to specialisation of visuoperceptual circuits in the same hemisphere as that which is innately predisposed to oral and spoken language. As reading develops, non-linguistic visual perceptual abilities that depend on foveal vision then

become more specialised in the non-language dominant hemisphere (Behrmann & Plaut, 2015; Centanni et al., 2018; Dehaene et al., 2010; Plaut & Behrmann, 2011).

In contrast, the statistical hypothesis (Bryden, 1990; Bryden & Allard, 1981) instead assumes that whatever underlies the lateralisation of a function is independent of that of another function, and may reflect independent probabilistic biases. Each function has an independent statistical probability of being lateralised to the right or the left hemisphere, and the fact a population level bias for language lateralised to the left hemisphere and, for example, face processing in the right hemisphere may arise, but reflect probabilities relating to independent causal sources.

One of the earliest investigations into the question of a relationship between functions was carried out by Bryden and colleagues (1983) with unilateral patient data. They examined data from 140 non-right-handers and 130 right-handers that were either classified as being aphasic or not aphasic, and as showing a visuospatial disorder or not, to examined if there was an association between the two functions. They found that only approximately 50% of the patients showed patterns of complementarity, which was roughly equal independent of side of lesion and patent handedness. Furthermore, many patients suffered deficits in both language and visuospatial function, suggesting that these are specialised in the same hemisphere in some individuals. It was also observed that right-hemispheric visuospatial function was not as prevalent as left hemisphere dominance for language, which also poses difficulties for the causal complementary account.

Harms and Elias (2014) examined complementarity of left-hemisphere processing of speech sounds and right hemisphere processing of emotional vocalisations in 52 right-handed participants using two dichotic listening tasks. Although they found an overall LEA for the emotional content and REA for the verbal content, they found no correlation between the two measures. Bryden and colleagues (1991) also examined complementarity of verbal stimuli and emotional stimuli in right-handed and non-right-handed participants using dichotic listening. Again, population level biases were found for the two tasks, but the data did not show that ear advantages for the two tasks anti-localised in individual people. These two studies give some evidence to suggest that hemispheric specialisation of auditory linguistic versus prosodic stimuli are not complementary. Of course, correlating different perceptual tasks is potentially very conservative, as this would imply that these tasks perfectly reflect underlying associated function. Even if the underlying functions depend on one another, they may not correlate very highly. On top of that, considering measurement error associated with any perceptual test, it is unsurprising that they are only crudely related to an underlying asymmetry. Perhaps a frequency count approach, with a sufficient number of atypically

lateralised individuals for a set of functions, is a different and potentially useful way of addressing this question.

A limited number of neuroimaging studies have tackled questions of complementary specialisation, and tend to be focused on language and visuospatial abilities (e.g. Ng et al., 2000; Powell, Kemp, & Garcia-Finana, 2012) rather than face perception, which is implicated in the recent models. A recent study by Cai and colleagues (2013) claims very strong support for complementary hemispheric specialisation of language and attentional functions, in non-right-handers, at least. Cai et al. (2013) used an fMRI-friendly variant of the landmark task to measure attentional asymmetry. It required participants to make judgments about pre-bisected horizontal lines, modelled after line bisection tasks used in studies of hemispatial neglect. They found that all 15 non-right-handed participants with right hemispheric language dominance identified from a previous experiment (Van der Haegen, Cai, Seurinck, & Brysbaert, 2011) were left hemispheric for attention. Similarly, 15 of the 16 non-right-handers who were left lateralised for language were right lateralised on the landmark task. However, for this study, a cut-off LI ≥ 0.5 or ≤ -0.45 was used to exclude participants who were classified as bilateral on their verbal fluency task. These, more weakly lateralised individuals, may be crucial in answering some of the questions relating to complementarity of specialisations.

Badzakova-Trajkov and colleagues (2010) also contrasted landmark and verbal fluency in a sample of 48 non-right-handers and 107 right-handers. Fortunately, Badzakova-Trajkov et al. (2010) provide scatterplots of individual LIs for their right-handers and non-right-handers. If a dichotomous classification with a cut-off of 0 is used, the scatterplot reveals that approximately 20% of both right-handers and non-right-handers did not show complementarity of language and attention. Zago et al. (2016) kindly provided individual LI values from a similar fMRI experiment using landmark and verbal fluency in a sample of 142 right-handers and 151 non-right-handers. The data from these two studies are remarkably similar: right-handers and non-right-handers differed in the expected direction on the proportion of people who are left lateralised for verbal fluency (Badzakova-Trajkov et al., 2010: 96% versus 81%, 95% CIs on the difference do not overlap zero; Zago et al., 2016: 94% versus 83%, 95% CIs on the difference do not overlap zero), but not in the proportions of participants with negative LIs (i.e. right hemispheric dominance) for the landmark task (Badzakova-Trajkov et al. 2010: right-handed 79.4% versus non-right-handed 79.2%, 95% CIs on the difference overlap with zero; Zago et al., 2016: right-handed 81.7%% versus non-right-handed 78.8%, 95% CIs on the difference overlap with zero). In other words, right-handers and non-right-handers, assessed for both language and attentional dominance differ in the predicted direction for language typicality, but are nearly identical for right hemispheric attentional dominance.

Whitehouse and Bishop (2009) examined complementarity of a language task and landmark task using functional transcranial Doppler sonography (fTCD), a non-invasive technique which uses ultrasound to measure event-related changes in blood-flow velocity in the middle cerebral artery serving each hemisphere. They found that 76% of right-handers and 73% of non-right-handers were right hemispheric for spatial attention. This is slightly lower than what is seen in the imaging studies by Badzakova-Trajkov et al. (2010) and Zago et al. (2016). However, they also used a bilateral category with 13% of participants respectively for both handedness groups. Similar to the two previous fMRI studies, they found the predicted proportional reduction in language asymmetry in the non-right-handed group. This independence of functions was replicated in a later study where task difficulty in the landmark task was taken into consideration (Rosch, Bishop, & Badcock, 2012).

In summary, most studies to date do suggest a statistical relationship between cognitive functions, for language and visuospatial tasks, at least. The fact that population level biases for cognitive functions are found would seem to suggest some complementarity in how they are organised in the brain, but that these are not constrained by, or, related to one another in a causal fashion.

1.6 Outstanding questions and thesis overview

An implicit assumption of complementary hemispheric specialisation is probably the main driver for the dearth of studies on non-language functional asymmetry in non-right-handers. This neglect is a shame, as data for language asymmetry at the very least is so skewed in right-handed samples that many interesting questions cannot be addressed by right-handers alone. Skew is a particular challenge in most of these lateralised tasks. Even worse, these experiments rely almost exclusive on reports of central tendency, masking the underlying data structure. Studies most often, explicitly or implicitly, conclude reduced asymmetries in non-right-handers based on the idea of a small number of the non-right-handed group showing reversed dominance, even for non-language asymmetries.

With contemporary techniques, such as fMRI, these questions can be readily addressed. In fact, language and attention have been major research topics since the start of fMRI. However, these domains were always examined independently, often by separate research groups. By examining multiple asymmetries in the same individual people, hemispheric asymmetries can be quantified and mapped out in order to start investigating which asymmetries go together. Neuroimaging studies are now occasionally including non-right-handers, but rarely with sample sizes sufficiently large to make any firm conclusion about proportion of typical and atypical dominance (in fact, even these large studies rarely provide

proportion data for their samples). Furthermore, the expenses of neuroimaging mean that using fMRI to determine an individual's hemispheric dominance is costly. Some way of pre-screening individuals before fMRI scanning to decrease the number of potential participants would be desirable. The alternative, mentioned above in the context of finding atypical dominance, is to scan many non-right-handed people in the hope that 15%, for example, are right hemispheric for language.

The principal aim of this thesis is to begin to fill the gap in the literature on asymmetries linked to the right hemisphere, in both right-handed and non-right-handed participants. The goal is to examine, describe and quantify several of these asymmetries in the same individual people. This thesis utilises both perceptual and neuroimaging techniques to attempt to answer these questions.

In Chapter 2, data from a large-scale behavioural battery of perceptual tests is reported. Examining frequency of typical and atypical biases can give estimates of the frequency of dominance in right-handed and non-right-handed individuals, but also help point to functional asymmetries that are likely to be related to language, versus ones that are more or less likely to be independent. The data from several indirect perceptual asymmetry tests are included, examining language processing, face processing, emotional processing and attentional processing.

In Chapter 3, fMRI is used to examine asymmetries in perception of emotional prosody, emotional vocalisations, bodies, and neutral and emotional faces, in individual people. To circumvent the threshold dependency problem, asymmetries were examined using the threshold independent bootstrapping technique developed by Wilke and colleagues (Wilke & Lidzba, 2007; Wilke & Schmithorst, 2006). A verbal fluency task is also included to examine hemispheric dominance for language processing, to examine its' complementarity with these right hemisphere functions.

Finally, in Chapter 4, fMRI data and behavioural data from individuals who took part in both experiments for the examination of how successful behavioural predictors, or a combination of behavioural predictors, are in predicting functional lateralisation.

CHAPTER 2

Perceptual asymmetries in right-handers and non-right-handers

2.1 Introduction

Measures of perceptual biases, such as dichotic listening (DL) tasks and visual half field (VHF) tasks, are often employed as indirect measures of brain asymmetry (e.g. Bourne, 2010; Bryden, 1965; Dagenbach, 1986; Grimshaw, 1998; Hilliard, 1973; Hugdahl & Anderson, 1986; Hugdahl & Franzon, 1985; Kimura, 1966; Levy & Reid, 1978; Nicholls, Bradshaw, & Mattingley, 1999). The assumption from these tests is that the visual field or ear advantage obtained is indicative of a person's hemispheric processing of that percept. Assuming that this is indeed the case, these tests provide a simple and cost-effective way of examining asymmetries in large number of right-handers and non-right-handers.

Unsurprisingly, language-related asymmetry has been the main focus of behavioural studies comparing handedness groups (Hugdahl & Franzon, 1985; Isaacs, Barr, Nelson, & Devinsky, 2006). In the case of language-related stimuli, a bias or processing advantage, often measured as accuracy or reaction time in tachistoscopic paradigms where stimuli are briefly presented to the right or left visual field, is frequently found for the right visual field (RVF; Barton, Goodglass, & Shai, 1965; Geffen, Bradshaw, & Wallace, 1971; Kimura, 1966; McKeever, & Huling, 1971; Willemin et al., 2016; Zurif & Bryden, 1969). This bias is thought to reflect the left hemisphere advantage most often found for language, as information presented to the RVF/right ear is initially sent to the contralateral hemisphere and vice versa. For example, in one variation of a VHF paradigm, Hunter and Brysbaert (2008) developed a lateralised naming task that consisted of the bilateral presentation of two words simultaneously, with an arrow that appeared at fixation indicating the stimuli that the participants had to name. They found that this behavioural task was moderately to strongly positively correlated with a fMRI study measuring hemispheric dominance for a word generation task in a non-right-handed sample (Hunter & Brysbaert, 2008).

Another way to examine language-related asymmetries is in the auditory domain by utilising dichotic listening techniques. Dichotic listening is one of the most common perceptual techniques to examine hemispheric organisation of speech processing (Hugdahl, 2000; Voyer,

1996; Voyer & Techentin, 2009). In the consonant-vowel (CV) dichotic listening task (Hugdahl et al., 2009; Shankweiler & Studdert-Kennedy, 1966), pairs of consonant-vowel syllables are presented simultaneously to the left and right ear. CV dichotic listening techniques has been found to produce some of the most robust perceptual asymmetries, and consistently produce average REAs for right-handed participants (see e.g. Bryden, 1988; Hirnstein, Westerhausen, Korsnes, & Hugdahl, 2013; Hugdahl, 2011; Voyer, 1998).

For non-right-handed groups, the prediction for these techniques is that a RVF advantage or REA asymmetry should be present, but reduced as compared to their right-handed counterparts, following the reduced proportions of non-right-handed individuals with left hemisphere specialisation for language (Carey & Johnstone, 2014; Hécaen & Sauguet, 1971; Knecht et al., 2000; Rasmussen & Milner, 1977). In fact, a reduced bias, on average, in the non-right-handed sample is frequently reported (Cowell, & Hugdahl, 2000; Curry, 1967; Foundas, Corey, Hurley, & Heilman, 2006; Hines & Satz, 1974; Hugdahl & Franzon, 1985; Isaacs et al., 2006). However, the relationship between handedness and language can be subtle and average differences are sometimes not found (e.g. Bless et al., 2015; Brysbaert, 1994; Hugdahl et al., 2009; Sequeira et al., 2006; Zurif & Bryden, 1969). Nevertheless, if a mean difference between right-handers and non-right-handers is not found, it is still possible that a larger proportion of right-handers has a bias towards the right ear or right visual field. In fact, authors who report mean differences often conclude that the they reflect rates of hemispheric bias for language, but often neglect to investigate or report the proportions of the sample with a left or right hemisphere bias.

Another indirect measure that has been associated with left hemisphere processing, and potentially with hemispheric processing for language, is the auditory octave illusion (Deutsch, 1974, 1978, 1983). In this auditory illusion, a sequence of two tones, separated by an octave, are presented to both ears simultaneously, but when one ear receives the higher pitch tone the other receive the lower pitch tone. Although both ears receive different stimuli, a common percept is that individuals hear the higher tones in the right ear, and the lower tones in the left (see Figure 2.1). The mechanisms behind the octave illusion have been debated (see e.g. Chambers, Mattingley, & Moss, 2002; Deutsch, 2004), but more importantly for this thesis, this percept has been found to vary depending on handedness and familial sinistrality (Deutsch, 1974, 1983; Oehler & Reuter, 2013).

Deutsch (1974) reported that a majority of right-handed participants (81%) reported hearing the high tones in the right ear, but that non-right-handed participants had no group level asymmetry. Similarily, a previous unpublished study from the lab (Johnstone, 2016) found that the proportion of non-right-handers with a right ear response was significantly lower

as compared to right-handed participants (54% of non-right-handers vs 65% of right-handers had a REA). The REA for the illusion has also been found to be decreased in individuals with siblings or parents that are mixed- or non-right-handed (Deutsch, 1983). The links to handedness led Deutsch (1983, 2004) to speculate that the perception of the octave illusion may be linked to degree and direction of cerebral dominance for language. In support of this, Ferrier, Huiskamp, Alpherts, Henthorn, and Deutsch (2013, as cited in Deutsch, 2013) found that out of 17 patient who underwent Wada testing, all heard the higher tones in the contralateral ear to the hemisphere that was determined as dominant for speech. This finding further suggests that the octave illusion should produce differences between right-handers and non-right-handers that mirrors those seen for language tasks.

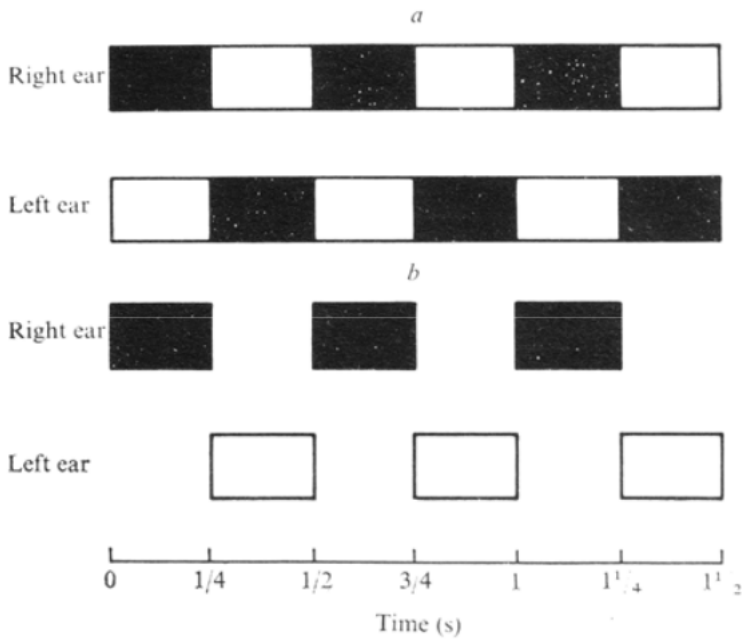


Figure 2.1. A graphical demonstration of the octave illusion. The black box represents the 800 Hz tone and the white box the 400 Hz tone. The panel *(a)* demonstrates the procedure and *(b)* the percept that is most commonly obtained. Reprinted from Deutsch (1974).

In contrast to the vast number of studies comparing right-handers and non-right-handers on language related asymmetry tasks, a small number of experiments seem to establish that at least some cerebral asymmetries favouring the right hemisphere result in a similar reduction in degree of lateralisation between non-right-handers and right-handers as that found for language. One of the most widely studied 'non-language' perceptual asymmetry is for processing faces. Multiple VHF studies have shown a superiority in the left visual field when face stimuli are presented (Geffen et al., 1971; Marcel & Rajan, 1975; Yovel, Tambini, &

Brandman, 2008), which has been attributed to a right hemisphere superiority in processing faces (Gilbert & Bakan, 1973; Yovel et al., 2008). Similarly, the use of centrally-positioned chimeric faces, comprising of one emotive hemiface and one neutral hemiface (see Figure 2.4), reliably produces biases to perceive the left side of the face as being more expressive (e.g. Bourne, 2005, 2008, 2010; Burt & Perrett, 1997; Butler et al., 2005; Ferber & Murray, 2005; Levy, Heller, Banich, & Burton, 1983; Luh, Rueckert, & Levy, 1991).

The chimeric face task has been found to produce preferences for emotions shown in the left visual field that were reduced in the non-right-handed group (e.g. David, 1989; Gilbert & Bakan, 1973; Heller & Levy, 1981; Levy et al., 1983; Roszkowski & Snelbecker, 1982). These experiments, despite power issues in some of them, had considerable face validity, given the reduced left-sided bias in the non-right-handed participants, together with the associations between hand preference and hemispheric dominance for language. The reduced bias seen in non-right-handers is often implicitly (and without comparing the same individuals on a face task and language task) interpreted as complementary to that seen for language. In theory, if asymmetry for processing faces is related to speech and language dominance in some causal way, then right hemispheric advantages for faces would parallel left hemispheric dominance for speech and language but in the opposite hemisphere. Thus, the conclusion of complementarity may seem particularly attractive. This argument should, of course, also hold true for any cerebral asymmetry that is 'yoked' to hemispheric dominance for language.

Since the early work on face processing, which included non-right-handers in some experiments at least, other behavioural asymmetries favouring the left visual field or left ear in right-handers have been revealed, but non-right-handers are almost never tested. One attentional bias task was developed by Mattingley, Bradshaw, Nettleton, and Bradshaw (1994), as part of a study on mechanisms underlying hemispatial neglect. Their 'greyscales' task requires individuals to choose which of two vertically-arranged horizontal bars with a black to white gradient is darker (see Figure 2.2). The bars are in fact mirror-images of one another, such that participants should chose the bar with the left side darkest and the right side darkest approximately an equal number of times. Instead, they found a small but significant mean bias to select the bar with the darker end on the left, which has been replicated in several laboratories (Friedrich & Elias, 2014; Nicholls et al., 1999; Tant, Kuks, Kooijman, Cornelissen, & Brouwer, 2002; Tomer et al., 2012). What is most interesting about these data is the '*breadth*' (i.e. how many, rather than 'depth', how biased on average) of the asymmetry in Mattingley et al. (1994): 80% of the right-handed control participants had a leftward bias. This proportion is an encouraging suggestion that greyscales tap into a function or functions that anti-localise relative to language. If it is indeed the case that greyscales

performance is indicative of a function that localises to the non-language hemisphere, then it is worthwhile comparing the breadth of asymmetry between right-handers and non-right-handers. There are, to date, currently no published studies that have examined this bias in a non-right-handed sample.

Figure 2.2. Sample greyscales stimulus. On average, people viewing this pair are more likely to rate the top bar as darker than the bottom, as the dark side of the gradient appears on the left in this stimulus pair.

Another function that has been linked to the right hemisphere is emotional prosody. The evidence for the perceptual lateralisation of emotional prosody in neurotypical samples (see General Introduction section 1.2 for a review of the patient literature) comes from studies utilizing the dichotic listening technique in healthy participants. Bryden and MacRae (1989) presented dichotically-paired words spoken in an emotional or neutral tone and asked their 32 right-handed participants to indicate if a target emotion was present or absent from the dichotomous pair. They found that 86% of participants were better at detecting the emotional tone when it was presented to their left ear. Several other studies have also found that right-handers, on average, were better at detecting the emotional prosody when presented to the left ear (Enriquez & Bernabeu, 2008; Grimshaw, Kwasny, Covell, & Johnson, 2003; Grimshaw, Séguin, & Godfrey, 2009; Hahn et al., 2011; Shipley-Brown, Dingwall, Berlin, Yeni-Komshian, & Gordon-Salant, 1988; Voyer, Bowes, & Soraggi, 2009; Voyer, Russell, & McKenna, 2002). However, studies who also included non-right-handed participants are rare, and most of those who do only include a small sample (e.g. Donnot & Vauclair, 2007; Elias et al., 1998; McNeeley & Netley, 1998; McNeely & Parlow, 2001; Turnbull & Bryson, 2001).

One exception to the omission of non-right-handers is an experiment by Bryden and colleagues (1991), who recruited 48 right-handed and 48 non-right-handed participants. They,

surprisingly, found that the LEA for emotional prosody processing was increased in the non-right-handed sample relative to the right-handed; 68% of right-handers and 74% of non-right-handers had a LEA. Grimshaw (1998) recruited 32 right-handers and 32 non-right-handers, but instead found that non-right-handers had a numerical REA; 59% of right-handers and only 41% of non-right-handers had a left ear advantage for emotional prosody. Elias et al. (1998) examined both hand and foot preference in a prosodic dichotic listening task. They found that the LEA was only reduced for strongly left-sided participants (participants with both a left hand and left foot preference). It has been suggested that strongly left-handed individuals are more likely to have right hemisphere dominance for language (Knecht et al., 2000), suggesting that perhaps these individuals are also more likely to have atypical (i.e. left hemisphere) brain organisation for emotional prosody. However, these results should be interpreted with caution as the study only had 8 participants in each hand/foot group.

In summary, there is good evidence, especially from right-handed samples, that attention, emotional prosody and face processing tend to depend more on the right hemisphere than the left. How these functions lateralise in non-right-handers, at least for attention and emotional prosody, is less clear. Furthermore, their relationships with one another remain unexplored.

There is a lack of research testing for multiple asymmetries within the same individuals, despite the inexpensive and relatively brief delivery time of these behavioural tests. Most of the studies who have included two or more tests have been restricted to examining language laterality using different modalities (i.e. one DL and one VHF task; Bryden, 1967, 1973; Dagenbach, 1986; Fennell, Bowers & Satz, 1977a,b; Hines & Satz, 1974). One possible explanation for why this is the case may be that these studies rarely find large, significant, positive correlations between the language related tasks (Fennell et al., 1977; Voyer, 1998; Zurif & Bryden, 1969). However, it should be noted that right-sided biases are still often reported for both measures. Therefore, regardless of poor intercorrelations, it is difficult to conclude that these tests are unrelated to language-related asymmetry.

Some studies examining one language task with a ‘non-language’ task do exist. For example, Piazza (1980) tested 64 participants, both right-handed and non-right-handed, with and without familial sinistrality, on five different tasks: a syllables DL, environmental sounds DL, melodies DL task, tachistoscopic VHF letter task, and tachistoscopic VHF face task. After correcting for multiple comparisons, no significant correlations were found between any the tasks. Harms and Elias (2014) examined complementarity of left hemisphere processing of speech sounds and right hemisphere processing of emotional vocalisations in 52 right-handed participants using two dichotic listening tasks. Although they found an overall LEA for the emotional content and a REA for the verbal content, they, again, found no significant

correlation between the two measures.

In contrast, Bryden and MacRae (1988) observed a significant correlation between ear advantages on dichotic measures of verbal and emotional prosodic speech functions in right-handed participants. In their sample, 79% of participants showed a typical complementary pattern (LEA for prosody, REA for words), but no participant had reversed complementary, the rest all had a same side bias for both tasks. McNeely and Parlow (2001) tested 73 participants (6 were non-right-handed) on the Fused Rhymed Words Test (Wexler & Halwes, 1983) and a dichotic listening emotional prosody test. Although there was a non-significant correlation between tests (r = .01), complementary pattern of functions was observed in 78% of the sample, and the remaining 22% showed a reversed complementary pattern. The authors interpreted this non-significant correlation as evidence for 'the statistical model', that functions lateralise independently (see Chapter 1, pages 21-22), but correlating different perceptual tasks is potentially very conservative, as this would imply that these tasks perfectly reflect its underlying associated function. Segalowitz (1987), for example, concluded that laterality measures tended to be reliable if groups are the focus of, for example, test-retest (unfortunately, reliability of individual participant scores was relatively poor). In fact, many of these correlational studies do find complementary patterns when examining absolute ear advantages alone, as compared to the non-significant correlational analyses often of focus.

Albeit weak predictors of hemispheric dominance, these tests may be able to act as a first step in providing valuable information on the possible, potential differences in hemispheric processing for right-handers and non-right-handers. The starting point and original idea of this battery of tests was to examine if a behavioural test, or combination of behavioural tests would be predictive in estimating brain asymmetry for speech and language (Johnstone, 2016). This idea has since evolved with the development of this thesis, as its main interest lies with asymmetries of the right hemisphere. These functions can be measured, and individuals categorised, much like previous work in the lab on language asymmetry from fMRI, resulting in individuals being labelled as 'typical' or 'atypical' for each process.

The aim of this chapter was to examine multiple perceptual asymmetries in the same individuals, in groups of right-handers and non-right-handers. The breadth of asymmetry for non-language asymmetries in the two handedness groups was the main theme of interest. Non-language asymmetries were investigated using versions of the chimeric face paradigm, emotional dichotic listening tasks, a bespoke version of the greyscales task, and a VHF face categorisation task. Language-related asymmetries were investigated using a dichotic listening task, a lateralised naming task, and a VHF words categorisation task. The octave illusion was also included due to its potential in being able to predict language asymmetry.

The working hypothesis at this stage was from a complementary theoretical perspective. The difference between the two handedness groups should be on the order of a 10-15% reduction in the proportion of non-right-handers who show the typical asymmetry for the language-related tasks included (Carey & Johnstone, 2014). If non-speech functions tend to lateralise to the opposite hemisphere, then similar differences should be obtained for *any* right hemispheric function that is complementary to language. Differences in the predicted direction in the proportion of the sample showing the asymmetry would provide initial strong prima facie evidence for complementarity of that function with speech/language asymmetry. No difference between the groups would suggest that the function is lateralised independently to speech and language.

It was predicted that the majority of participants in both groups would show a bias in the predicted direction for that particular function, but that this would be reduced in the non-right-handed sample. It was also predicted that the reduced breadth of a typical side bias in the non-right-handed group would reflect in the average asymmetry, and that the right-handed group would show increased averaged asymmetries in comparison to the non-right-handed group.

2.2 Methods

2.2.1 Participants

The participants were students and staff members from Bangor University recruited opportunistically and via a student participation panel. Participant recruitment had a specific focus on finding left-handed and left-footed individuals, in order to compare handedness and footedness groups. Thus, left-sided individuals are overrepresented in the current sample as compared to the population representation. In total, 412 individuals participated. Most participants took part in several experiments; however, the experiments were divided into two testing phases and total participant demographics for each experiment can be seen in Table 2.1. Participants were granted course credits or compensated £7 per hour for their time. The protocols were approved by the Bangor University Ethics Board.

2.2.2 Apparatus

All experiments were presented using E-Prime 2.0 Professional (Psychology Software Tools, Pittsburgh, PA) running in Microsoft Windows XP Professional (version 2002, service pack 3). Computer-based tasks were displayed on a 1920x1080, 60 Hz, monitor and responses were entered on a standard keyboard. To maintain head position throughout the visual tasks, a chin rest positioned at 50 cm from, and aligned with the centre of the monitor, was used for all tasks. All auditory stimuli were presented through a pair of Beyerdynamic (DT770 PRO 80 OHM) headphones. A decibel meter was used to ensure the two channels were matched for sound pressure level (balanced at +/- 0.1 dB). A voice key comprising of a Labtec AM-22 Deluxe microphone connected to a sound relay-detector and timer was used to record reaction times in the naming task.

Table 2.1

Participant demographics for all behavioural perceptual experiments. Group means and standard deviations in parenthesis are displayed in the age and WHQ columns. NRH = non-right-handed, RH = right-handed

Experiment	Hand group	Sex	WHQ	Age
Chimeric faces 1.0	NRH	F = 50, M = 20	-19.31 (13.87)	23.23 (6.28)
	RH	F = 49, M = 20	+27.04 (3.32)	21.96 (4.78)
Chimeric faces 2.0	NRH	F = 95, M = 33	-19.85 (13.91)	24.30 (8.99)
	RH	F = 127, M = 46	+25.64 (5.94)	21.76 (4.86)
Colourscales	NRH	F = 127, M = 45	-20.02 (13.28)	24.22 (8.56)
	RH	F = 170, M = 67	+25.86 (5.56)	21.90 (5.04)
CV dichotic listening	NRH	F = 126, M = 46	-20.20 (13.20)	24.23 (8.55)
	RH	F = 169, M = 67	+25.97 (5.44)	21.91 (5.05)
EmoDL long	NRH	F = 50, M = 20	-19.31 (13.87)	23.23 (6.28)
	RH	F = 50, M = 21	+27.07 (3.30)	22.37 (5.70)
EmoDL short	NRH	F = 95, M = 34	-22.22 (13.88)	24.26 (8.97)
	RH	F = 126, M = 46	+25.80 (5.79)	21.78 (4.87)
Lateral naming	NRH	F = 95, M = 34	-19.87 (13.85)	24.26 (8.97)
	RH	F = 126, M = 47	+25.67 (5.95)	21.77 (4.85)
Octave illusion	NRH	F = 49, M = 20	-19.19 (13.93)	23.28 (6.31)
	RH	F = 52, M = 21	+27.10 (3.28)	22.44 (5.70)
VHF face categorisation	NRH	F = 124, M = 46	-20.09 (13.30)	24.08 (8.49)
	RH	F = 169, M = 66	+25.83 (5.57)	21.90 (5.06)
VHF word categorisation	NRH	F = 126, M = 46	-20.09 (13.27)	24.18 (8.57)
	RH	F = 166, M = 67	+25.89 (5.56)	21.89 (5.06)

2.2.3 Stimuli, materials, and procedures

2.2.3.1 Waterloo Handedness Questionnaire.

A modified version of the Waterloo handedness questionnaire (WHQ, Steenhuis & Bryden, 1989) was used to assess participants' direction and strength of hand preference. The inventory asked participants to indicate hand preference for 15 common manual activities such as 'writing' and 'throwing' from alternatives of 'left always', 'left mostly' 'either' 'right mostly' or 'right always'. The questionnaire items add up to a total score ranging from -30 (complete left-hand preference) to +30 (complete right-hand preference) Phone ear preference, foot preference for kicking, and eye dominance (using the Miles A-B-C test) was also recorded for each participant.

2.2.3.2 Emotional prosodic dichotic listening (EmoDL) long version.

2.2.3.2.1 EmoDL development.

2.2.3.2.1.1 Recording procedure.

The stimuli were recorded in a sound-insulated booth in the School of Psychology, Bangor University. The words were recorded using a high quality Sennheiser microphone (MKH 40-P48) and Yamaha mixer (MG124c), and were recorded on a PC with a high-quality sound card (M-audio delta 1010) using Cool Edit Pro 2.0 (Cool Edit Pro 2002, version 2.0 Syntrillium Software Corporation, Phoenix, Arizona, USA). Sound files were recorded using one channel (mono) at 16-bit resolution and 44.1 kHz sampling rate.

Nine females were invited to have their voices recorded and were recruited from adverts distributed to the School of Creative Studies and Media, and the Bangor English Dramatics society at Bangor University. They were native English speakers without strong regional accents and reimbursed £10 per hour for their time. Separate recording sessions were conducted with each speaker lasting approximately one hour each. A list of the words and the emotions they were asked to produce were given to each speaker ahead of the recording session so that they could familiarise themselves with the materials. The list provided contained a total of 30 different words and syllables.

The actresses were told that each word and syllable was to be produced in varying intonations to portray neutrality and six emotional states (happy, surprised, sad, angry, fear disgust). The general instruction was to produce the words as if they were feeling each of the target emotions, and it was emphasised that they should try to act the emotions out as strongly as they could. To enhance expressiveness, the speakers were encouraged to imagine situations where they had experienced the target emotion, and hypothetical scenarios were provided (e.g. 'imagine that it is your birthday and your best friend who lives in a different town

shows up to surprise you'). However, specific instructions on how to achieve the emotional tones were not given as the most natural and spontaneous expression was desired, and did not want to impact on the actresses' perception of that emotion.

The actresses were asked to repeat each word 4-5 times for each emotional prosody (or until they felt happy with the expression), or until being evaluated by the experimenter as a clearly recognisable instance of the intended expression. Four out of the nine females were then chosen for inclusion based on their ability to produce several of the emotional expressions. The voice recordings from these four individuals were edited using Cool Edit Pro 2.0. Two different versions of each word and emotion were edited into individual sound files and normalised in energy (root mean square).

2.2.3.2.1.2 Validation of emotions.

A total of 240 stimuli were submitted to the validation procedure (6 words [ball, call, fall, hall, mall, wall] x 5 intonations [happy, sad, angry, fear, disgust] x 4 speakers x 2 [validated for two versions of the same words/affect]). Ten independent raters (all right-handed; 6 females) were asked to identify the emotional prosody conveyed in the voice ('please categorise the emotion') and intensity of the emotion, using a slider, ranging from 'not intense at all' to 'extremely intense'. The stimuli were presented via high-quality headphones (Beyerdynamic DT770 PRO 80 OHM) and the responses were given by pressing pre-specified buttons on the keyboard, and sliding the slider using the computer mouse. Once decided, participants clicked a 'next' button, and the next sound would play automatically. The rating procedure was self-paced, and participants had the option of listening to the stimuli several times, but were encouraged to rate it based on their initial impression. The rating session lasted approximately 25 minutes.

2.2.3.2.1.3 Selection.

The mean percentage of correct identifications and mean intensity ratings were computed for each stimulus (see Table 2.2). Four emotions were selected for inclusion in the experiment: anger, fear, happiness, and sadness. Disgust was excluded as it was the least recognisable emotion. Four rhyming words were used: ball, call, fall, and mall. These words were chosen as sufficient number of items passed the validation process for each of the four actresses. The items chosen had emotional tones that were correctly identified with a minimum accuracy of 80%, and the mean accuracy for each sound category did not differ (p = .134). There was a difference in the intensity ratings, $F(3,47) = 5.12$, p = .004, with happiness rated less intense

as compared to anger ($p = .003$) and fear ($p = .018$). There was no other differences in intensity ratings.

Each word/emotion combination were paired with each other with the constraint that two different words and two different prosodies were present in each trial. The same actress generated both words in any pairing. This resulted in a total of 144 unique stimulus pairs. The stimulus pairs were chosen so that each actress appeared an equal number of times, both for each word and each emotional expression. If two versions of an emotion with the same word passed the validation process, the word with the highest rating, or the one closest in length to its word pair was chosen. Every matched pair was always the identical stimuli but reversed (so that one member of each identical pairing would be presented once to the left ear and once to the right ear).

Table 2.2

Mean F0, F0 variability (SD), duration, and intensity ratings of the stimuli included in the emoDL task

Emotion category	F0 (Hz)	F0 variability (SD)	Duration (ms)	Mean intensity rating (0-1)	Mean accuracy %
Anger	314.59 (67.04)	95.23 (32.65)	679.13 (11.02)	.74 (.11)	95.33 (8.34
Fear	448.31 (88.42)	56.71 (39.30)	543.30 (7.84)	.72 (.08)	92.31 (7.25)
Happiness	347.93 (35.20)	123.66 (25.31)	609.99 (8.73))	.61 (.07)	90.00 (7.07)
Sadness	287.80 (58.51)	57.68 (27.84)	706.60 (10.39)	.70 (08)	96.43 (4.97)

2.2.3.2.2 Procedure.

Participants heard two stimuli simultaneously in each dichotic trial, one in the left ear and one in the right ear. Participants were informed that they would be presented with two words spoken in two different emotional tones simultaneously in each trial, and were instructed to report back the emotional tone that that they heard, or if they heard two, the one that they heard best or clearer. They were instructed to focus on the emotional tone of the speaker, and to ensure that attention was centred and allocated equally to each emotional tone. Participants were given a response sheet which depicted the four emotions in line drawn facial expressions and were told to focus their attention on the sheet throughout the task. They were asked to give their answers by pointing to the image depicting the emotion and to verbally report the emotion to the experimenter. The experiment was divided into four blocks of trials, with 36 trials in each block, and participants were offered breaks in between each block.

2.2.3.2.2 EmoDL Pilot.

The stimuli were first piloted to examine if a significant ear advantage would be obtained in the task. Fifteen right-handed participants (10 female, 5 male) with a mean age of 28.00 (*SD* = 8.82) took part in the piloting. The scores from each ear was converted to a LI (see section 2.2.4 below), were a negative score indicates that participants chose the emotional tone presented in the left ear more often, and a positive score reflects a preference for the emotional tone in the right ear. The mean LI score was -22.81 (*SD* = 28.80), and this was a left ear advantage (LEA) significantly different from no ear advantage (NEA – a score of 0), $t(14) = -3.02$, $p = .009$. From a proportional approach, only two individuals (.13) had an overall REA. It was concluded that these results, albeit with a small number of participants, were consistent with the left ear advantage reported in the literature and decided to include the task in the testing battery of perceptual asymmetry.

2.2.3.3 EmoDL short version (emoDL short).

In developing emoDL, a goal was always to develop a short version of the test. As the current long version had a long administration time (~15-20 minutes to administer; was the longest out of all behavioural tasks), the aim was to develop a test to be ~10 minutes or less. A colleague, at a conference, confirmed that they also had success obtaining significant mean LEA with a shorter 72-trial version of the task. Thus, a shorter version of the task was created.

One issue with dichotic listening tasks is stimulus dominance; when one stimulus in the pair is so salient that participant always report back that item regardless of the ear it is presented to. For example, if an angry tone and a sad tone is paired, and the participants always report back the angry tone, angry is thought to be the dominant stimulus. Although this does not have an effect on the direction of a person's ear advantage, it adds noise, thus reducing the overall ear advantage (Grimshaw, McManus, & Bryden, 1994). By reducing the influence of dominant pairs, a 'purer' ear advantage can be obtained. Therefore, the potential effect of stimulus dominance within the data set was investigated, and pairs were eliminated if they produced stimulus dominance effects for more than 70 percent of all participants, in order to obtain a more representative measure of a person's ear advantage.

2.2.3.3.1 Stimulus dominance analysis emoDL.

Analysis was carried out to investigate stimulus dominance in the first 130 participants who had taken part in the original version of emoDL. As each stimulus pair only appeared twice in the data set (once with stimulus A presented to the right ear, B in the left ear and the next time reversed), stimulus dominance effects were investigated across participants. Firstly,

stimulus dominance analysis was carried out on an individual person basis for each stimulus pairing (e.g. ball_happy/fall_sad and fall_sad/ball_happy). Secondly, each stimulus pairing was compared across participant to examine how often it was chosen as dominant. Eight items from the original version were found to dominate in 70% of participants.

2.2.3.3.2 Development emoDL short.

The original 4-block version of emoDL was organised so that two of the blocks contained half of the item pairings. This meant that all stimuli could be divided into two sets. Since a strong correlation for LI ear advantages was found between the two sets ($r = .81$, $p < .001$, $N = 134$), one half of the long version was chosen for the short version. The remaining dominant items in that set (4 items) were taken out and replaced with non-dominant items from the other set. The final version consisted of 72 trials that were split over two experimental blocks, and were balanced as well as possible in regard to how many times each word and each emotion appeared from each actress. As in the longer version, a different word and a different emotional tone was presented to each ear in the different trials.

2.2.3.3.3 Procedure.

Participants heard two stimuli simultaneously in each dichotic trial, one in the left ear and one in the right ear. Participants were informed that they would be presented with two words spoken in two different emotional tones simultaneously in each trial, and were instructed to report back the emotional tone that that they heard, or if they heard two, the one that they heard best or clearer. They were instructed to focus on the emotional tone of the speaker, and to ensure that attention was centred and allocated equally to each emotional tone. Participants were given a response sheet which depicted the four emotions in line drawn facial expressions and were told to focus their attention on the sheet throughout the task. They were asked to give their answers by pointing to the image depicting the emotion and to verbally report to the experimenter.

2.2.3.4 Chimeric faces 1.0.

The stimuli for this experiment were kindly provided to us by Dr. Mike Burt (Burt & Perrett, 1997) and were based upon Ekman and Friesen's facial expression images (Ekman & Friesen, 1976). The faces consisted of symmetrical average images created from four male and four female faces, each with a neutral or emotional expression (see Burt & Perrett, 1997; and Innes, Burt, Birch, & Hausmann, 2016, for more information). Four emotional facial expressions were used for the current experiment: anger, disgust, happiness, and sadness.

The faces were vertically split down the middle of the face and paired so that one emotive hemiface was attached to another, and then blended at the midline (see Figure 2.3). These were paired in all possible combinations, resulting in 16 individual stimuli presented to the participant twice in a total of 32 trials.

The participants were seated in front of the computer, positioned in the chinrest. They were instructed to focus on the fixation cross shown in the center of the screen at all times. Each trial started with the fixation cross for 1000ms, followed by the presentation of the emotional chimeric face for 400ms (see Figure 2.3). The participants were asked to verbally report to the experimenter the emotion seen in the face, which was a forced choice out of the four present emotions. The experimenter inputted the response using a key press on keyboard which triggered the next trial. The trials were presented in a randomised order.

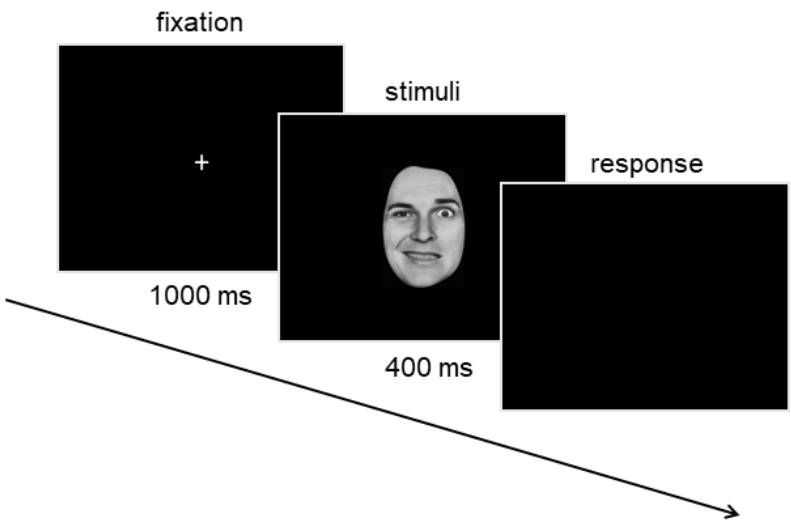


Figure 2.3. Trial procedure for the chimeric faces 1.0 task. Participants were asked to name the emotion they saw in the face. The next trial began after a response had been inputted by the experimenter.

2.2.3.5 Chimeric faces 2.0.

The chimeric face task was modified for phase 2 of the behavioural testing as participants were not always accurate when identifying the emotion from the face. The mean accuracy for chimeric faces 1.0 was 0.82 and did not differ between right-handers ($M = 0.82$, range = 0.44 – 1.00) and non-right-handers ($M = 0.82$, range = 0.63 – 1.00), $p = .958$. As LIs were calculated from correct trials only, the task was modified so that all trials in the experiment could be included.

Stimuli for this experiment were from the same database as the previous chimeric faces

task. Six emotional expression were used; happy, sad, disgust, anger, surprise and fear. This time, each chimeric face stimuli consisted of one emotive expression paired with one neutral expression. Two versions of each face pair were used, one with the emotive expression on left side, and one with emotive expression on right side, resulting in a total of 12 images (see Figure 2.4) shown on a black background. Stimuli were presented in pairs, centered at 1° of visual angle above and below central fixation. Each pair was presented four times, resulting in a total of 48 trials.

In each trial, a question was presented for 2000ms, instructing the participants about which emotion they were responding to in the trial. The question was followed by the presentation of the face pair. The participants were instructed to indicate the face that displayed the target emotion (as prompted at the start of the trial) more. To indicate their decision participants pressed the 'T' key indicating the top face or the 'B' key indicating the bottom face using their left and right index fingers. Participants were free to attend to both faces; however, they were asked to go with their initial reaction and to report their decision as quick as possible. Once the response was registered the next trial was initiated immediately.

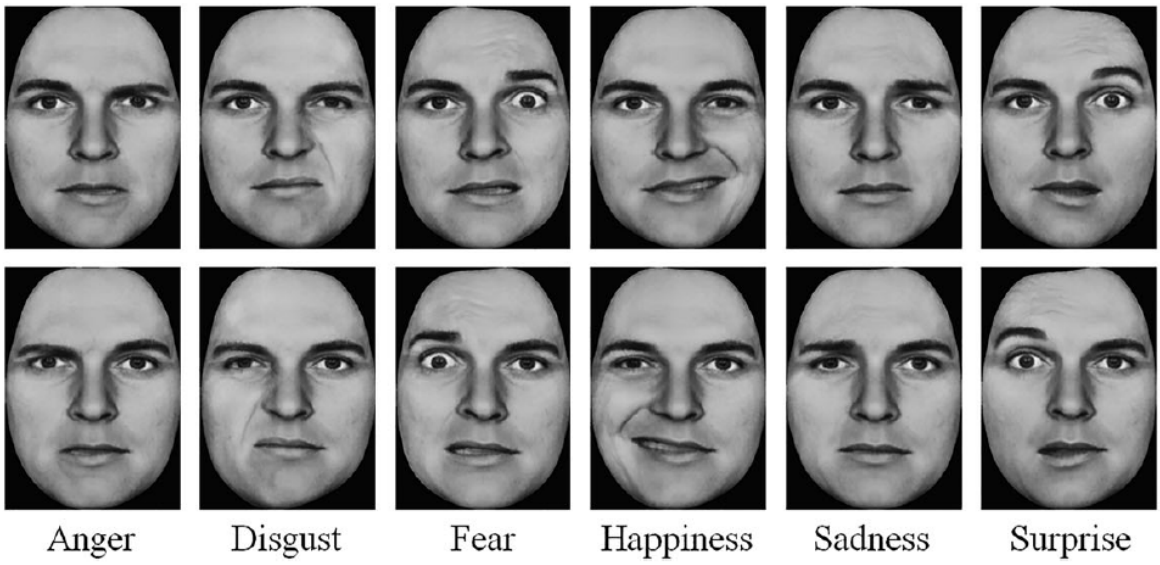


Figure 2.4. Stimuli for chimeric faces 2.0. The top row shows chimeras with the emotive expression on the right side, and the neutral expression on the left side. The bottom row shows the mirror images, with the emotive side on the left and neutral on the right. Reprinted from Innes et al. (2016).

2.2.3.6 Colourscales.

Colourscales is an in-house bespoke version of the greyscales task, invented by Mattingley, Nicholls and colleagues (Mattingley et al., 1994, 2004; Nicholls et al., 1999). Stimuli consisted of images of two left-right mirror reversal colour gradient bars, presented on a white background. Bars between white and four different colours respectively were used; blue, green, purple and red (see Figure 2.5 for examples). Each stimulus was 5° high and each colour was presented at two different lengths (at a visual angle of 28° and 34°). Each bar pair was presented twice so that the bars with the left to right colour/white gradient was shown at the top in one trial and at the bottom in one trial. Four black and white greyscales-like stimuli were also included, resulting in a total of 20 stimulus pairs. The horizontal midline of each stimulus pair was aligned with the screen's centre, and the upper and lower stimuli were placed 2° above and below the centre, respectively. Each stimulus pair was presented twice; once targeted for the colour gradient, and once targeted for the white gradient, resulting in a total of 40 trials.

Participants were positioned in the chinrest. Each trial began with a question centred on the screen for 1500ms, such as 'Greener?', 'Whiter?', or 'Bluer?', informing which colour to respond to in the trial. The stimulus presentation of the associated colourscale bars followed and remained on the screen until the participants responded by pressing the 'T' key on the keyboard indicating the top bar, or the 'B' key indicating the bottom bar, initiating the next trial. The participants were instructed to respond as quickly as they could. Participants were reminded of this if they took time inspecting the bars, rather than making an instant judgment. The presentation was randomised for each participant.

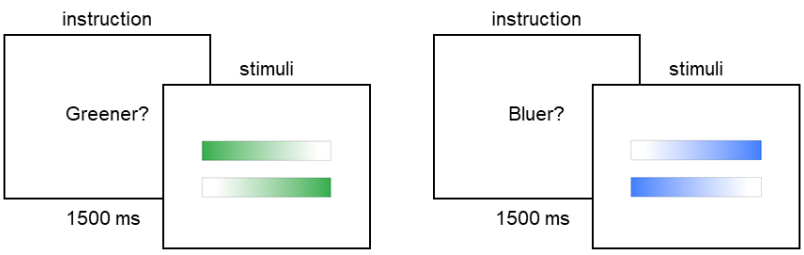


Figure 2.5. Two sample colourscales stimuli. The instruction screen is illustrated in the panel before its companion colourscale figure.

2.2.3.7 CV dichotic listening.

The stimuli for the consonant-vowel (CV) dichotic listening paradigm (Hugdahl et al., 2009) were kindly shared with us by Dr Rene Westerhausen, and a description of the stimulus creation process can be found in Rimol, Eichele and Hugadahl (2006). The consonant-vowel syllables were paired presentations of the six stop-consonants /b, d, g, p, t, k/ with the vowel /a/ to form six consonant-vowel (CV) syllables: /ba/, /da/, /ga/, /pa/, /ta/, /ka/. The six syllables were combined in pairs played in each sound channel (eg. /pa/-/ga/), which resulted in 36 stimulus pairings, including homonyms. The syllables were temporally synchronised at the energy release in the consonant and vowel segment between channels.

The experiment consisted of three blocks of 36 trials each (108 in total). Each block contained all possible syllable pairings including homonyms. The 18 trials of homonyms were excluded from laterality calculations. The three-block version of this task is traditionally used to measure cognitive control by directed attention, here comprising of three conditions; a 'non-forced attention' condition, and two 'forced right/ left' conditions where the participants are specifically asked to focus their attention on the right and left ear (see Hugdahl & Andersson, 1986). In the current experiment, all bocks were given under non-forced conditions in order to calculate an ear advantage LI score from a larger number of trials.

Participants were given a set of headphones and were instructed they would hear a pair of syllables presented in each trial. They were instructed to report back the syllable they heard or if it seemed like they heard two different sounds, the one they heard best or most clearly. They were instructed that they should try and center their attention to their best ability, and not focus their attention by listening to the syllables presented to a particular ear. The participants were also told that they may not report all syllables an equal amount of time, and not to worry if they reported the same syllable several times in a row. The participants were encouraged not to spend time thinking about the sounds, but to report one back as soon as the sound had been presented by verbally reporting the sound and to point to it on a response sheet that was given at the start of the experiment. The experimenter entered the response using keyboard which triggered the next trial. A rest period was offered between each block with optional short breaks.

2.2.3.8 Lateral naming.

The methodology used for this VHF naming task was a partial replication of Hunter and Brysbaert (2008), only using the three-letter and four-letter words (24 of each category) from the original experiment. Each word was accompanied by a controlled pair word that would never start with the same initial letter/phoneme to reduce the risk of a participant correcting

themselves mid-word after initially naming the control word. All words were matched based on their initial phoneme and initial letter to make sure that the reaction time differences were not caused by any shorter/longer initial phonemes/letters. The words were presented once in each visual field, resulting in a total of 96 trials distributed over two blocks, positioned with the inner edge at 3° of visual angle left or right to central fixation. The participants' vocal reaction times (VRT), were recorded through a voice key comprising a 20mm in diameter microphone, which was placed on the desk between the monitor and the participant. The microphone was connected to a sound relay-detector and timer. A trigger to start the timer was sent from the presentation PC at stimulus onset, and the relay-detector sent a trigger back to the recording PC upon voice detection.

Each trial began with a central fixation cross which the participants were asked to fixate on. The onset of each trial was initiated by the experimenter, by pressing the enter bar on the keyboard. This was followed followed by the bilateral presentation of the two words for 200ms after a random delay (200, 400, 600, or 800ms). Simultaneously, an arrow appeared instead of the fixation cross in the centre of the screen pointing to one of the two words, and the participant was instructed to name the word the arrow was pointing to (see Figure 2.6). The arrow stayed on screen while the words were masked with a sequence of ASCII codes 35 (#) for another 200ms. The onset of speech was registered as reaction time for each stimulus. The experimenter reported whether the response was correct or incorrect using the keyboard and was completed without feedback of whether they had reported the correct word or not.

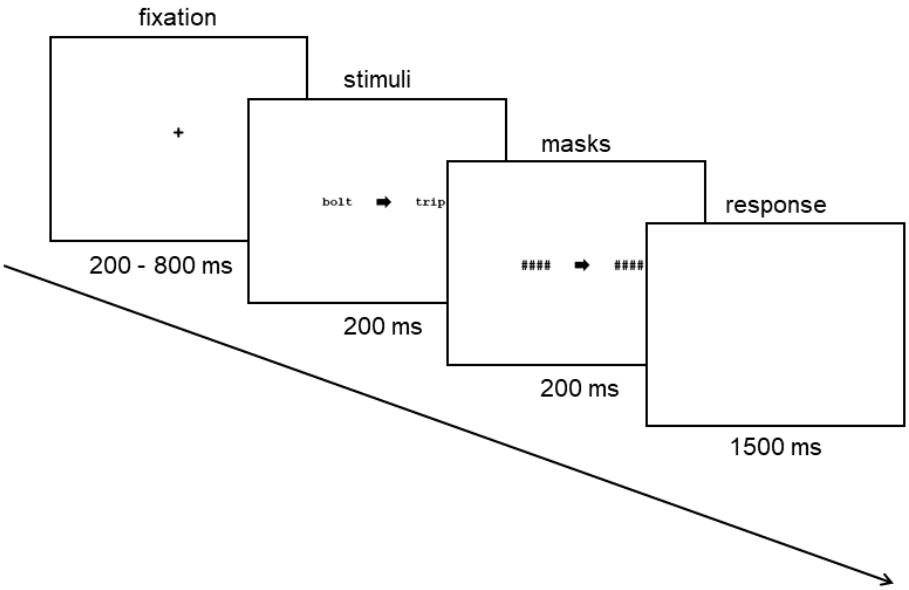


Figure 2.6. Trial procedure for the lateral naming task.

2.2.3.9 The octave illusion.

The stimulus was a sound file shared by Prof Diana Deutsch (http://deutsch.ucsd.edu/psychology/pages.php?i=202). The sound file was one minute long and consisted of a sequence of sine wave tones with frequencies alternating between 400 Hz and 800 Hz in durations of 250ms. The sequence was played to both ears simultaneously but in a staggered fashion, so when the high tones were presented to one ear, low were presented to the other (see Figure 2.1, panel a).

The participants were instructed that they through headphones would be presented with a complex sequence of higher pitched and lower pitched tones, and that their task was to report back to which ear they heard more higher tones. This forced choice version is modified from the original experiment where participants were given the choice to report that they either heard the higher pitched tones on one ear and then the other, or that they heard no difference between the ears (Deutsch, 1974). It was not made clear to the participants that the two ears were experiencing the same stimuli. Participants were asked to respond as soon as they had decided by pointing to the ear that they felt had more of the high tones.

2.2.3.10 VHF face categorisation.

The face stimuli were 60 greyscale faces (30 male and 30 female) from the Vienna face database (Endl et al., 1998). The faces were cropped and covered with an oval mask (see Figure 2.7). Forty-eight of the faces were presented with the inner edge 7° to the left or the right of the centre of the screen in peripheral vision, and with 12 presented at fixation.

Participants were instructed to fixate centrally on the screen throughout the experiment. Each trial began with a central fixation cross on the screen for 2000ms. This was followed by a random delay (200, 400, 600, or 800ms), and then the presentation of the face stimuli for 250ms. This was followed by a 100ms mask where the face had been presented and 3000ms to respond before the next trial was initiated. The participants were asked to categorise the face as either male or female using the ‘Z’ or ‘M’ key on the keyboard using their left and right index finger respectively. Participants were instructed to respond as quickly but as accurately as possible, without breaking focus from central fixation. The tasks were counterbalanced so that half of the participants responded to female faces with the ‘Z’ key and half with the ‘M’ key. The task was preceded with three practice trials before the experimental session started.

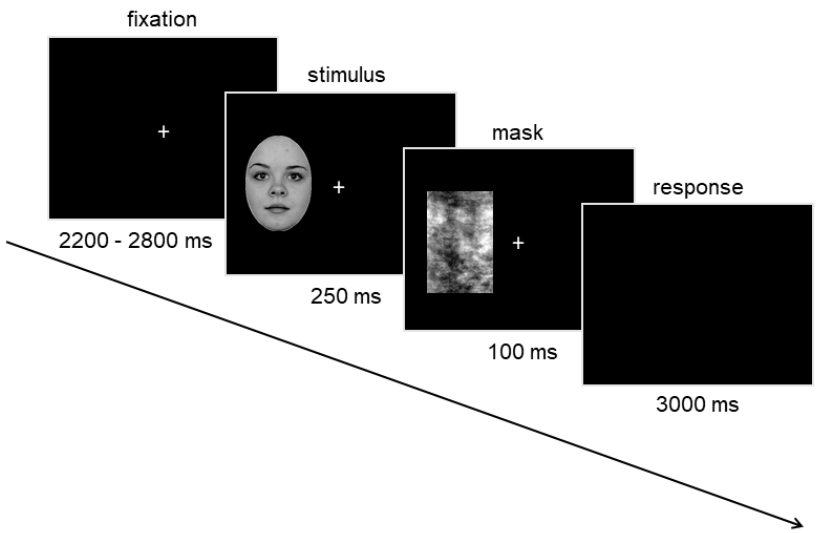


Figure 2.7. Trial procedure for the VHF face categorisation task.

2.2.3.11 VHF word categorisation.

This task required participants to categorise written words on the screen. A total of 60 words were used in this task, 24 were animal names and 24 names of fruits or vegetables. Out of the words, 48 were presented with the inner edge 6° to the left or right out in the periphery, and the remaining 12 presented in the centre of the screen. The words were taken from a revised version of the Battig and Montauge (1969) category norms (Van Overschelde, Rawson, & Dunlosky, 2004) and were selected based on length and word frequency according to the British National Corpus (BNC). All the words were 4-6 letters long and had a frequency of between 1 and 15 (per 1 million words) in the BNC. The words from each category were divided into two sets of 12 (presented to each visual field) matched for mean word length and frequency (see Table 2.3).

Table 2.3

Word frequency and length information for the VHF word categorisation task

	Mean frequency	Range	Mean word length
Animals 1	5.46	1.23 - 13.93	5.0
Animals 2	5.84	1.91- 13.04	5.0
Fruit/Vegetable 1	5.0	1.10 - 11.62	5.25
Fruit/Vegetable 2	4.81	1.22 - 11.90	5.08

Participants were instructed to stay fixated on the central fixation cross throughout the experiment. Each trial began with the central fixation cross on the screen for 2000ms. This was followed by a random delay (200, 400, 600, or 800ms) and then the presentation of the word stimuli for 250ms, followed by a 100ms mask where the word had been presented (see Figure 2.8). The participants had 3000ms to respond before the next trial was initiated. The participants were asked to categorise the word as either an animal or a fruit/vegetable using the 'Z' or 'M' key on the keyboard using their left and right index fingers respectively. Participants were instructed to respond as quickly but as accurately as possible, without breaking focus from central fixation. The tasks were counterbalanced so that half of the participants responded to animals faces with the 'Z' key and half with the 'M' key. The task was preceded with three practice trials before the experimental session started.

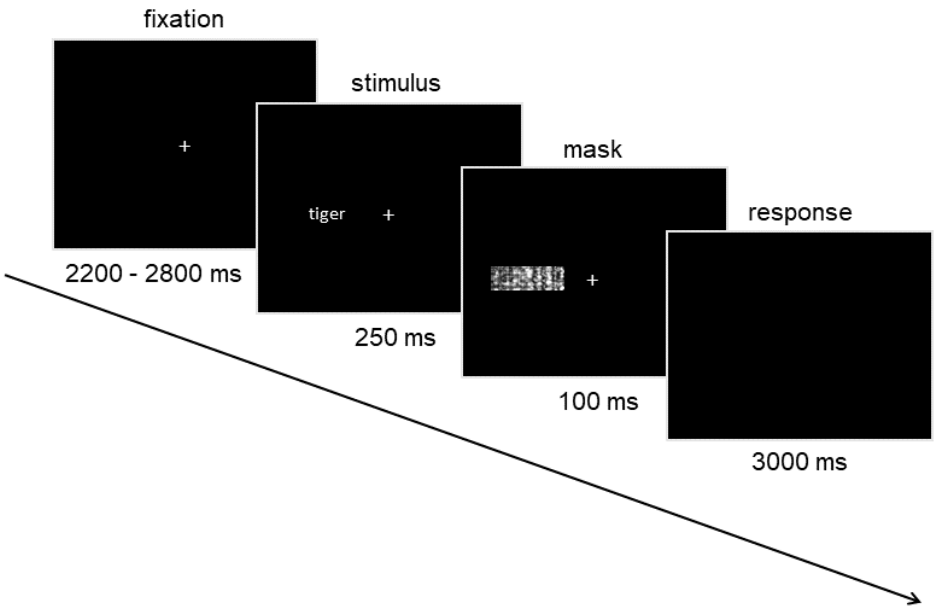


Figure 2.8. Trial procedure for the VHF word categorisation task.

2.2.4 Laterality Index

Results from most of the experiments reported within this thesis are expressed as an LI unless otherwise stated. The LI was calculated using the following traditional formula:

$$\text{Laterality Index} = \frac{(\text{right}-\text{left})}{(\text{right}+\text{left})} \times 100$$

where 'right' equals the number of stimuli where the chosen member of the pair was presented to the right ear or right visual field. Therefore, response bias scores range from -100 to +100, with negative scores reflecting a leftward perceptual bias and positive scores reflecting a rightward perceptual bias. A score of 0 reflects no bias (i.e. the participant reported stimuli from the left and right equally).

The LIs for reaction time-based experiments were calculated somewhat different. Only correct trials were used for the calculations. Mean reaction times or VRT were calculated for the RVF and LVF and the LI score for each task and each individual was derived through the following formula: LI = (LVF VRT/RT – RVF VRT/RT)/(LVF VRT/RT + RVF VRT/RT)*100, meaning that a positive score indicates an average advantage for RVF and negative faster on average to respond to items presented in LVF. Accuracy difference scores for the same experiments were calculated as proportion of correct trials in the RVF - LVF, so that a negative score indicated a LVF advantage. For all behavioural tasks it is important to note that these sides refer to the percept rather than the associated hemisphere.

2.2.5 Data analysis

A mean LI and proportion of visual field bias/ear advantage was calculated for all tasks separately for the two handedness groups. Firstly, mean LIs were compared against 0 using a one-sample t-test in order to examine if the handedness group was, on average, significantly lateralised for the specified task. Secondly, mean LI scores were compared for the two different handedness groups using one-tailed independent samples t-tests. It is worth to note that not all data were normally distributed according to Kolmogorov-Smirnov normality tests. However, it has been argued that t-tests are valid for any distributions with large (>100) sample sizes (Lumley, Diehr, Emerson, & Chen, 2002). The two tasks with sample sizes below 100 participants (chimeric faces 1.0 and emoDL long) both had data that was normally distributed for both handedness groups. Histograms of distributions for all tasks as a function of handedness group can be found in Appendix A.

A z-test was used to examine proportional differences between the two handedness groups for all tasks. Only participants with a directional LI were included for this analysis

(participants with an LI of 0 were excluded). It is specified how many participants were excluded (if any) for each task based on this criterion.

Sex was not included as a variable for any of the analyses. Meta-analyses of sex differences demonstrate null or very small effects. There is a well-established sex difference in incidence of left-handedness, with more males being left-handed, but no differences in dichotic listening, planum temperate asymmetry, or of fMRI assessed language lateralisation (Hirnstein, Hugdahl, & Hausmann, 2019; Hirnstein et al., 2013; Papadatou-Pastou et al., 2008; Sommer, 2010). In order to limit the number of comparisons made (Gelman & Loken, 2013), there was no reason to examine sex differences without any strong theoretical underpinnings to do so.

2.3 Results

2.3.1 Chimeric faces 1.0

It was predicted that most participants would name the emotion shown on the left half of the face more often, but that the *breadth* (how many) and *depth* (how biased on average) of this bias would be reduced in the non-right-handed sample. Figure 2.11(a) shows pirate plots of chimeric faces 1.0 LI scores as a function of handedness group. This and all subsequent pirate plots contain raw scores, means, smoothed densities, and 95% confidence intervals for each handedness group. Right-handers (M = -15.32, SD = 24.13) were found to be lateralised on the task, displaying an overall bias towards the left side of the face, $t(68) = -5.27$, $p < .001$. Non-right-handers (M = -4.85, SD = 25.96) were not lateralised for the task, showing no overall bias towards one side of the face, $t(69) = -1.56$, $p = .123$. It was found that the left-sided bias was, on average, significantly increased in right-handed as compared with non-right-handed participants, $t(137) = 2.46$, $p = 008$ (one-tailed), $d = 0.42$.

The proportion of each sample showing a LFA can be seen in Figure 2.9. To examine the breadth of the bias, the proportion of individuals with biases to the left half of the face were compared for the two handedness groups using a z-test. Only individuals with a visual field bias were included for the proportional analysis. Four right-handers (5.80%) and six non-right-handers (8.57%) had LIs of 0 and were excluded from this analysis. Out of participants with a directional bias, the proportions of right-handers (48/65 = .74), 95% CI [.62, .83], and non-right-handers (39/64 = .61), 95% CI [.49, .72], did not differ, $z = 1.56$, $p = .059$, and the 95% CI of the difference (-0.13) overlapped with zero [-0.28, +0.03].

2.3.2 Chimeric faces 2.0

It was predicted that most participants would choose the chimera with the emotional half displayed on the left more often, and that the breadth and depth of this bias would be reduced in the non-right-handed sample. Pirate plots of LI scores for each handedness group can be seen in Figure 2.11(b). As with the previous task, right-handers (M = -22.90, SD = 34.73), were found to be lateralised on average, displaying an overall bias towards the face with the emotional half on the left, $t(172) = -8.68$, $p < .001$. Non-right-handers (M = -5.73, SD = 41.22) were, again, not lateralised on the task, $t(127) = -1.57$, $p = .118$. It was found that right-handed participants, on average, had a stronger bias to the left side of the face as compared to non-right-handed participants, $t(245.43) = -3.82$, $p < .001$ (one-tailed), $d = 0.45$.

The proportion of each sample showing a LFA can be seen in Figure 2.9. For the proportional analysis, seven right-handers (4.05%) and six non-right-handers (4.69%) and had LIs of 0 and were excluded from the analysis. Out of participants with a directional bias, the proportions of right-handers (120/166 = .72), 95% CI [.65, .79], with a leftward bias was significantly higher than that of non-right-handers (71/122 = .58), 95% CI [.49, .67], $z = 2.50$, $p = .006$ (one-tailed), and the 95% CI of difference (-0.14) did not overlap with zero [-0.25, -0.03].

2.3.3 Colourscales

It was anticipated that the majority of both groups would choose the colored bars with the target colour presented on the left, but that this response would be more frequent in the right-handed sample. Pirate plots of LI scores for each handedness group can be seen in Figure 2.11(c). Right-handers (M = -17.28, SD = 38.73) were found to have a significant left side bias on the task, $t(236) = -6.87$, $p < .001$. Non-right-handers (M = -23.55, SD = 40.68) were also found to have a significant left side bias, $t(171) = -7.59$, $p < .001$. As mean LIs for the right-handed group were numerically smaller than those of the non-right-handers, and in opposite direction to our one-tailed prediction, a t-test was not performed.

The proportion of each sample showing a LFA can be seen in Figure 2.9. Sixteen right-handers (6.76%) and 11 non-right-handers (6.40%) had LIs of 0. Of people with a directional bias, .67 of the right-handers (149/221), 95% CI [.61, .73], and .73 of the non-right-handers (117/161), 95% CI [.65, .79], had leftward biases. As this goes against the predictions, no further analysis was performed.

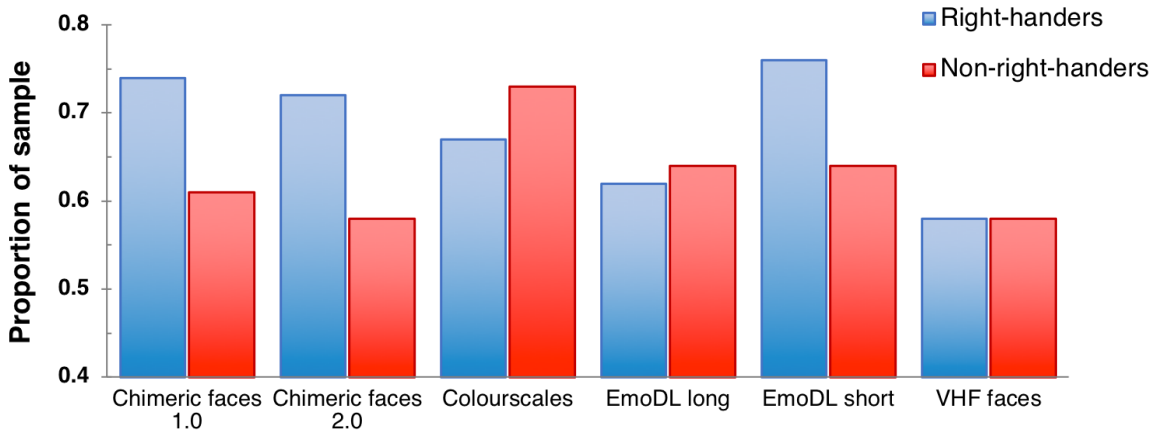


Figure 2.9. Proportion of each sample showing a LEA/LFA on the perceptual tasks related to the right hemisphere. Three of the tests differed significantly in proportions of right-handers and non-right-handers (chimeric faces 1.0, chimeric faces 2.0, and emoDL short), but three of the tests did not (colourscales, emoDL long, and the VHF faces task).

2.3.4 CV dichotic listening

It was predicted that both groups would exhibit an overall REA, but that the breadth and depth of this bias would be decreased in the non-right-handed sample. Pirate plots containing LI scores for each handedness group can be seen in Figure 2.11(d). The hypothesised REA was found for both handedness groups (right-handers, $t(235) = 14.30$, $p < .001$; non-right-handers, $t(171) = 7.48$, $p < .001$). Furthermore, right-handers ($M = 25.41$, $SD = 27.30$) were found to have a higher average LI score compared to non-right-handers ($M = 19.34$, $SD = 33.90$), $t(318.95) = 1.94$, $p = .027$ (one-tailed), $d = 0.20$.

The proportion of each sample showing a REA can be seen in Figure 2.10. The proportion of participants with a REA was found to be higher in the right-handed (.85 = 200/236), 95% CI [.80, .89], compared to non-right-handed group (.78 = 133/170), 95% CI [.71, .84], $z = 1.69$, $p = .046$ (one-tailed), however, the 95% CI of difference (-0.07) overlapped with zero [-0.14, +0.01].

2.3.5 Emotional dichotic listening (emoDL)

It was predicted that participants would exhibit an overall LEA, but that the depth and breadth of this bias would be reduced in the non-right-handed group. Pirate plots of LI scores for each handedness group can be seen in Figure 2.11(e). Both handedness groups had a small but significant bias overall towards the left ear (right-handers: $t(70) = -2.20$, $p = .031$; non-right-handers: $t(69) = -2.80$, $p = .007$). Mean LIs for the right-handers ($M = -8.30$, $SD =$

31.86) and non-right-handers (*M* = -11.00, *SD* = 32.91) were numerically in the unpredicted direction and no statistical tests were performed.

The proportions of each sample showing a LEA or REA can be seen in Figure 2.9. When investigating the proportions of right-handers and non-right-handers with LEA, it was found that .62 of right-handers (44/71), 95 % CI [.50, .72], and .64 of non-right-handed (45/70) 95% CI [.53, .75] had a LEA, which again is numerically in the unpredicted direction and no statistical tests were performed.

2.3.6 Emotional dichotic listening (emoDL) short version

As with the long version, it was predicted that participants would exhibit an overall LEA, but that the depth and breadth of this bias would be reduced in the non-right-handed group. Pirate plots of LI scores for each handedness group can be found in Figure 2.11(f). Both right-handers (*M* = -15.55, *SD* = 29.50) and non-right-handers (*M* = -9.00, *SD* = 31.10) had an overall significant bias towards the left ear (right-handers: $t(171) = -6.92$, $p < .001$; non-right-handers: $t(128) = -3.29$, $p = .001$). Right-handers were found to have a higher average LI score compared to non-right-handers, $t(299) = -1.86$, $p = .032$ (one tailed), $d = 0.22$.

The proportion of each sample showing a LEA can be seen in Figure 2.9. When comparing proportions of individuals with a left ear advantage, .76 of right-handers (130/172), 95% CI [.69, .81], and .64 of non-right-handers (83/129), 95% CI [.59, .72], had a bias towards the left ear. This difference was found to be significantly decreased in the non-right-handed sample, $z = 2.12$, $p = .017$ (one-tailed), however, 95% CI of the difference (-0.11) did not overlap with zero [-0.22, -0.01].

2.3.7 Octave illusion

It was expected that a majority of both groups would give a right ear response but with a decreased frequency in the non-right-handed sample, consistent with previous findings in our lab (Johnstone, 2015). The proportion of each sample showing a REA can be seen in Figure 2.10. In this sample of participants, the proportion of right-handers (38/72 = .53), 95% CI [.41, .64] and non-right-handers (34/69 = .49), 95% CIs [.38, .61] with a right ear response did not differ, $z = 0.42$, $p = .337$. Neither was there a group level bias on this task, assessed using a binomial test against 50% for right-handers ($p = .724$), or non-right-handers ($p = 1$).

2.3.8 Lateral naming

It was predicted that participants would be faster/more accurate when the cued word was presented in the RVF, but that both breadth and depth of this bias would be reduced in the non-right-handed group. For this experiment LI scores for VRT and accuracy were analysed separately. Naming corrections or errors were excluded from VRT analysis. Voice key failures were excluded from VRT analysis but not accuracy analysis. As followed by Van der Haegen et al. (2011), VRTs of less than 200ms, greater than 1500ms or latencies below/above 2.5 SD from the participant mean VRT were excluded. Two participants were excluded from VRT analysis as they did not have sufficient items to analyze in one visual field (one right-handed male with an accuracy of .02 in the LVF, and one non-right-handed male with an accuracy of .02 in the RVF).

VRT for right-handers and non-right-handers can be seen in Figure 2.11(h). Right-handers had a mean VRT of 634.08ms (SD = 204.48) in the LVF and 606.08ms (SD = 187.93) in the RVF. Non-right-handers had a mean VRT of 581.11ms (SD = 168.22) in the LVF and 560.58ms (SD = 160.02) in the RVF. Right-handers had an LI of +1.98 (SD = 8.69) and were on average lateralised for the task, $t(171) = 2.98$, $p = .003$. Non-right-handers had an average LI of +1.66 (SD = 9.20) and also had bias towards the RVF, $t(127) = 2.04$, $p = .043$. There was, however, no difference in average LI scores for right-handers and non-right-handers, $t(298) = 0.30$, $p = .383$.

The proportion of each sample showing a RFA can be seen in Figure 2.10. When investigating the proportions of right-handers and non-right-handers with a bias towards the word presented in the right, it was found that .56 of right-handed (97/172), 95% CI [.49, .64], and .58 of non-right-handers (74/128), 95% CI [.49, .66], had a right-side bias, which was numerically in the unpredicted direction and no statistical tests was performed.

When examining the error data, total accuracy scores did not differ between right-handers (M = .74, SD = .15) and non-right-handers (M = .72, SD = .14), $t(300) = 1.33$, $p = .183$. The average accuracy score for right-handers was .80 (SD = .14) in the RVF and .68 (SD = .19) in the LVF; for non-right-handers .79 (SD = .16) in RVF and .65 (SD = .19) in LVF. An accuracy difference score was calculated as proportion of correct trials in the RVF - LVF, so that a positive score indicated a RVF advantage. Accuracy difference scores for right-handers and non-right-handers can be seen in Figure 2.11(g) The average accuracy difference score was .12 (SD = .17) for right-handers, and .15 (SD = .21) for non-right-handers. As non-right-handers were more accurate in their RVF, no statistical tests were performed.

The proportion of individuals with a better score in their right or left visual field was also calculated and can be seen in Figure 2.10. Out of the right-handers .78 (131/169), 95% CI

[.71, .83], had a LFA, and .81 of non-right-handers (103/127), 95% CI [.73, .87]. This difference was again in the unpredicted direction and no statistical tests was performed.

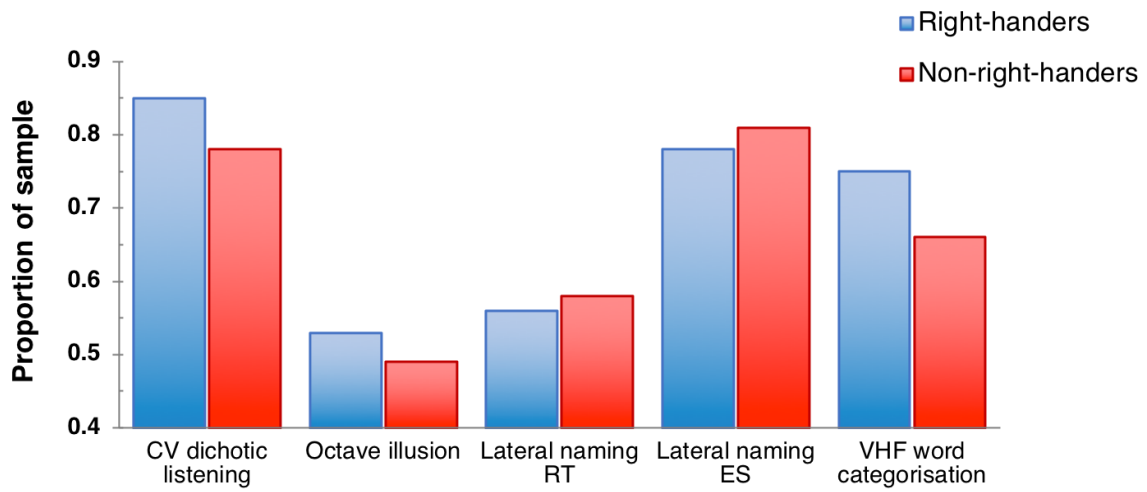


Figure 2.10. Proportion of each sample showing a REA/RFA on the perceptual tasks related to the left hemisphere. There were significant differences in proportions for CV dichotic listening and VHF word categorisation, but not for the other three measures.

2.3.9 VHF face categorisation

It was predicted that participants would categorise faces faster when shown in the LVF, compared to the RVF, but that the breadth and depth would be reduced in non-right-handed sample. For this task, participants with accuracy scores below 40% were eliminated in order to have sufficient trials available for analysis (~20 trials or more survived). This was rare as the average accuracy score was 83.18% (*SD* = 10.38). Five participants were excluded based on this criterion. One participant was also excluded due to having one category accuracy of 0 and most likely pressed the wrong button. The average RT for right-handers was 350.05ms (*SD* = 128.02) for the LVF, 314.81ms (*SD* = 129.47) for faces presented in the middle and 360.36ms (*SD* = 134.13) for faces presented in the RVF. The average RT for non-right-handers was 376.37ms (*SD* = 176.47) for faces in the LVF, 338.75ms (*SD* = 173.58) for faces presented in the middle, and 381.96ms (*SD* = 175.01) for the RVF.

Pirate plots of LI scores for each handedness group can be found in Figure 2.11(i). Both right-handers (M = -1.48, SD = 6.64) and non-right-handers (M = -0.90, SD = 6.66) were on average faster to respond when the face was shown in the LVF. Right-handed participants were, on average, found to be right lateralised for the task, $t(169) = -1.77$, $p = .079$, but the non-right-handed group was not lateralised, $t(169) = -1.41$, $p = .160$. There was, however, no

difference in average LI scores for right-handers and non-right-handers, $t(403) = -0.87$, $p = .193$ (one-tailed).

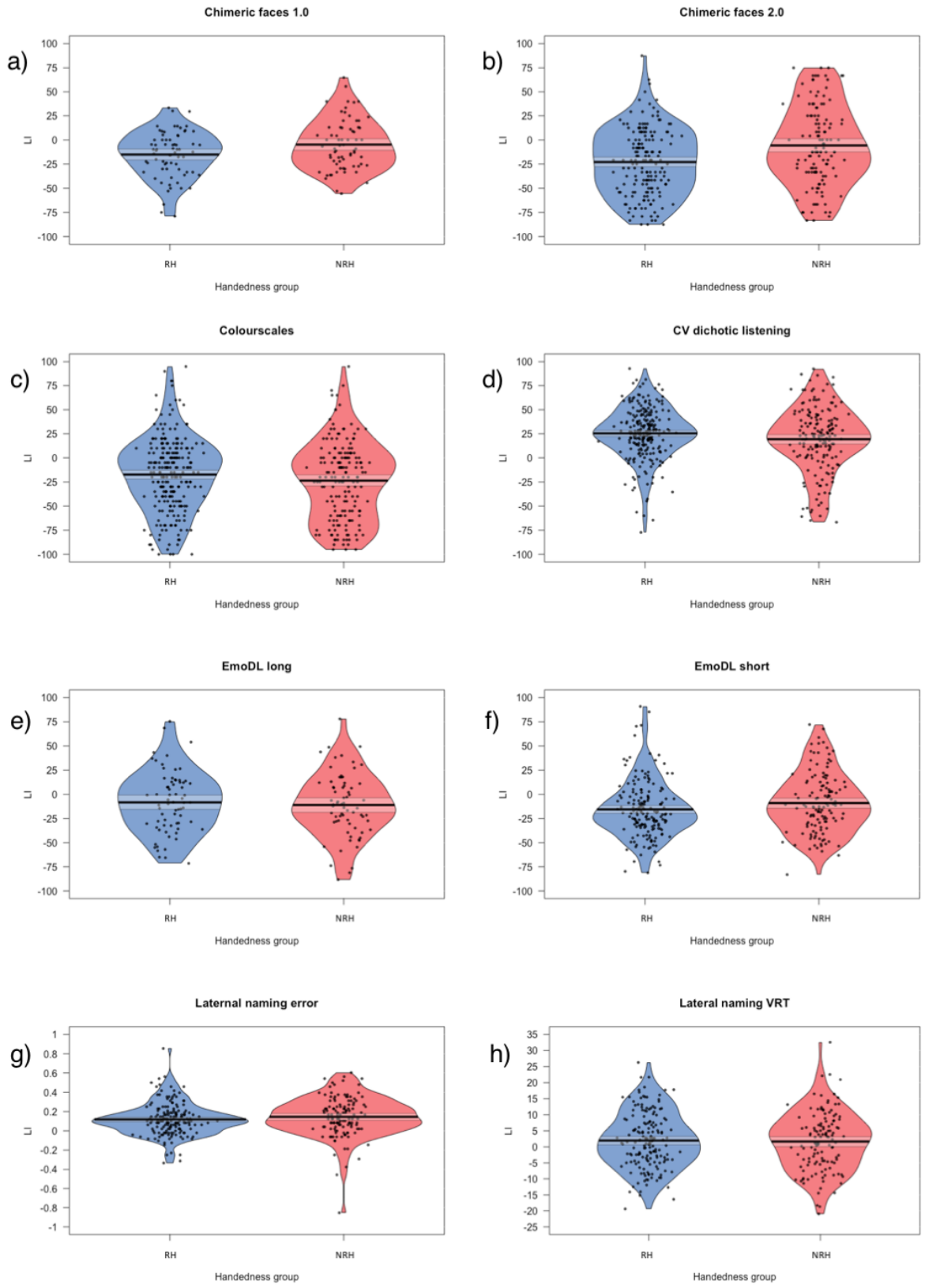
The proportion of each sample showing a LFA can be seen in Figure 2.9. Out of the right-handers, .58 (137/235), 95% CI [.52, .64] had a LFA and .58 (99/170), 95% CI [.51, .65], of non-right-handers, and this difference in proportions was not significantly different, $z = 0.01$, $p = .496$ (one-tailed), and 95% CI of the difference (< -0.01) overlapped with zero [-0.10, +0.10].

2.3.10 VHF word categorisation

It was predicted that participants would categorise words faster when shown in the right visual field, compared to the left visual field. Participants with total accuracy scores below 40% were eliminated in order to have sufficient trials included for analysis (~20 trials or more survived). This was again rare as the average accuracy score was 87.39% (*SD* = 10.53). Four participants were excluded based on this criterion. Two participants were also excluded due to having one category accuracy of 0 and most likely pressed the wrong button with one hand. The average RT for right-handers was 471.85ms (*SD* = 174.62) for the LVF, 376.80ms (*SD* = 167.26) for the middle, and 438.87ms (*SD* = 168.53) for the RVF. The average RT for non-right-handers was 495.40ms (*SD* = 189.53) for the LVF, 388.11ms (*SD* = 155.70) for the middle words, and 464.58ms (*SD* = 164.35) for the RVF.

Pirate plots of LI scores for each handedness group can be found in Figure 2.11(j). Both right-handers ($M = 3.72$, $SD = 7.20$) and non-right-handers ($M = 2.79$, $SD = 6.45$) were on average faster to respond when the face was shown in the RVF and were, on average, both found to be right lateralised for the task (right-handed: $t(232) = 7.89$, $p < .001$; non-right-handed: $t(171) = 5.67$, $p < .001$). Average LI scores did not differ between the groups, $t(403) = 1.35$, $p = .089$ (one-tailed).

The proportion of each sample showing a RFA can be seen in Figure 2.10. There was a significant difference between the proportion of the right-handers (174/233 = .75), 95% CI [.69, .80], and non-right-handers (114/172 = .66) 95% CI [.59, .73], who showed a right visual field bias, $z = 1.84$, $p = .033$ (one-tailed), but the 95% CI of difference (-0.08) overlapped with zero [-0.17, +0.01].


a)
Chimeric faces 1.0
b)
Chimeric faces 2.0
c)
Colourscales
d)
CV dichotic listening
e)
EmoDL long
f)
EmoDL short
g)
Laternal naming error
h)
Lateral naming VRT
LI
RH
NRH
Handedness group

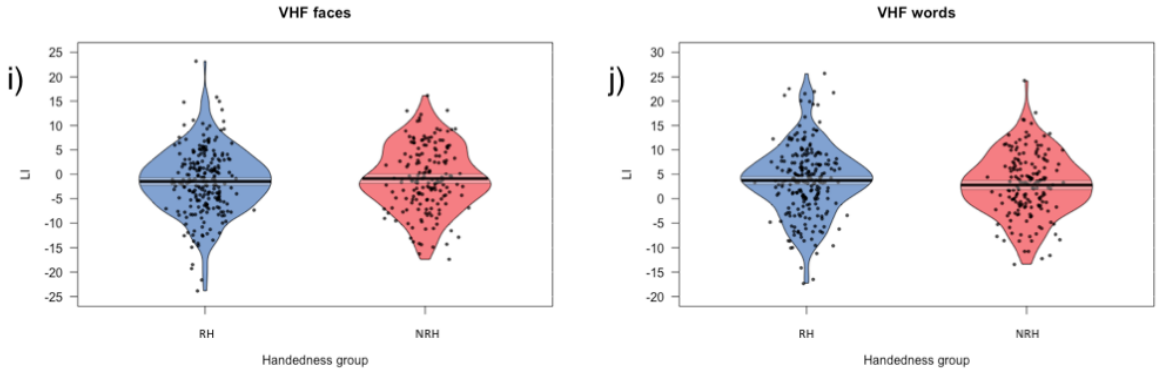


Figure 2.11. Pirate plots showing distributions of if LI scores for each of the perceptual measures separate for right-handers (blue) and non-right-handers (red). The bold line indicates the mean, and the highlighted area the 95% confidence intervals. Plots are shown for (a) chimeric faces 1.0, (b) chimeric faces 2.0, (c) colourscales, (d) CV dichotic listening, (e) emoDL long version, (f) emoDL short version, (g) lateral naming error scores, (h) lateral naming RTs, (i) VHF face categorisation, and (j) VHF word categorisation. RH = right-handers, NRH = non-right-handers

2.3.11 Correlations between language tasks

Three different correlations were carried out between the three different language-related measures (CV dichotic listening, lateral naming, and VHF words task – for scatterplots of these, see Appendix B). After correcting for multiple comparisons (α = .017), none of the correlations were significant (all one-tailed - CV dichotic listening and lateral naming: $r = .10$, $p = .038$; CV dichotic listening and VHF words: $r = .08$, $p = .058$; lateral naming and VHF words: $r = .01$, $p = .428$).

2.4 Discussion

For the perceptual tests presented in this chapter, it was predicted that the majority of participants would show a bias in the predicted direction of that specific function, but that this bias would be reduced in the non-right-handed sample. It was also predicted that the reduced breadth of the typical side bias in the non-right-handed group would be reflected in the average asymmetry, and that the right-handed group would show increased average asymmetries in comparison to the non-right-handed group. All the tests, except for the octave illusion, produced biases in the expected direction, suggesting the tasks measured the relevant underlying asymmetry. The octave illusion did not produce an overall ear bias for either handedness group and appeared to be the only task that was not lateralised, for the sample as a whole, in the battery.

For the tasks linked to the right hemisphere, the right-handers were, as a group, lateralised in the predicted direction on all tasks. Non-right-handers were, as a group, lateralised for colourscales, emoDL long, and emoDL short, but not for chimeric faces 1.0, chimeric faces 2.0, or the VHF face task. The predicted proportional differences, with increased typical biases for right-handers, were found for chimeric faces 2.0 and emoDL short, but not for chimeric faces 1.0, emoDL long, the VHF face task, or colourscales. A mean difference, with an increased average LI score for right-handers were found for chimeric 1.0, chimeric 2.0, emoDL short, but not for colourscales, emoDL long, or the VHF face task.

The three different language tasks produced slightly inconsistent results. Right-handers and non-right-handers were, as groups, lateralised as predicted for all three tasks. Significantly more right-handers, as compared to non-right-handers, had a REA on the CV dichotic listening task, and the right-handers also had a significantly higher mean LI. The VHF word task also yielded a difference in the proportions of right-handers and non-right-handers with a RFA favouring the right-handers, but there was no mean difference between the groups. For the lateral naming task, both groups were lateralised, but no mean or proportional difference were found in either RT or error scores. Additionally, lateral naming means and proportions were in the unpredicted directions, with more non-right-handers as compared to right-handers having a bias towards the RVF.

The results for the different language tasks are consistent with previous studies that did not find associations between different VHF and DL measures of language asymmetries (Boles, 2002; Bryden, 1965; Fennell et al., 1977; Hellige et al., 1994). One possibility is that the VHF tasks are poorer measures of asymmetries as compared to DL tasks. One reason may be that participants rarely fully fixate, unless their fixation is continuously monitored (Jordan, Patching, & Milner, 1998). It has been found that the laterality effects can be

increased and made more reliable if two different stimuli are presented simultaneously in each visual field as compared to the one visual field (Boles, 1987, 1990, 1994). However, this did not seem to apply to the current set of experiments, as the lateral naming task did not produce more robust LIs as compared to the VHF words task, which consisted of the single presentation of words. In fact, the VHF word task did produce proportional differences between the two handedness groups, whilst the lateral naming task did not.

It has been argued that it is crucial to include a sufficient number of trials for the reliability of laterality effects (Berenbaum & Harshman, 1980; Brysbaert & d'Ydewalle, 1990b; Hunter & Brysbaert, 2008). All tasks in the current battery were designed to have short administration times. Perhaps these short tasks are not sensitive enough to detect handedness differences in the visual domain. Behavioural experiments are inherently noisy due to a range of experimental factors such as lack of stimulus control, as well as factors relating to participant responses, such as lack of attention and development of strategies. Therefore, it is possible that noise in the data combined with a relatively small number of trials masks any underlying differences that may exist between the groups.

The CV dichotic listening task was the only language-related task that found a mean and proportional difference between the two handedness groups. Perhaps dichotic listening paradigms are more sensitive and less noisy as compared to VHF tasks. Voyer (1998) for example found that laterality effects, albeit modest, were most reliable when verbal in the auditory modality ($r = .7$) with CV pairs the highest ($r = .8$). Gadea, Gomez, and Espert (2000) also found test-retest for the standard non-forced condition of CV dichotic listening ($r = .8$), indicating temporal stability for the ear advantages. Dichotic listening has also been reported to predicts language dominance reliably, as measured with fMRI, using a small number of trials (Hughdahl, 2005; Hugdahl et al., 2009; Van der Haegen, Westerhausen, Hugdahl, & Brysbaert, 2013).

Sensitivity of these behavioural tests is still a concern. The effects are not as dramatic as the 15-20% difference suggested by Wada test data and other more direct measures such as neuroimaging. The group difference in CV dichotic listening is not large, only a 7% increase in prevalence of REAs in right-handers. This reduced sensitivity is not particularly unexpected, given intact interhemispheric communication (c.f. Springer & Gazzaniga, 1975), attentional biases in dichotic listening, noise introduced by subtle differences in hearing between ears, and so on. However, these data at least suggest that, despite their indirect assessment of the underlying asymmetry, they do capture some or most of the difference between right-handed and non-right-handed in terms of speech and language dependence on the left hemisphere. Of course, the fact that these differences are not seen for the other two language tasks does

not mean that the task(s) are not useful in predicting language dominance, on its own – perhaps in terms of the tails of the distributions – or as a part of a combination of different tests. This will be further examined in Chapter 4.

The results from the right hemisphere related tasks suggests that whilst a difference between right-handers and non-right-handers may be found for some functions, it may be the case that other functions do not differ between handedness groups. Colourscales suggest that the left-sided bias frequency does not differ between right-handed and non-right-handed samples, despite its' rather impressive breadth (~70% left sided bias). These data suggest that whatever function (or functions) that colourscales performance depends on is not complementary in nature to the typically obtained asymmetries in these handedness groups on speech and language functions (Carey & Johnstone, 2014). The working hypothesis is that some right hemispheric functions are not yoked to language in a type of complementary hemispheric fashion (see Bryden, 1990; Harms & Elias, 2014; Whitehouse & Bishop, 2009; reviewed recently by Badzakova-Trajkov, Corballis, & Häberling, 2016) that is often assumed in the handedness and cerebral asymmetries literature. However, first non-cerebral models that could account for a left-sided visual bias of the breadth seen in the task must be eliminated.

The most obvious explanation which does not depend on a right-hemisphere specialisation account is the attentional and/or scanning bias consequence of left to right reading in English. A life history of reading in a particular direction may lead to a scanning or attentional preference to the left (see Chung, Liu, & Hsiao, 2017, for evidence for very acute effects of reading on greyscales for Chinese people who can read in both directions). This concern has repeatedly been expressed for other behavioural asymmetries, including line bisection and face processing (e.g.; Chokron, Bernard, & Imbert, 1997; Sakhuja, Gupta, Singh, & Vaid, 1996; Vaid & Singh, 1989). Fortunately, this reading direction bias hypothesis can be addressed.

Nicholls and Roberts (2002) compared 20 English readers with 20 Hebrew-reading Israeli tourists on the greyscales task and a line bisection task. Although the mean greyscale LIs were numerically lower in the Hebrew readers, they were not significantly less left biased, on average, compared to the English readers. However, a later study did find that right to left readers show reduced breadth in the left bias for greyscales. Friedrich and Elias (2014) gave the task to 54 English readers and 43 Hebrew readers. In the left to right readers, the bias was found in 81% of the 53 right-handers with a directional bias. In the right to left sample, the left bias was present in 60% of the 42 right-handers who had a directional bias, suggesting that there is a reduced left-sided bias in participants who read in a right to left direction.

Nevertheless, reading direction is unlikely to completely account for the bias in English reading participants, at least on this evidence, as the majority of right to left readers are not right-biased on this task. This point has been made several times in other literatures on left-sided biases and reading direction (Fagard & Dahmen, 2003; Nicholls & Roberts, 2002; Rinaldi, Di Luca, Henik, & Girelli, 2014; Vaid & Singh, 1989). This is also strengthened by the fact that right field biases are obtained for the two VHF language measures. If reading direction causes a generalised bias to the left, then virtually any VHF study should result in a left-sided bias.

One puzzle about the colourscales findings is that the results differ from what would be expected given the neuroimaging study by Cai and colleagues (2013) which provides strong support for complementary hemispheric specialisation of language and attentional functions, in non-right-handers, at least. As discussed in Chapter 1, there is more evidence from landmark tasks using both fMRI and fTCD that diverges from the findings of Cai et al. (e.g. Badzakova-Trajkov et al., 2010; Rosch et al., 2012; Whitehouse & Bishop, 2009; Zago et al., 2016). Of course, it is unknown whether or not any underlying mechanisms driving colourscale left-sided biases are shared with whatever participants 'use' when they perform the landmark task, but most neuroimaging and fTCD results are consistent with the suggestion that at least *some* attentional functions do not differ in breadth in right-handers and non-right-handers.

One task that did produce differences between the handedness groups was the chimeric face task. This difference is seen in both the first and second versions and supports previous studies that suggest that right hemispheric face processing is less prevalent in non-right-handed samples (David, 1989; Gilbert & Bakan, 1973; Heller & Levy, 1981; Levy et al., 1983; Roszkowski & Snelbecker, 1982). Interestingly, the two chimeric face tasks, and VHF face task are the only three studies in which non-right-handers show no average lateralised performance in. However, there were no differences between right-handers and non-right-handers in the VHF face task. This discrepancy may be down to methodological differences in the tasks. One possibility is that there is, in some sense, more control over participant behaviour in chimeric face tasks, as it is forced choice between two alternatives. In VHF tasks participants are asked to fixate, but without eye tracking, there is no guarantee that all participant do so properly on the majority of what was a fairly small number of trials. There was, however, an effect in the predicted direction of handedness group difference in the VHF words task, so perhaps the limitation has something to do with the stimuli used in the face task.

Behavioural asymmetry estimates might lack sufficient sensitivity to provide accurate proportions of typical and atypical cerebral dominance for any lateralised function.

Nevertheless, the chimeric face data are at the very least suggestive; a reduced prevalence of left side bias in the non-right-handers. It may be a coincidence, but language and face processing are the only two functional domains that are explicitly hypothesised to be complementary to one another in current accounts (Behrmann & Plaut, 2015; Centanni et al., 2018; Dehaene et al., 2010). Nonetheless, the results from both chimeric face tasks are encouraging for the notion that right-handers and non-right-handers may lateralise differently for face processing.

The evidence for emotional prosody through dichotic listening is somewhat less convincing. In the long version of emoDL, numerically more non-right-handers, as compared to right-handers, had a bias to the left ear, against expectations. In the short version, a difference of 11% in the predicted direction was found for the handedness groups, and the confidence intervals around this estimate did not overlap with zero. Neuroimaging studies of prosody have focused exclusively on right-handed participants, and so cannot to date speak to a potential difference between right-handers and non-right-handers. Chapter 3 focuses on quantifying the depth and breadth of prosody asymmetry measured by fMRI in both right- and non-right-handed individuals with known cerebral dominance for language. These data might speak to difference in prosody asymmetry between handedness groups.

In conclusion, some evidence is suggestive of complementarity with language asymmetry, for example, face processing and, less convincingly, processing of emotional prosody. Of course, drawing such conclusions from behavioural data alone must be made with caution. Fortunately, the opportunity to explore some of these questions with somewhat more direct measures of asymmetry in individuals was possible. The next chapter is the subject of these preliminary, albeit extensive, set of investigations.

CHAPTER 3

Functional asymmetries in right-handers and non-right-handers

3.1.1 Introduction

Advances in cognitive neuroscience allow for inferences to be made about neural processes in vivo in healthy individuals. There is now a wealth of neuroimaging research which has suggested asymmetrical neural networks underlining face processing, emotional processing and body processing (confirming many such assertions from patient-based neuropsychology). However, neuroimaging research designed to understand cerebral asymmetries in individual people is still relatively rare. Most work on individual differences is still limited to attempts of evaluating the ability of fMRI to determine hemispheric dominance for language in individuals (Rutten, Ramsey, van Rijen, Alpherts, & van Veelen, 2002; Spreer et al., 2002). Largely, this literature involves analysing concordance between functional imaging data and data from the Wada test (e.g. Binder et al., 1996; Deblaere et al., 2004; Sabsevitz et al., 2003; Janecek et al., 2013), and is not designed or intended to explore the underlying asymmetry in the individuals per se. The aim of the current chapter is to examine incidence of hemispheric dominance in cerebral asymmetries related to right hemisphere processing for five different functions: emotional prosody, emotional vocalisations, neutral faces, emotional faces and bodies. Surprisingly, non-right-handers are remarkably absent from previous experiments, a gap which this chapter is designed to address.

3.1.2 Emotional Prosody

Speech prosody provides a wealth of information from the speech stream beyond the semantic meaning of words. For example, whether someone is perceived as happy or sad is greatly reliant on the sound of their voice. This kind of voice modulation has been referred to as ‘emotional’ or ‘affective’ prosody (Monrad-Krohn, 1947). Numerous studies suggest remarkable accuracy in identifying a variety of emotions, such as anger, happiness, fear, and sadness, from vocal qualities of speech (for a meta-analysis see Juslin & Laukka, 2003). However, relative to linguistic aspects of speech, the neural underpinnings of this ability to comprehend prosodic emotional signals are rather understudied (Paulmann, 2016).

Crucially, in contrast to the left hemisphere superiority for speech and language, emotional prosody is thought to be lateralised to the right hemisphere. This right hemisphere bias was first implicated by studies in behavioural neurology, where it was often found that right hemisphere lesions resulted in more severe impairments of emotional prosody recognition and expression, in comparison to left hemisphere lesions.

Imaging studies that have examined perception of emotional prosody, by contrasting emotional prosody with neutral prosody, tend to report right-lateralised activation in the superior temporal cortex (Bach et al., 2008; Beacousin et al., 2006; Buchanan et al., 2000; Ethofer, Van De Ville, Scherer, & Vuilleumier, 2009; Grandjean et al., 2005; Mitchell, Elliott, Barry, Cruttenden, & Woodruff, 2003; Wiethoff et al., 2008; Wildgruber et al., 2002, 2005; Zhang, Zhou, & Yuan, 2018), and bilateral or right-lateralised activation in frontal cortices (Bach et al., 2008; Buchanan et al., 2000; George et al., 1996; Kotz et al., 2003; Imaizumi et al., 1997; Mitchell et al., 2003; Wildgruber et al., 2002, 2004, 2005). Some studies also report subcortical activation in the basal ganglia (Kotz et al., 2003; Morris, Scott, & Dolan, 1999; Pell & Leonard, 2003; Wittforth et al., 2010), amygdala (Ethofer et al., Vuilleumier, 2009; Sander et al., 2005), and insula (Bach et al., 2008; Ethofer et al., 2009; Imaizumi et al., 1997; Wildgruber et al., 2002, 2004). Note that all of the studies presented in this chapter, if not otherwise stated, compare the extent of cluster sizes and/or t-values in grouped-averaged activations using threshold-dependent data. Statistical tests comparing activation in the two hemispheres are rarely performed, and comments about hemispheric differences are mainly based on trends in the data alone.

One of the more consistent findings is greater activation in the right, compared to left, superior temporal cortex. For example, Ethofer and colleagues (2012) contrasted emotional prosody (angry, sad joyful, relieved) with neutral prosody for pseudo-sentences in 22 right-handed participants, judging the sex of the speaker. They found that both left and right superior temporal gyrus (STG), posterolateral to the primary auditory cortex, were activated, but with increased activation for both statistical strength and extent in the right hemisphere. The greater involvement of the right hemisphere is further supported by a meta-analysis by Witteman, Van Heuven, and Schiller (2012). They examined 16 studies where emotional prosody had been compared to neutral prosody or synthesised speech devoid of prosody. When examining laterality effects in these studies, by flipping the data around the x-axis and comparing activation in the two hemispheres, the one surviving cluster that was significantly lateralised was found in the right Heschl's gyri at a lenient threshold (uncorrected at $p = .05$), although no differences between the hemispheres were found at more conservative thresholds.

Beacousin et al. (2006) also examined emotional prosody processing in 23 right-handed participants. What is rare about this study is that *all participants* had confirmed leftward language asymmetry, assessed in a separate task. They used sentences spoken in emotional prosody, contrasted with a text-to-speech program that produced the same sentences from naturally spoken syllables lacking in any prosodic contour. Contrasting emotional prosody with neutral prosody activated bilateral anterior STG, right posterior STG, bilateral precentral gyri, right supplementary motor area (SMA) and subcortical structures, including bilateral amygdala, putamen and hippocampal gyri. Hemispheric asymmetries were evaluated by computing asymmetrical contrast maps. This procedure required the subtraction of individual flipped contrast maps in their x axis, with their corresponding non-flipped maps, entered into a group analysis. This comparison was confined to the temporal lobes only. Two significant clusters were found: one in the right anterior superior temporal sulcus (STS), that closely matched the temporal voice area (TVA; Belin Zatorre, Lafaille, Ahad, & Pike, 2000), and one in the right posterior STG. Unfortunately, data from individual participants was not reported in this study, so it is unknown how many individuals that showed lateralised activity to the right hemisphere.

All the studies examining emotional prosody to date present results from threshold dependent averaged data (asymmetries may change depending on the chosen threshold - see General Introduction, pages 18-20). *None* of these experiments provide data on the number of imaged participants who showed right, left or no hemispheric bias. The lack of these data is understandable, given the focus in neuroimaging on group-averaged data. Differences between participants therefore tend to fade amongst these average values and are treated as noise, rather as being interpreted in a meaningful way (Kanai & Rees, 2011). Furthermore, these studies are all restricted to samples of right-handers.

In summary, the neuroimaging data to date confirms suspicions from neuropsychology and neurology of a right hemispheric specialisation for some aspects of emotional prosody processing (some even argue for a role of this hemisphere in linguistic prosody, see Friederici, 2017, for discussion). What they cannot speak to, given their chosen analytical strategy, is the frequency of this specialisation in right-handers, for whom 90-95% should be more 'left hemispheric' for non-prosodic aspects of speech and language processing. It would be tempting to assume that these individuals process prosody more in their right hemisphere, if prosody *anti-localises* with language.

3.1.3 Emotional Vocalisations

One disadvantage with using speech in neuroimaging studies of emotional prosody is that it contains semantic information, which may interfere or facilitate the listener's judgment of the emotional tone of the speech (Ben-David, Multani, Shakuf, Rudzicz, & van Lieshout, 2016; Kim & Sumner, 2017; Kotz & Paulmann, 2011). One method to avoid this limitation is to use pseudo-speech (nonsense words and/or sentences, e.g., Banse & Scherer, 1996; Grandjean et al., 2005; Price et al., 1996; Sander et al., 2005). However, it has also been found that unintelligible speech activates perisylvian semantic areas of the left hemisphere (Meyer et al., 2002). The typical interpretation of this finding is that left lateralised speech perception mechanisms are modular in nature and will be utilised to attempt to process any speech-like signal if it is sufficiently structured. In any case, this stimulus type may not be optimal for detecting right hemispheric contributions to the prosodic elements of the signal, per se. A promising alternative is to examine paralinguistic emotional expressions with purely emotive non-verbal vocalisations like sobs, laughter, or screams (Frühholz & Grandjean, 2013). In fact, information gathered from these signals may be just as valuable for the listener as knowledge gathered from speech or speech-related vocal phenomenon such as emotional prosody.

Non-verbal emotional expressions have many acoustic features in common with emotional prosody in speech streams (Banse & Scherer, 1996; Patel et al., 2011), and listeners rapidly perceive and infer the emotional state of the speaker (Sauter & Eimer, 2009; Sauter, Eisner, Ekman, & Scott, 2010). Emotional vocalisations, like emotional prosody, elicit responses in mid to superior temporal regions (Cervolo, Frühholz, & Grandjean, 2016; Fecteau, Belin, Joanette, Armony, 2007; Joly, 2012; Meyer, Zysset, Von Cramon, & Alter, 2005; Phillips et al., 1998), as well as subcortical regions like thalamus and amygdala (Bestelmeyer, Maurage, Rouger, Latinus, & Belin, 2014; Phillips et al., 1998; Sander & Scheich, 2001).

Meyer et al. (2005) recruited 12 right-handed participants for a passive listening fMRI experiment where they compared laughter with speech (short sentences such as 'Peter sleeps') or sounds (non-vocal sounds). When laughter was compared with speech, activation was found in the right precentral gyrus, right planum temporale, right Heschl's gyrus, and STG in the left hemisphere. When compared with sounds, activation could be seen in the right STG including the primary auditory cortex, and right fusiform gyrus. Fecteau and colleagues (2007) contrasted emotional vocalisations with neutral vocalisations such as coughs and throat clearings whilst asking participants to judge the gender of the speaker in 14 right-handed participants. They reported increased activity in left middle STG, right middle STS, right

anterior STG, bilateral amygdala, left and right primary auditory cortex, with the strongest activation clusters in right primary auditory and right middle STS.

In summary, this small literature suggests that emotional vocalisations, such as cries or sobs, are right lateralised in a fashion that is similar to what is seen for emotional prosody. These two types of stimuli have yet to be compared in the same participants in terms of their lateralisation. In fact, this type of comparison is potentially of use in evaluating claims about the right hemisphere's role in emotional processing, rather than more specific modality- or stimulus-category claims. This kind of question can also be asked about the better documented right hemispheric dominance for face processing.

3.1.4 Face perception

There are several well-defined cortical regions that generate stronger neural responses to faces compared with various control stimuli. These regions, arguably, form a network that is specialised for face processing. This network has been subdivided into a core and an extended system (Haxby, Hoffman, & Gobbini, 2000; Ishai, 2008), with core regions found in the inferior occipital cortex (occipital face area, OFA), the fusiform gyrus (the fusiform face area, FFA) and the posterior part of the superior temporal sulcus (pSTS).

The first (and one of very few, in fact) data that describes the depth (i.e. frequency) of a right hemisphere bias for faces using neuroimaging came from Kanwisher and colleagues (1997). It was the first study to describe the fusiform face area, and noted that five out of ten right-handed participants only showed significant activation in the right FFA, whilst the rest had bilateral activation patterns. This result supported the right hemispheric dominance for face perception already characterized in the prosopagnosia literature (Benton, 1990; De Renzi et al., 1994; Sergent & Villemure, 1989; Wada & Yamamoto, 2001).

In fact, the tendency for face activations to be right-lateralised *at a group level in right-handed participants* is well established (e.g. Rossion, Hanseeuw, & Dricot, 2012; Cabeza & Nyberg, 1997, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Haxby et al., 1999; Ishai, Schmidt, & Boesiger, 2005; McCarthy, Puce, Gore, & Allison, 1997), although it is rarely discussed. Authors often mention a greater proportion of significant voxels and/ or higher t-values in the right hemisphere (eg. Davies-Thompson & Andrews, 2012; Rossion, 2012; Rossion et al., 2012; Ishai et al., 2005), but rarely compare the hemispheres explicitly.

For example, Dien (2009) noted that only seven out of over 100 published studies had compared the lateralisation of the FFA using any kind of statistical test. Some research groups also restrict examination to face selective regions in the right hemisphere because 'previous studies have reported that face selective regions in the right hemisphere are more consistently

activated than those in the left hemisphere' (Zhang et al., 2016, p. 79). Nonetheless, as activation patterns are commonly reported in tables, group level lateralisation effects can be calculated from thresholded data. Dien (2009) went on to review FFA activation described in 59 published studies comparing static neutral faces versus a control and found that 51 of these reported greater right hemisphere activation and 8 reported greater left hemisphere activation. This finding supports that the FFA, at least, seems to be relatively right lateralised in groups of right-handed participants.

Though this finding provides evidence for group-level right hemispheric superiority, it does not provide evidence on frequency (or magnitude) of individual participants' dominance. This lack is not a consequence of weak signal, for example requiring grouped data to reveal an FFA. Most experts agree that the FFA, at least, can be localised in almost every individual person, even with short simple face localiser paradigms (Kanwisher & Yovel, 2006). Rossion, Hanseeuw, and Dricot (2012), for example, are one of few who reports individual activation patterns for 40 right-handers with statistically significant activation in a pre-determined region of interest defining the FFA. Thirty-six out of the 40 participants had a significant right hemisphere activation and were included for analysis. Of these, 31 also had significant left hemisphere activation. Unfortunately, these data do not reveal how many of the participants had stronger activation in one hemisphere over the other, per se. Furthermore, significant activation of the right FFA was used as an inclusion criterion for the analysis. It is not clear in this paper if any of the excluded participants instead showed left FFA activation above threshold.

Frequency data on greater activation in one hemisphere or the other, in right-handers, is not readily available. Such data alone (i.e. even without measures of speech/language dominance) could be extremely useful for models of complementary hemispheric specialisation. Most studies on face perception are restricted to right-handed participants, however, in contrary to the prosody and vocalisation literature, some evidence from non-right-handers on face processing asymmetry does exist. In the early study from Kanwisher and colleagues (1997), two non-right-handed participants were included; one which showed bilateral FFA activation and one with greater activity in the left FFA. Willems, Peelen, and Hagoort (2010) also examined FFA activation in 16 right-handed and 16 non-right-handed participants. They compared number of activated voxels in their ROIs (9mm spheres using the local maxima reported in previous literature as the mid-point). They found that the FFA was right lateralised in the right-handed group, but not lateralised in the non-right-handed group. Unfortunately, this study does not mention individual lateralisation patterns, or the language dominance of individual participants.

Bukowski, Dricot, Hanseeuw, and Rossion (2013) did examine individual patterns of face processing in 11 non-right-handed participants using FFA, OFA and pSTS as ROIs in both hemispheres, as well as conducting a whole-brain analysis. They also compared the number of significant voxels for their analyses using thresholded data. In the whole-brain averaged activation maps, 62% of the statistically significant activation was present in the right hemisphere, suggesting an overall right hemisphere superiority at the group level. However, when examining individual patterns for their ROIs, all regions were found to be right lateralised, except for FFA which was only right hemisphere dominant in 27% (n = 3) of the non-right-handers, whilst 3 individuals had bilateral activation (bilateral at the individual level was defined as when the proportion of voxels in each hemisphere was between 45% and 55% of one another) and 5 left hemispheric. The FFA was also the only region that differed in a comparison to a separate sample of 40 right-handers tested on the same task in a previous study (Rossion et al., 2012; 72% of right-handers were lateralised to the right hemisphere for FFA but otherwise very similar for the other ROIs, see Figure 3.1). There was no difference between lateralisation patterns when comparing whole-brain activation (73% of left-handers versus 75% of right-handers were right lateralised). They conclude that some non-right-handers may not have the same competition of word and face representation in left FFA, leading to increased face localised activity in this region (Bukowski et al., 2013). Of course, in a sample of 11 individuals, statistically perhaps one person might have been atypical for language. At best one could consider these findings as preliminary.

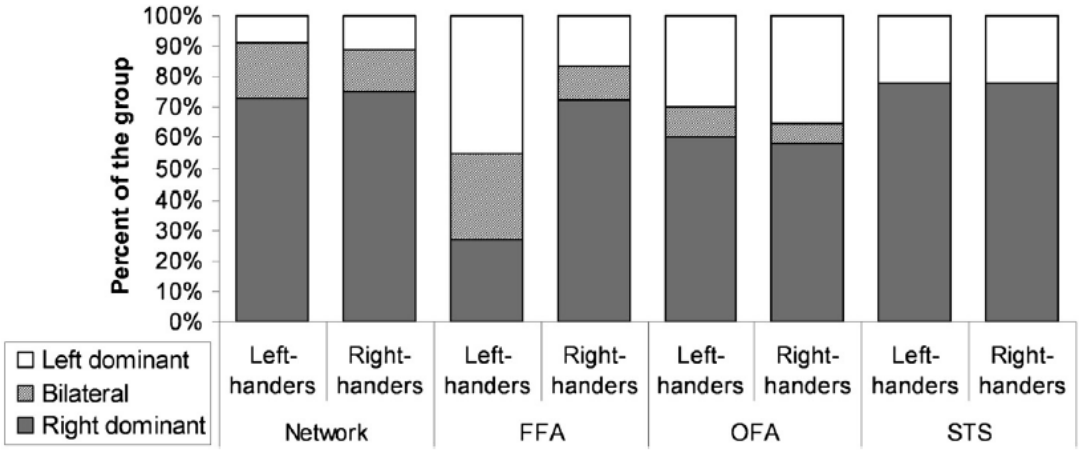


Figure 3.1. Proportions of non-right-handed and right-handed participants with more right, left, or bilateral activations in different regions in the face perception network in Bukowski et al. (2013) and Rossion et al. (2012). 'Network' refers to the whole-brain analysis. It should be noted that these proportion graphs, with no estimate of variance, might be misleading with a sample of n = 11. Reprinted from Bukowski et al. (2013).

To summarise, both the study from Willems et al. (2010) and Bukowski et al. (2013) claim that FFA is not as consistently lateralised in non-right-handers as compared to right-handers, unfortunately, the relationship between face processing and language processing is not addressed.

There are a lack of data that addresses the question of complementarity of face processing and language processing in right-handers and non-right-handers. This absence of data is surprising considering the theories regarding the direct relationship between vVFA and FFA (discussed in more detail in Chapter 1). There is only one neuroimaging study to date that investigated faces processing and language processing in both handedness groups. Sadly, this study only had a small number of individuals with language lateralised to the right hemisphere, as these individuals are very hard to find. Badzakova-Trajkov and colleagues (2010) used a verbal fluency task to examine language processing, and a face task consisting of videoclips of faces making emotional expressions, using moving non-biological objects as the control task, in the same individuals. They used the LI toolbox to avoid thresholding confounds and used the entire temporal lobes (frontal lobes for word generation) when examining face related activity, a less stringent mask than the ROIs used by Bukowski et al. (2013) and Willems et al. (2010). Their sample consisted of 52 right-handers and 33 non-right-handers, and of these, 94% of right-handers and 73% of non-right-handers were right hemisphere dominant for faces. They also found a weak, but significant, negative correlation between face dominance and language dominance (r = -.34). Their conclusion from these provocative data is interesting, but somewhat surprising. Rather than refer to the left hemispheric superiority for speech and language processing per se, they focus on a little known claim for left-hemispheric bias in the processing of facial speech movements (Smeele, Massaro, Cohen, & Sittig, 2004). They concluded that this right-hemispheric bias of emotional expressions implied a complementary relation with processing of facial speech movements (Smeele et al., 2004). Interestingly, there is no evidence to suggest that biases of processing facial speech movements are related to speech/language, which was measured in their verbal fluency task.

In fact, their data allows for a more direct test of the relationship between face and language asymmetry than they actually provide. Their study identified 9 participants with language lateralised to the right hemisphere (7 non-right-handed and 2 right-handed). If language and face processing is complementary, these individuals should process faces preferentially in their left hemisphere. Fortunately, they included their data as supplementary material, thus this question of anti-localising patterns in language atypically lateralised individuals can be addressed. Irrespective of hand preference, of individuals that were left

lateralised for language, 90% were right lateralised for face processing. When considering those who were right lateralised for language, right hemispheric processing was reduced to 56% (thus 44% of the participants were complementary lateralised). Although this is a significant reduction (z = -2.76, p = .003), language atypical participants did not show a reversed asymmetry for faces in this small sample. With a small number of language atypicals, the confidence in this particular estimate of complementarity is limited, with 95% CIs of right hemispheric rates ranging from 80.6% to 94.6% for language typicals, and 26.7% to 81.1% for the language atypicals. Of course, these authors also opted to use dynamic emotional faces as their face expression, which may elicit responses slightly different to those of neutral faces.

3.1.5 Emotional face perception

As in the auditory modality, emotional facial perception has traditionally been linked with right hemisphere specialisation, mostly from early work with unilateral brain damage (for recognising and/or producing facial emotional expressions, e.g. Benowitz et al., 1983; Blonder, Burns, Bowers, Moore, & Heilman, 1993; Borod, Koff, Lorch, & Nicholas, 1986; Bowers, Bauer, Coslett, & Heilman, 1985; DeKosky, Heilman, Bowers, & Valenstein, 1980; Mandal, Asthana, & Tandon, 1993). For example, Borod and colleagues (1985) found that patients with right hemisphere damage had deficits in in both perception and expression of facial emotion, which was not found in individuals with left hemisphere damage or healthy controls. Similarly, anesthetising the right hemisphere makes patients judge facial emotional expressions as less intense as compared to when the left hemisphere is anesthetised (Ahern et al., 1991). As such, clinical data implicate the right hemisphere in facial emotion perception.

Unfortunately, to confuse the issue somewhat, a surprisingly large literature claims that the two hemispheres preferentially process different types of emotions (Reuter-Lorenz & Davidson, 1981; Reuter-Lorenz, Givis, & Moscovitch, 1983; Rodway, Wright, & Hardie, 2003; Natale, Gur, & Gur, 1983). This ‘valence’ theory proposes that emotional processing is depending on valence, with negative emotions processed in the right hemisphere and positive emotions in the left hemisphere (Ahern & Schwartz, 1979; Reuter-Lorenz & Davidson, 1981), whilst the ‘right hemisphere’ theory proposes that the right hemisphere have a dominant role in the processing of all emotions (Bourne 2010; Bourne & Maxwell, 2010; Gainotti, 1972; Levy et al., 1983).

The hemispheric processing of faces displaying emotional expressions has more recently been explored in healthy individuals using neuroimaging techniques. fMRI studies of emotional face processing typically contrast the emotional face with a neutral stimulus, such

as an unexpressive face, or neutral scene, in order to specifically examine the neural underpinnings of the emotional process(es). Due to the links to the right hemisphere in both the face domain and emotional processing domain it may not be unreasonable to assume that emotional face perception would elicit even greater responses from the right hemisphere as compared to neutral faces if the right hemisphere plays a dominant role in both types of processing. Emotional faces have, for example, been found to activate traditional face selective areas such as the fusiform gyrus and STS, even when neutral faces are used as the comparison condition (Furl, Henson, Friston, & Calder, 2013; Morris et al., 1998; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Vuilleumier, Armony, Driver, & Dolan, 2001; Vuilleumier, & Pourtois, 2007). Additionally, emotional faces are found to activate regions such as the amygdala (especially the left amygdala with fearful faces), cingulate gyrus, right orbitofrontal cortex, somatosensory and insula cortex (Blair, Morris, Frith, Perrett, & Dolan, 1999; Dolan et al., 1996; O'Doherty et al., 2003).

There is at least some support for right hemisphere lateralisation of emotional face processing from neuroimaging studies. Narumoto, Okada, Sadato, Fukui, and Yonekura (2001) found that emotional faces resulted in right lateralised activity in the STS, as compared to neutral faces, in 12 right-handed participants. Kesler/West et al. (2001) also found right lateralised STS activity in a sample of 21 right-handed participants. Engell and Haxby (2007) found that emotional faces, compared to neutral faces, activated STS and occipital lobe bilaterally, with right lateralised activity in the IFG in a sample of 12 right-handed participants.

In contrast, a more recent fMRI study by Beraha et al. (2012) did not find evidence for a right hemisphere superiority for emotional face processing. Instead, they found that the lateralisation of different emotional categories differed between different structures; positive stimulus processing was lateralised towards the left in the medial prefrontal cortex, but towards the right in the premotor cortex and temporo-occipital junction. Instead, negative stimulus processing was lateralised towards the left in the amygdala, uncus, and middle temporal gyrus, and lateralised towards the right in the dorsolateral prefrontal cortex (extending to the premotor cortex) and the temporo-parietal junction. Here they found support for the valence theory, but in prefrontal cortical areas only.

A couple of meta-analyses have tried to consolidate the literature in terms of hemispheric specialisation. Wager (2003) meta-analysed 65 PET and fMRI studies focusing on the effects of emotional valence on regional brain activations, with particular emphasis on hypotheses concerning lateralisation of brain function in emotion. No overall differences between hemispheres was found, thus, finding no support for a right hemisphere superiority or valence hypothesis. Left lateralisation was found in some brain structures, and right lateralisation in

others. Fusar-Poli et al. (2009) also meta-analysed neuroimaging studies of facial emotion but failed to support either the right hemisphere or the valence hypothesis. These meta-analyses indicate that the right-hemisphere effects may be smaller than some of the studies above suggest. It is, however, worth noting that both of these meta-analyses included a variety of different emotional tasks, such as static faces and videoclips of facial expressions, with a variety of different control conditions. It is also not clear how many of these studies involved passive viewing or if participants were asked to perform some type of task whilst viewing the stimuli. Thus, the unclear results may be confounded by both methodological and experimental factors, and to the verbal or nonverbal nature of the stimuli used in the different experiments. It would be useful to separately meta-analyse studies which did not require explicit judgment about the stimuli presented, such as passive viewing or n-back tasks. In conclusion, although there is some evidence for right lateralisation, it does not seem to be as robust as for the other stimulus types presented in this chapter.

3.1.6 Body perception

Similar to faces, there are distinct cortical regions that responds preferentially to bodies. One of these is located in the lateral occipitotemporal cortex, and was first described by Downing and colleagues (2001). They conducted a series of studies comparing human bodies and body parts with a variety of visual control stimuli, such as objects, mammals, faces and scenes. It was found that human bodies and body parts preferentially activated an area in the lateral occipitotemporal cortex they referred to as the extrastriate body area (EBA). The EBA was found to be activated in the right hemisphere in all 19 participants that were scanned, with a majority of these showing a significant, but weaker, activation in the left hemisphere.

The lateralisation of body selective activity is generally accepted but not well characterized, and it is common practise in the literature to only define and report data obtained from ROIs in the right hemisphere (e.g. Peelen, Glaser, Vuilleumier, & Eliez, 2009; Schwarzlose, Baker, & Kanwisher, 2005; Taylor, Wiggett, & Downing, 2007). For example, Downing and colleagues justify this exclusion of the left hemisphere as ‘only right-hemisphere FBA was examined because significant body selective activity in the left fusiform gyrus is rare’ (Taylor et al., 2007, pp. 1628), of course, indicating a lack of symmetry. Out of papers that do report activation from both hemispheres, a rightward asymmetry for the EBA (Bracci, Ietswaart, Peelen, & Cavina-Pratesi, 2010; Downing, Chan, Peelen, Dodds, & Kanwisher, 2005; Downing, Wiggett, & Peelen, 2007), FBA (Peelen & Downing, 2005) or whole-brain analysis (Greven, Downing, & Ramsey, 2018, supplementary materials) can sometimes be inferred from tables of group activations, or supplementary materials.

Aleong and Paus (2009) is one of the few papers which explicitly examined the lateralisation of body selective areas, measured as percent signal change for bodies as compared to scrambled bodies. They found a greater response in the right EBA and FBA compared to the left, but only in women and not men. This response was characterised by an increase of right hemisphere activity in females and a surprising absence of asymmetry in male participants, However, it is worth noting that this study has a sample size of nine participants in each gender group.

Only one study has included a group of non-right-handed participants using bodies as stimuli in fMRI. In addition to the face areas previously discussed, Willems et al. (2009) localised body selective responses in EBA and FBA using ROIs (9mm^3 sphere) based on local maxima in both hemispheres from previous literature using chairs as the control contrast. They found that the EBA was lateralised in both handedness groups, but the FBA was only lateralised in the right-handed group. Thus, they found evidence to suggest that both FFA and FBA were not lateralised in the non-right-handed group. Again, this study relies on activation patterns from thresholded data. No study to date has examined body-related processing using a technique like the threshold-independent one utilised by the LI toolbox. Furthermore, it would have been interesting to see if lateralisation patterns for body processing and face processing were linked in individual participants (such a linkage might have implications for the models of complementary hemispheric specialisation that link face and vWFA asymmetry). No one has examined if right hemisphere processing for bodies goes hand in hand with right hemisphere processing for faces, or if these asymmetries are complementary to language processing.

3.1.7 Outstanding questions

Averaging data across non-right-handed samples, where the variability between participants' underlying cortical organisation (for language at least) is higher than within right-handed samples, is a common weakness in laterality research, especially when coupled with the relatively low sample sizes typical of neuroimaging research. An even more serious limitation of averaging, in non-right-handed groups, in particular, is the ambiguity regarding a reduced asymmetry. As discussed previously, weakened asymmetries in *most* non-right-handers participants (relative to the right-handers) would have quite a different interpretation than if the reduction is accounted for by a *small subgroup of non-right-handers with reversed* asymmetries. This distinction is of crucial importance. What is needed is frequency data in right-handed and non-right-handed samples.

In this chapter, cerebral asymmetries for emotional prosody, emotional vocalisations, neutral and emotional faces, and bodies are explored. These asymmetries are thought to

depend more on the right hemisphere in right-handed samples, and are either unknown or hypothesised to be reduced in non-right-handers. Furthermore, the argument regarding 'complementary hemispheric specialisation', the idea that the lateralisation of one function is determined/dependent on the lateralisation of another (eg. Cai et al., 2013), is largely unexplored for all these asymmetries (bar the one study by Badzakova-Trajkov et al., 2010, on face processing and language). Distinct lateralised functions are often investigated in isolation, if investigated at all. One lateralised function that we know is dominant to the left hemisphere in most, but not all, individuals is speech/language (Carey & Johnstone, 2014). Individuals with right hemisphere (atypical) language processing enable examination of the possible relationship between dominance for language and functions that normally depend on the right hemisphere. These individuals should show the reversed relationship if complementarity is assumed. Furthermore, right-handed and non-right-handed participants that have confirmed leftward asymmetry for language should for the majority, be right hemispheric for these functions, for strong evidence of complete complementarity. Non-right-handed language typicals should show similar breadth and depth as the right-handed typicals if these functions are related to language, but not handedness per se. The objectives of the current chapter were therefore to:

1) Examine how often (i.e. the breadth) and the average degree (the depth) of the asymmetry for several hypothesised right hemispheric functions in right-handed and non-right-handed participants with known hemispheric dominance for speech/language.
2) Examine for the presence of reduced average asymmetry in non-right-handers, controlling for the confounding effects of reversed language dominance in a proportion of this group.
3) Examine if the language atypical participants show reversed asymmetry for what are typically right hemispheric functions. Furthermore, the breadth of asymmetry favouring their non language dominant hemisphere should be similar in magnitude to the breadth of asymmetry seen in language typical right-handers and language-typical non-right-handers.

The working hypothesis for these experiments was that the direction of typical asymmetries would be reversed in language atypical participants, based on if these functions are related to language in a complementary fashion. If this is not the case, there is evidence for independence of functions.

3.2 Methods

3.2.1 Participants

Sixty-nine individuals took part in the experiment. The data from one right-handed participant was removed before data analysis as they failed to understand the task instructions. Thus, there were 68 participants in total; 24 males (M_{age} = 23.88, *SD* = 6.09) and 44 females (M_{age} = 24.80, *SD* = 7.03). All participants had normal or corrected to normal vision, and normal hearing. Hand preference, as assessed by the modified version of the WHQ (Steenhuis & Bryden, 1989), was +28.25 (*SD* = 1.80) for the right-handers, and -23.20 (*SD* = 11.82) for non-right-handers.

The participants were students and staff members from Bangor University, recruited opportunistically and via a student participation panel. Participants were either compensated with course credit or £10 for their time. Informed consent was obtained from all individuals and the study protocol was approved by the local Psychology Ethics and Research Committee and the Bangor Imaging Unit committee. Although anyone enrolled in the student participation panel who had taken part in the perceptual test battery was eligible to take part, the final sample is not entirely random. Eleven participants who had been identified as right hemisphere dominant for a verbal fluency task in a previous fMRI study in the lab were scanned as part of this experiment. Individuals with a strongly left-sided behavioural profile, including a left ear preference on the behavioural CV dichotic listening task, were actively invited as they are more likely to be right lateralised for language (Carey, Karlsson, & Johnstone, unpublished study; Knecht et al., 2000). In total, 5 non-right-handed participants (not obtained from the previous neuroimaging study) were scanned based on their behavioural profile.

3.2.2 fMRI Paradigms

3.2.2.1 Auditory Emotions localiser.

A five-condition localiser was used to identify activated areas whilst hearing emotional prosody and emotional vocalisations. The experiment consisted of auditory stimuli presented in a blocked design.

3.2.2.1.1 Stimuli.

3.2.2.1.1.1 Emotional and neutral spoken words.

Words in neutral and emotional prosody were selected from the same recordings as described in Chapter 2 (see page 36). In order to avoid using rhyming words when possible,

as these have shown to produce increased left hemisphere activity as compared to non-rhyming words (Baciu et al., 2005; Cousin et al., 2007; Lurito, Kareken, Lowe, Chen, & Mathews, 2000; Niskanen et al., 2012), an additional 240 sound files conveying anger, fear, sadness and happiness were validated from the same four speakers, but using different words (see below), in an additional sample of 10 independent raters (6 female, 4 male). Words were included if one emotion per actress and per word was recognisable 80% of time. The final set of words were: ball, call, kit, pan, and tar. For the neutral prosody condition, one set of each word from each actress were used (20 stimuli in total). For the emotional prosody condition, stimuli were paired so that each word was presented in each emotional tone (anger, fear, sadness, happiness). The stimuli were counterbalanced so that each of the actresses were heard expressing each of the words and each of the emotional tones, with one emotional tone presented by each of the actresses twice (as four emotional tones were used from five actresses). A total of 20 unique stimuli were used for this condition.

3.2.2.1.1.2 Emotional vocalisations.

Recordings of emotional vocalisations were taken from the Montreal Affective Voices database (Belin, Fillion-Bilodeau, & Gosselin, 2008), in which actors and actresses were instructed to produce emotional outbursts using the vowel /a/. Expressions of anger, fear sadness, and happiness were used; one emotional expression each from five identities (all female), resulting in a total of 20 stimuli.

3.2.2.1.1.3 Neutral vocalisations.

Voices from five identities (all female) expressing coughs, sneezes, hiccups, and throat clearings and were recorded in a sound-insulated booth in the School of Psychology, Bangor University. The words were recorded using a Rode NT-1 microphone, Yamaha mixer (MG124c) using a PC with a high-quality sound card (M-audio delta 1010) using Cool Edit Pro 2.0 (Cool Edit Pro 2002, version 2.0 Syntrillium Software Corporation, Phoenix, Arizona, USA). Sound files were recorded using one channel (mono) at 16-bit resolution and a 44.1 kHz sampling rate. The stimuli were recorded in four separate recording sessions and were edited into separate sound files using Cool Edit Pro 2.0. One sample of each vocalisation from each actress was used (20 stimuli in total).

3.2.2.1.1.4 Non-words.

Voices from four new identities (all female) were recorded in a sound-insulated booth in the School of Psychology, Bangor University. The recording and editing procedures were the

same as that described above for neutral vocalisations. Non-words were created using the pseudo-word generator Wuggy (Keuleers & Brysbaert, 2010). Each of the words used in the neutral and emotional prosody part of the experiment (ball, call, kit, pan, and tar) were entered into the program in order to produce non-words comparable with each of the spoken words. The non-words used were: bave, cags, pag, tas, and vit, spoken by each of the four speakers (20 words in total).

3.2.2.1.2 Localiser creation procedure and fMRI paradigm.

All sound files from the five different categories were first normalised (RMS) to an equal amplitude. More detailed acoustic measures as a function of category can be found Appendix C. The localiser consisted of within-category blocks. Blocks were 16 seconds (Henson, 2006) with a 2 second silence between each block. Sounds were presented continuously with 200ms of silence in between each sound within each of the blocks. The number of sound files within each block and category varied slightly due to differences in sound durations, but were balanced as much as possible for the number of times each actress and word/vocalisation appeared within the block. Experimental scripts were run in GNU Octave version 4.0.0 (http://www.octave.org). Psychophysics Toolbox Version 3 (version 3.0.14; Brainard, 1997) was used for stimulus presentation. Each participant completed five runs of the task. Each run consisted of two blocks of each sound category together with three rest blocks; one at the start, one in the middle and one at the end of each run. The blocks were presented in a palindromic sequence and the run order was counterbalanced across participants. Auditory stimuli were presented binaurally through an MR compatible electrostatic NNL headphone system (NordicNeuroLab, Inc.) at an intensity of 81 dB SPL(C). A sound level meter was utilised to ensure that the sound level was equal in the right and left ear ($\pm$ 0.2 dB as maximum deviation) for each participant. Participants were asked to keep their eyes closed for the duration of all scans. They were also asked to complete a one-back task during the scan, where they pressed a button if a sound file was repeated.

3.2.2.2 Verbal fluency.

Verbal fluency tasks are commonly used in laterality research to determine language dominance (e.g. Häberling, Badzakova-Trajkov, & Corballis, 2011; Knecht et al., 2000; Hunter & Brysbaert, 2008; Whitehouse & Bishop, 2009). In fact, an earlier in-house study resulted in rates of typical (left) and atypical (right) lateralisation in non-right-handers and right-handers that are remarkably similar to estimates derived from Wada testing (Rasmussen & Milner, 1977). It was also chosen as the task is sufficiently well characterised that group averages of

threshold dependent statistical maps can be compared to previous publications for validity comparisons.

For this experiment, seven different letters, 'T' 'A' 'S' 'H' 'W' 'I' 'O', were presented in individual blocks lasting 15 seconds each. The seven letters chosen were the letters that begin the most words in English (as reported in the Natural Language Toolkit 3.0 - http://www.nltk.org/). The letters were presented in white font (pt. 48 Helvetica) on a black background and centred on the screen. The letters were contrasted with seven control blocks where the letter strings 'RARA' or 'LALA' (Hunter & Brysbaert, 2008) were shown on the screen, also lasting 15 seconds. In between the experimental blocks and control blocks were 15 seconds of fixation, where a central fixation cross was shown on the screen (15 rest blocks in total). The experiment started and finished with fixation blocks and lasted for 435 seconds in total. The presentation order of fixation, letters and control was fixed, but with random allocation of each letter and letter string within each run. Only seven letters were used for this experiment, as this task was found to have a highly reliability across two separate 7-letter runs in a previous study conducted in the lab (r = .93, Johnstone & Carey, unpublished data).

Participants were instructed to silently, without moving their mouths or jaws, generate as many words as they could starting with the letter for as long as it was shown on the screen. A demonstration was given outside of the scanner with the letter 'D' before the session. During the control blocks, participants were instructed to silently repeat the letter string for the duration it was shown on the screen. When the fixation cross was on the screen, they were instructed to clear their minds.

3.2.2.3 Body localiser.

A four-condition localiser was used to identify body-selective brain areas. The experiment consisted of images of hands, hand-held tools, human bodies without heads, and chairs; presented in a blocked design (results from hands and hand-held tools will not be discussed within the scope of this thesis). The stimuli were randomly selected from a total set of 20 stimuli per category depicting isolated objects on a white background (see Figure 3.2). The hands consisted of ten left hand images and ten right hand images in various orientations. Tools consisted of ten unique tools, such as a wrench or a hammer, depicted in two variants and balanced so that half of the tools were presented diagonally from left to right, and half diagonally right to left. Bodies were of 10 males and 10 females, and chairs were 20 various chairs in different styles.

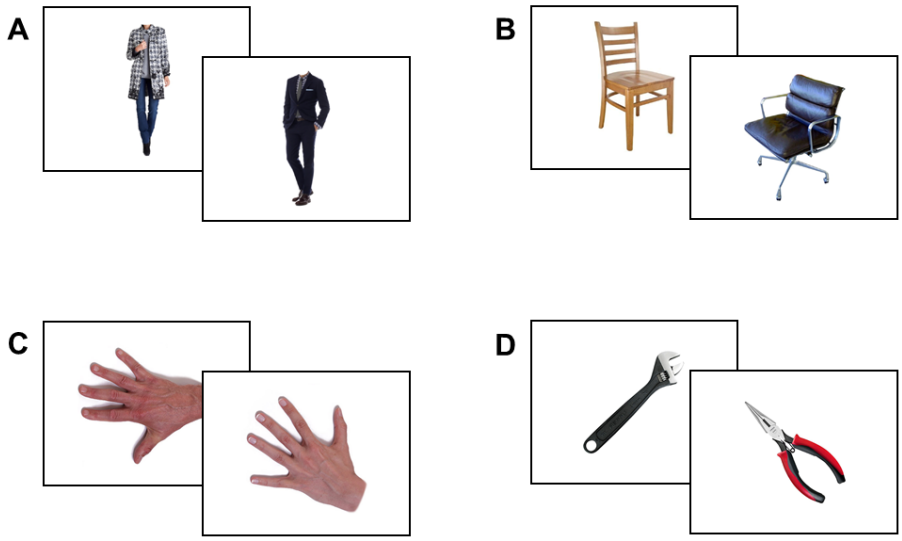


Figure 3.2. Two example stimuli for each of the different categories presented in the body localiser. A: bodies, B: chairs, C: hands, D: tools.

The experiment was presented using Psychophysics Toolbox Version 3 (version 3.0.14; Brainard, 1997) implemented in GNU Octave version 4.0.0 (http://www.octave.org). The participants completed two runs, each lasting 336 seconds. Each functional run consisted of 21 blocks of 16 seconds each. Five out of these, including the first and last block, were fixation-only baseline epochs were a single central fixation point was presented on the screen. Within each experimental block, 12 items from one category were presented for 392ms, with a 941ms inter stimulus interval (ISI), during which the central fixation point appeared on the screen. There were two different fixed stimulus orders which were counterbalanced across participants. Participants were instructed to detect image repetitions in a one-back task, were they pressed a button whenever an image occurred in immediate succession. The repetitions appeared twice at random selected times for each block.

3.2.2.4 Face localiser.

A four-condition localiser was used to identify areas activated when viewing faces and faces with emotional expressions. The experiment consisted of images of faces with neutral expressions, faces with emotional expressions, butterflies, and flowers, in a blocked design. The stimuli were randomly selected from a total set of 20 stimuli per category depicting each item on a white background (see Figure 3.3). The neutral faces consisted of 10 male faces and 10 female faces from The Karolinska Directed Emotional Faces (KDEF) database (Lundqvist, Flykt, & Öhman, 1998) with neutral facial expressions. The faces with emotional

expressions were also taken from KDEF and have been validated as a valid set of affective facial pictures (Goeleven, De Raedt, Leyman, & Verschuere, 2008). Four emotive facial expressions were used; anger, fearful, happiness, and sadness. Each expression was shown in five different faces, and half of the images were of male faces and half of female faces, with each emotional expression shown by either two or three individuals of each gender. The emotional faces were from different individuals than those chosen for the neutral expression to avoid repetition effects. The butterflies and flowers were both of images depicting 20 unique variants of different butterflies and flowers.

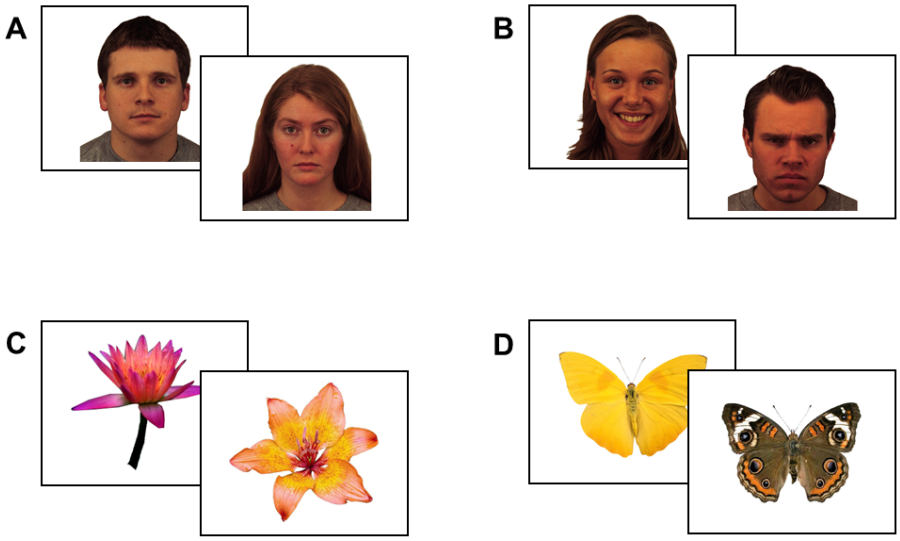


Figure 3.3. Examples of stimuli used for the different categories in the face localiser. A: neutral faces, B: emotional faces, C: flowers, D: butterflies.

The experiment was presented using Psychophysics Toolbox Version 3 (version 3.0.14; Brainard, 1997) implemented in GNU Octave version 4.0.0 (http://www.octave.org). The participants completed two runs, each lasting 336 seconds. Each functional run consisted of 21 blocks of 16 seconds each. five out of these, including the first and last block, were fixation-only baseline epochs were a single central fixation point was presented on the screen. Within each experimental block, 12 items from one category were presented for 392ms, with a 941ms ISI, during which the central fixation point appeared on the screen. There were two different fixed stimulus orders which were counterbalanced across participants. Participants were instructed to detect image repetitions in a one-back task, were they pressed a button whenever an image occurred in immediate succession. The repetitions appeared twice at random selected times for each block.

3.2.3 fMRI data acquisition

A Philips 3 Tesla Achieva magnetic resonance (MR) scanner located at the Bangor Imaging Unit at Bangor University, using a 32-channel phased-array receive-only head coil, was used to acquire T1-weighted anatomical and functional images.

Functional images for the auditory emotions localiser were acquired with the following parameters: a T2-weighted gradient-echo single-shot echo planar imaging (EPI) pulse sequence (sensitivity encoding (SENSE), acceleration factor = 2); repetition time (TR) = 2000ms, echo time (TE) = 30ms, acquisition time = 234 seconds, flip angle (FA) = 77°, field of view (FOV) = 240 x 240 x 105, acquisition matrix = 80 x 79 x 35; 35 slices (width = 3mm, no gap) were acquired; acquired voxel size (mm) = 3 x 3.04 x 3 (reconstructed voxel size (mm) = 3 x 3 x 3). Fat suppression was implemented with spectral pre-saturation with inversion recovery (SPIR). The first 5 scans of each run were discarded before image acquisition to establish steady-state magnetisation.

Functional images for verbal fluency were acquired with the following parameters: a T2-weighted gradient-echo single-shot EPI pulse sequence (SENSE, acceleration factor = 2); TR = 2500ms, TE = 30ms, acquisition time = 435 seconds, FA = 83°, FOV = 240 x 240 x 105, acquisition matrix = 80 x 79 x 35; 35 slices (width = 3mm, no gap) were acquired; acquired voxel size (mm) = 3 x 3 x 3 (reconstructed voxel size (mm) = 3 x 3 x 3). Fat suppression was implemented with SPIR. The first 5 scans of each run were discarded before image acquisition to establish steady-state magnetisation.

Functional images for the body localiser and face localiser were acquired with the following parameters: a T2-weighted gradient-echo single-shot EPI pulse sequence (SENSE, acceleration factor = 2); TR = 2000ms, TE = 30ms, acquisition time = 336 seconds, FA = 77°, FOV = 240 x 240 x 105, acquisition matrix = 80 x 79 x 35; 35 slices (width = 3mm, no gap) were acquired; acquired voxel size (mm) = 3 x 3.04 x 3 (reconstructed voxel size (mm) = 3 x 3 x 3). Fat suppression was implemented with SPIR. The first 5 scans of each run were discarded before image acquisition to establish steady-state magnetisation.

A high resolution T1-weighted structural images were obtained with the following parameters: T1-weighted image acquisition using a multi echo, multi-shot turbo field echo pulse sequence, with a five echo average, TR = 12ms, TE = 3.5ms, acquisition time = 329 seconds, FA = 8°, FOV (mm) = 240 x 240 x 175, acquisition matrix = 80 x 79; 175 contiguous slices were acquired, voxel size (mm) = 1 x 1 x 2 (reconstructed voxel size = $1mm^3$).

3.2.4 Data analysis

All MRI data were pre-processed and analysed using SPM12 (Wellcome Department of Cognitive Neurology, University College London, http://www.fil.ion.ucl.ac.uk/spm/) implemented in MATLAB R2015b 8.6 (Mathworks Inc., Sherborn, MA, USA).

3.2.4.1 Pre-processing.

Anatomical images were first manually aligned to the anterior and posterior commissure (AC-PC). This re-orientation matrix was then applied to all functional images acquired in the same scanning session. The functional data was corrected for head motion by aligning all scans to the first scan of the last run (the run closest to the anatomical scan) to create a mean image. At this point data was inspected to assess for excessive or problematic head movement (within-run movement that exceeded 1 voxel or more). No participants were excluded based on this criterion. The anatomical image was then co-registered to the mean functional image. The anatomical image was segmented, and functional and anatomical data transformed to Montreal Neurological Institute (MNI) space. The normalised data was then spatially smoothed with a $6mm^3$ full-width half maximum (FWHM) Gaussian kernel.

3.2.4.2 fMRI analysis.

General linear model (GLM) analysis was implemented in SPM12. Onsets and durations were modelled for each experimental condition and participant using a boxcar reference vector and convolved with a canonical hemodynamic response function (HRF). Realignment parameters were included to account for motion artefacts. The boxcar function was fitted to the time series at each voxel resulting in a weighted beta-image used to generate contrast images and t-statistic images for the following contrasts presented in Table 3.1.

Table 3.1

fMRI contrasts used for LI analysis and the localiser they were obtained from

Localiser	fMRI contrast
Verbal fluency task	Verbal fluency > control
Auditory emotions localiser	Emotional prosody > neutral prosody
Auditory emotions localiser	Emotional vocalisations > neutral vocalisations
Auditory emotions localiser	Emotional vocalisations > non-words
Face localiser	Neutral faces > flowers, butterflies
Face localiser	Emotional faces > flowers, butterflies
Body localiser	Bodies > chairs

3.2.4.3 Laterality analysis.

To assess hemispheric processing for each participant and contrast, lateralisation indices (LI) were calculated using the SPM extension LI toolbox (Wilke & Lidzba, 2007; also see Wilke & Schmithorst, 2006). The LI toolbox uses a bootstrapping method to generate threshold-independent LI values, which involves iterative resampling and calculation of LIs over multiple threshold levels. The bootstrapping method works such that for a chosen input image (such as a t-map), contrast images are created at 20 equally sized thresholds between 0 and the maximum t-value in the dataset for each hemisphere. The values of the voxels at each threshold, for each hemisphere (or ROI), are then converted into vectors and resampled 100 times with replacement. LIs are then calculated from all possible left/right combinations from this resampling using the standard LI equation (LI = (right-left)/(right+left)). The whole procedure is repeated at each threshold. All LIs are then plotted in a histogram where only the central 50% of the data is kept in order to reduce the effect of outliers. A final weighted mean is calculated from the remaining data were higher thresholds are assigned larger weightings. The toolbox gives indices ranging from -1 to +1, with a negative value indicating relative greater right hemisphere activation, and a positive value indicating greater left hemisphere activation.

3.2.5 Analysis

As the main hypothesis in this chapter relates to complementarity with language, and proportions of hemispheric processing in handedness groups, participants were first divided into three groups based on their language dominance and handedness. Participants were categorised into groups based on LI values for verbal fluency and based on hand preference. Zero was used as a cut-off for all tasks, thus each participant with an LI value of > 0 were categorised as left hemisphere lateralised, and participants with LIs of < 0 as right hemisphere lateralised. Language typical right-handers and language typical non-right-handers were separated into groups in order to examine for handedness differences independent of language dominance. The third group were the language atypically lateralised individuals. As language atypical right-handers are rare, this group included both the two right-handed and the 20 non-right-handed individuals.

Mean LI values were first compared against 0, using a one-sample t-test, in order to examine if *the group*, on average, was significantly lateralised for the specified contrast. The approach here utilises one-tailed significance tests, as it was predicted that each the group would be lateralised for the specified function (either in the typical direction for groups that were left hemisphere dominant for language, or in the opposite direction for the right hemisphere language dominant group). Although two published papers (Bukowski et al., 2013;

Willems et al., 2010) claim no significant laterality in non-right-handers for face or body processing, these studies had small participant numbers and language lateralisation was unknown.

Differences in mean LI values for each of the non-language functions were assessed using one-way ANOVA's comparing the three language/handedness groups. If there is no complementarity, then differences defined by language processing and handedness should have no bearing on how asymmetrical anyone is for any of these functions.

To examine if there was a statistical majority of individuals with dominance in one hemisphere over the other (i.e. the breadth of asymmetry), the proportion of individuals with right and left hemisphere processing was compared against 50% using a binomial test. Furthermore, z-tests were used to examine proportional differences in 'typical' processing between the three language/handedness groups for all tasks. This means that proportions of right hemisphere processing in the two language typical groups were compared with proportions of left hemisphere processing in the language atypical group. The z-test between the language typically lateralised groups and the language atypically lateralised group were two-tailed, as the proportions were assumed to be similar if complementarity of functions exists. The examination of proportional differences between language typical right-handers and language typical non-right-handers was two-tailed for the same reason. There was no reason to suspect that one group would be more lateralised than the other in terms of proportions.

Many researchers employ cut-off values that excludes data or defines it as bilaterally organised. To examine the potential influence of using a cut-off when defining individuals as right hemisphere dominant or left hemisphere dominant, rates of complementarity were examined for different LI cut-offs (0, 0.1, 0.2, 0.3, and 0.4).

Finally, to examine if there is a difference in LI values between handedness groups whilst controlling for typical and atypical lateralisation, participants were grouped as either typical or atypical for each separate contrast, and mean LI values for right-handers and non-right-handers were compared using independent samples t-tests.

3.3 Results

3.3.1 Verbal fluency

The verbal fluency task was used to classify participants' language dominance within the current study (see Chapter 1, section 1.4, for a discussion on different language paradigms used in fMRI). Three groups were created: *language typical* (left hemisphere lateralised) right-handers (n = 23), *language typical* non-right-handers (n = 22) and *language atypical* (right hemisphere lateralised) individuals (n = 22, as two atypically-lateralised right-handers were identified, these were grouped with the non-right-handed atypical group). Demographics for these groups can be seen in Table 3.2. After first level analysis for each individual participant, when language lateralisation had been established, average activation maps were created, displaying whole-brain activation patterns for each of the three groups. Group average activation maps for verbal fluency in these three groups are illustrated in Figure 3.4. Activations are reported in Table 3.3 at a threshold of $p < .001$ with FWE-correction at the cluster level. For the verbal fluency task, significant activations were observed mostly in the left hemisphere in the IFG and in the supplementary motor area, for both typically lateralised groups. The typically lateralised right-handers had additional activation in the right cerebellum. Non-right-handers additionally showed activation in the left parietal lobe, including precuneus and supramarginal gyrus, and the left STG. These activation patterns are in agreement with those seen in previous fMRI studies using the verbal fluency task (e.g. Badzakova-Trajkov et al., 2010; Biduła, Przybylski, Pawlak, & Króliczak, 2017; Cai et al., 2013; Gaillard et al., 2003). The atypically lateralised group show a similar pattern of activations, but reversed for the two hemispheres.

Table 3.2

Participant demographics for the fMRI experiments after being classified in the verbal fluency task. Group means, and standard deviations in parenthesis, are displayed in the age and WHQ columns. NRH = non-right-handed, RH = right-handed

Group	Sex	Age (*SD*)	WHQ (*SD*)
Language typical RH (n = 23)	F = 17, M = 6	23.64 (4.10)	+28.14 (1.83)
Language typical NRH (n = 23)	F = 15, M = 8	25.43 (6.64)	-18.52 (14.84)
Language atypical RH (n = 2)	F = 1, M = 1	24.00 (7.07)	+29.50 (0.71)
Language atypical NRH (n = 20)	F = 11, M = 9	22.80 (7.60)	-28.10 (3.60)

Table 3.3

Statistics of whole-brain analysis for the contrast fluency > control for all three language/handedness-defined groups. Activation patterns were obtained at a threshold of p < .001 with FWE-correction at the cluster level. RH = right-handers, NRH = non-right-handers

		MNI coordinates (peak voxel)				*Cluster*
Group	Anatomical definition	*x*	*y*	*z*	*t-value*	*size*
Typical RH	Right cerebellum	36	-64	-28	11.72	313
	Right cerebellum	6	-82	-22	7.30	
	Left cerebellum	-33	-61	-31	5.43	
	Left inferior frontal gyrus, pars opercularis	-57	14	17	10.96	2836
	Left inferior frontal gyrus, pars opercularis	-42	5	26	10.67	
	Right inferior frontal gyrus, pars orbitalis	33	23	-7	10.18	
	Left supplementary motor area	-9	14	50	8.63	736
	Left anterior cingulate gyrus	-9	23	29	8.35	
	Left anterior cingulate gyrus	-3	8	23	8.25	
Typical NRH	Supplementary motor area	0	11	50	10.08	633
	Left supplementary motor area	-9	17	47	9.89	
	Right middle cingulate gyrus	3	17	41	9.35	
	Left inferior frontal gyrus, pars triangularis	-45	14	26	10.03	3623
	Right midbrain	3	-22	-16	9.99	
	Left insula	-30	23	-1	9.99	
	Left precuneus	-27	-67	38	9.32	248
	Left supramarginal gyrus	-42	-43	38	6.38	
	Left inferior temporal gyrus	-51	-55	-16	6.56	118
	Left inferior temporal gyrus	-42	-43	-10	5.20	
	Left middle temporal gyrus	-42	-40	-1	3.85	
	Right precentral gyrus	42	2	29	5.30	65
	Right precentral gyrus	48	8	32	4.83	
	Right inferior frontal gyrus, pars opercularis	60	11	26	3.61	
Atypicals	Left middle cingulate gyrus	-3	20	38	13.10	598
	Right middle cingulate gyrus	9	17	35	12.71	
	Supplementary motor area	0	14	47	9.69	
	Right insula	36	23	-1	12.82	3328
	Right inferior frontal gyrus, pars triangularis	48	26	20	11.85	
	Right inferior frontal gyrus, pars opercularis	42	17	-4	10.74	
	Right cerebellum	39	-61	-28	10.22	126
	Right cerebellum	33	-55	-31	7.63	
	Left cerebellum	-30	-58	-28	9.03	166
	Left cerebellum	-33	-70	-25	8.03	
	Left cerebellum	-6	-79	-22	7.18	
	Right superior parietal lobule	24	-67	59	5.65	97
	Right angular gyrus	33	-55	38	5.11	
	Right superior parietal lobule	36	-58	56	4.89	
	Right superior temporal gyrus	48	-31	2	5.10	49
	Right superior temporal gyrus	42	-37	2	5.10	
	Right middle temporal gyrus	51	-40	2	3.60	

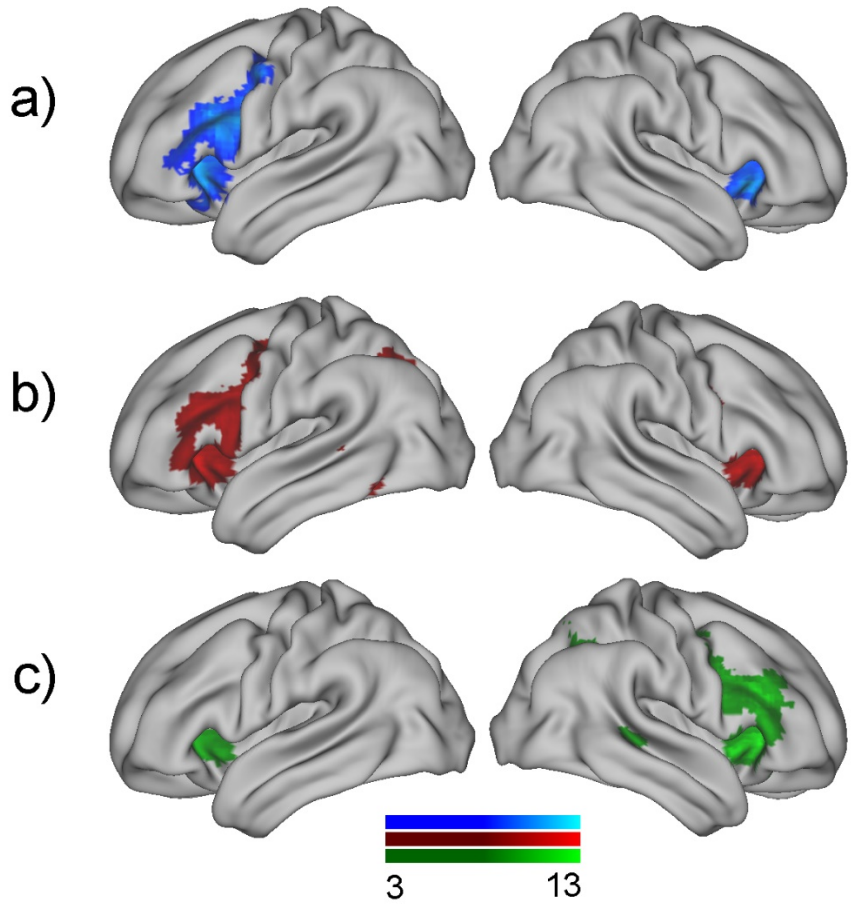


Figure 3.4. Group-level whole-brain activation maps for the contrast fluency > control. The data is visualised at a threshold of $p < .001$ with FWE-correction at the cluster level. Blue activation maps (a) represent the typical right-handed group (n = 23); red activation maps (b) the typical non-right-handed group (n = 23); and green activation maps (c) the atypical group (n = 22). The coloured bars represent t-values.

The following results are based on the LI values calculated for each individual participant for the whole-brain excluding the cerebellum, as cerebellar involvement in language processing is contralateral to the activation of the cerebral cortex (e.g. Gelinas, Fitzpatrick, Kim, & Bjornson, 2014; Schmahmann, 1996). Average LI values for typical right-handers (M = +0.67, SD = 0.17), typical non-right-handers (M = +0.60, SD = 0.16), and atypical participants (M = -0.57, SD = 0.22) are illustrated in Figure 3.5. All three groups were, on average, significantly lateralised for verbal fluency as assessed with a one sample t-test against 0 (language typical right-handers, $t(22) = 18.61$, $p < .001$; language typical non-right-handers, $t(22) = 17.88$, $p < .001$; language atypicals, $t(21) = -12.00$, $p < .001$). To make sure that the three groups were comparable in terms of magnitude of their LI values, a one-way ANOVA was carried out to compare mean LI verbal fluency values for the three groups. To

assess whether the atypical group were as lateralised as the two typical groups, the direction of the individual LIs for the atypical language group was inverted, i.e. absolute values were used for the analysis. The one-way between subjects ANOVA was performed comparing values of the two typical groups with the atypical modified values (M = 0.57, SD = 0.22), and the magnitude of the LI's for the groups did not differ, $F(2, 65) = 1.84$, $p = .166$.

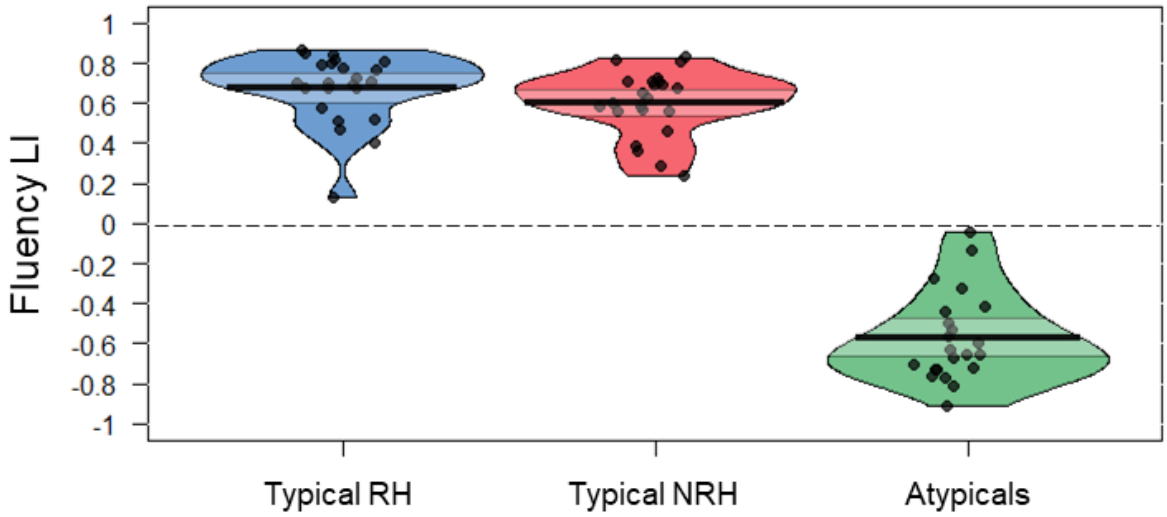


Figure 3.5. Pirate plot (Phillips, 2017) showing distributions of individual verbal fluency LI values for each language-defined group (typical right-handers n = 23; typical non-right-handers n = 23; atypicals n = 22). The bold line indicates the mean and the lighter highlighted area the 95% CIs. All participants in the groups fall above and below the zero line, as this is how the groups were composed. Note that individual in all groups, on average, were highly lateralised for this task. Of relevance is also the scarcity of individual data points near zero.

3.3.2 Emotional prosody

Anatomical regions showing significant activation for emotional prosody processing in the three groups are reported in Table 3.4 and illustrated in Figure 3.6 at a threshold of $p < .001$ with FWE-correction at the cluster level.

Table 3.4

Statistics of whole-brain analysis, for the contrast emotional prosody > neutral prosody for all three language/handedness defined groups. Presented at a threshold of p < .001 with FWE-correction at the cluster level. RH = right-handers, NRH = non-right-handers. The decreased activity in non-right-handed participants, despite being matched in numbers, is noteworthy

		MNI coordinates (peak voxel)				*Cluster*
Group	Anatomical definition	*x*	*y*	*z*	*t-value*	*size*
Language typical RH	Left superior temporal gyrus	-54	-10	-4	10.11	496
	Left superior temporal gyrus	-54	-4	-13	7.21	
	Left insula	-36	-1	-13	6.26	
	Right middle temporal gyrus	60	-4	-13	9.56	838
	Right superior temporal gyrus	54	-7	-1	6.41	
	Right hippocampus	30	-7	-22	5.84	
	Left inferior frontal gyrus, pars orbitalis	-51	26	-4	5.81	84
	Left inferior frontal gyrus, pars triangularis	-45	35	-1	5.26	
	Left inferior frontal gyrus, pars triangularis	-42	32	14	4.06	
	Right inferior frontal gyrus, pars triangularis	57	26	2	5.74	191
	Right inferior frontal gyrus, pars triangularis	45	20	20	5.43	
	Right inferior frontal gyrus, pars triangularis	45	35	2	4.99	
	Left superior temporal gyrus	-45	-34	2	4.97	42
	Left middle temporal gyrus	-51	-34	-7	4.84	
Language typical NRH	Left middle temporal gyrus	-60	-4	-13	4.88	78
	Left middle temporal gyrus	-42	-4	-22	4.74	
	Left middle temporal gyrus	-51	-16	-10	4.25	
Language atypicals	Right superior temporal gyrus	45	14	-19	6.01	132
	Right superior temporal gyrus	39	5	-22	5.91	
	Right superior temporal gyrus	51	-1	-13	5.27	
	Left hippocampus	-24	-7	-25	5.97	45
	Left hippocampus	-21	-13	-16	4.48	
	Left inferior frontal gyrus, pars triangularis	-48	32	11	5.49	67
	Left inferior frontal gyrus, pars triangularis	-39	32	11	4.53	
	Left superior temporal gyrus	-36	17	-25	5.24	235
	Left superior temporal gyrus	-51	-7	-7	5.22	
	Left superior temporal gyrus	-36	5	-25	5.19	
	Right middle frontal gyrus	48	32	17	4.56	42
	Left inferior frontal gyrus, pars triangularis	51	38	5	4.31	

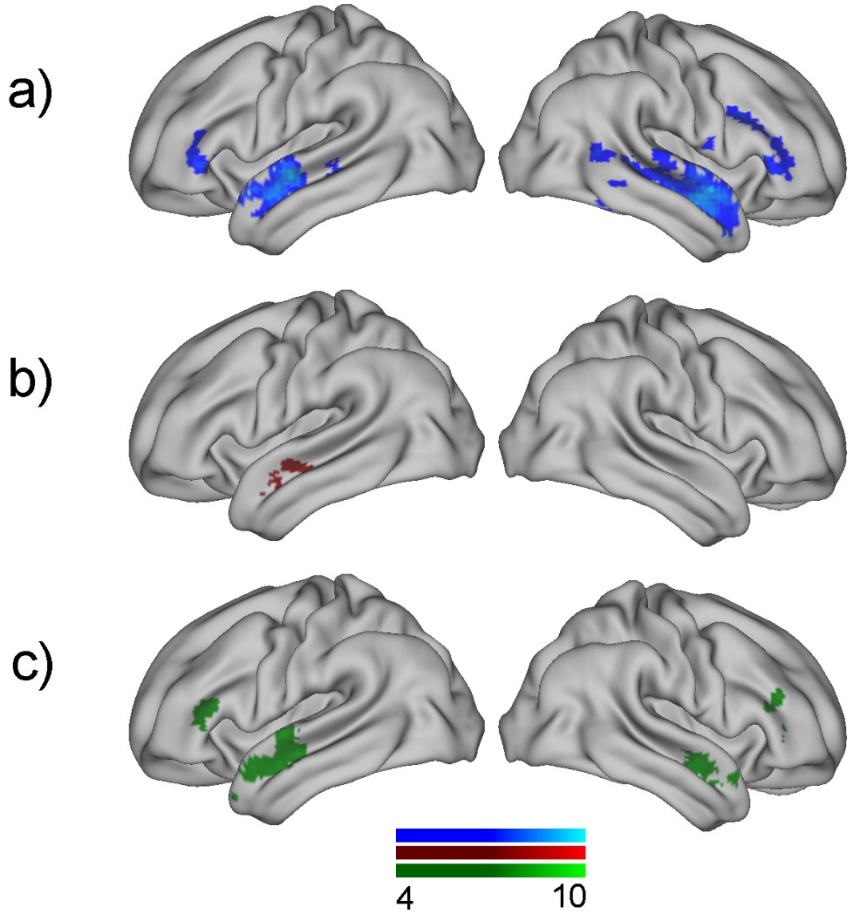


Figure 3.6. Group-level whole-brain maps for the contrast emotional prosody > neutral prosody. Blue activation maps (a) represent the language typical right-handed group; red activation maps (b) the language typical non-right-handed group; and green activation maps (c) the language atypical group. The coloured bars represent t-values.

To examine if the groups, on average, were lateralised for emotional prosody, one sample t-tests against 0 were performed. LI values for each group can be seen in Figure 3.7, and a scatterplot of emotional prosody and verbal fluency LI values for each participant, grouped by handedness, can be found in Appendix D. It was found that language typical right-handers (M = -0.21, SD = 0.32) were significantly right lateralised, $t(22) = -3.11$, $p = .003$. Language typical non-right-handers were significantly right lateralised (M = -0.14, SD = 0.28), $t(22) = -2.38$, $p = .014$. The language atypical group (M = -0.04, SD = 0.40) was not significantly lateralised for prosody processing ($p = .313$). A one-way between subjects ANOVA found no significant difference in mean LI values for the groups, $F(2, 65) = 1.37$, $p = .261$).

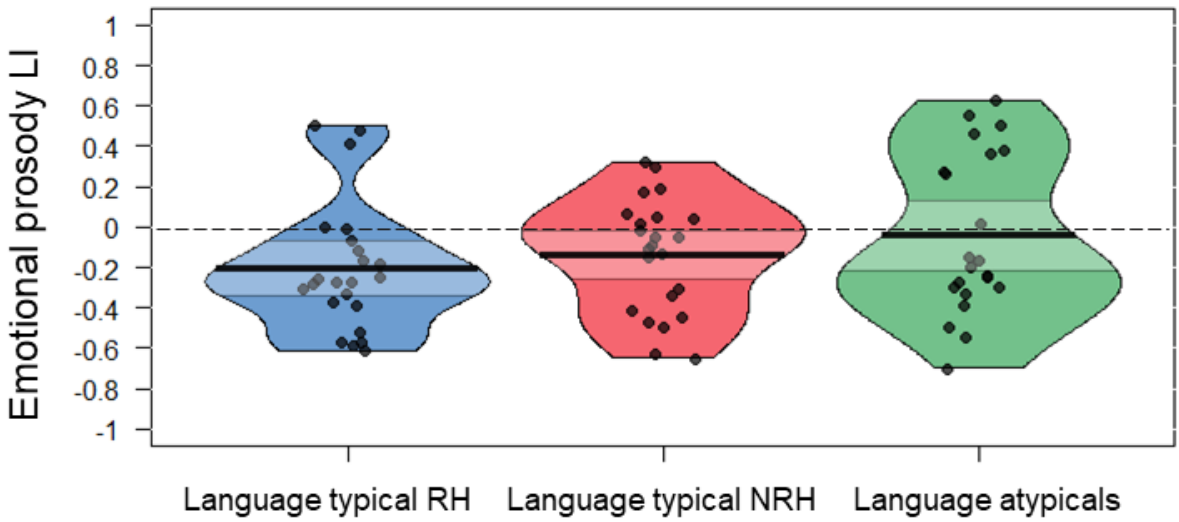


Figure 3.7. Pirate plot showing distributions of individual emotional prosody LI values for each of the language-defined groups. The bold line indicates the mean and the highlighted areas the 95% CIs.

The proportion of individuals with typical hemispheric processing in each group can be seen in Figure 3.12, and was compared against .50 using binomial tests. The proportion of right hemisphere processing in language typical right-handers (.87) was significantly higher than .50, $p < .001$. The proportion of right hemisphere processing in language typical non-right-handers (.65) was not significantly different, $p = .210$. The proportion of left hemisphere processing in language atypicals of *.41* was not significantly different, $p = .523$.

A z-test was used to compare if there were differences in the proportions of right hemisphere emotional prosody processing in the two language typical groups. There was no significant difference in the proportion of right prosody processing in language typical right-handers (20/23 = .87) 95% CI [.68, .96], and language typical non-right-handers (15/23 = .65), 95% CI [.45, .81], $z = 1.73$, $p = .084$. To examine if there was a difference in the complementary patterns found for language and emotional prosody in the two language typical groups with the language atypical group, z-tests between proportion of right hemisphere processing in the typical groups and left hemisphere processing in the atypical group was compared. It was found that the proportion of language typical right-handed participants with right hemisphere dominance was significantly higher than the proportion of left hemisphere prosody processing in the language atypicals (9/22 = .41), 95% CI [.23, .61], $z = 3.23$, $p = .001$, and 95% CI of the difference (.41) did not overlap with zero [-0.66, -0.18]. There was no significant proportional difference between language typical non-right-handed and atypical group (z = 1.63, $p = .103$).

3.3.3. Emotional vocalisations

3.3.3.1 Emotional vocalisations > neutral vocalisations.

Anatomical regions showing significant activation for emotional vocalisations > neutral vocalisations in the three groups are reported in Table 3.5 and illustrated in Figure 3.8 at a threshold of $p < .001$ with FWE-correction at the cluster level.

Table 3.5

Statistics of whole-brain analysis for the contrast emotional vocalisations > neutral vocalisations for all three language/handedness defined groups

		MNI coordinates (peak voxel)				*Cluster*
Group	Anatomical definition	*X*	*y*	*z*	*t-value*	*size*
Language typical RH	Left medial orbitofrontal cortex	0	62	-7	6.55	176
	Right medial frontal gyrus	9	56	14	5.91	
	Left medial frontal gyrus	-6	59	8	4.81	
	Left precuneus	-3	-49	35	6.39	233
	Right precuneus	6	-49	20	4.69	
	Left precuneus	-6	-52	20	4.29	
	Left hippocampus	-24	-10	-22	5.67	118
	Left hippocampus	-27	-37	5	5.18	
	Left parahippocampal gyrus	-33	-43	-7	4.73	
	Right hippocampus	30	-10	-19	5.38	42
	Right amygdala	24	-4	-22	5.04	
Language typical NRH	Right medial frontal gyrus	9	53	23	5.82	103
	Left medial frontal gyrus	-6	59	32	5.10	
	Right superior frontal gyrus	18	47	35	4.30	
	Right precuneus	12	-49	32	4.91	43
Language atypicals	Right medial frontal gyrus	9	59	17	6.15	77
	Left medial frontal gyrus	-3	68	14	4.51	
	Right medial frontal gyrus	6	65	26	3.62	
	Left posterior cingulate gyrus	-6	-52	17	5.28	282
	Right cuneus	15	-61	20	5.10	
	Right precuneus	24	-61	23	4.80	
	Right medial orbitofrontal cortex	3	44	-10	4.83	52
	Left anterior cingulate gyrus	-12	47	-4	4.14	
	Left caudate nucleus	-6	14	-13	4.71	48
	Left caudate nucleus	-3	5	-7	4.30	
	Right caudate nucleus	9	11	-13	3.86	

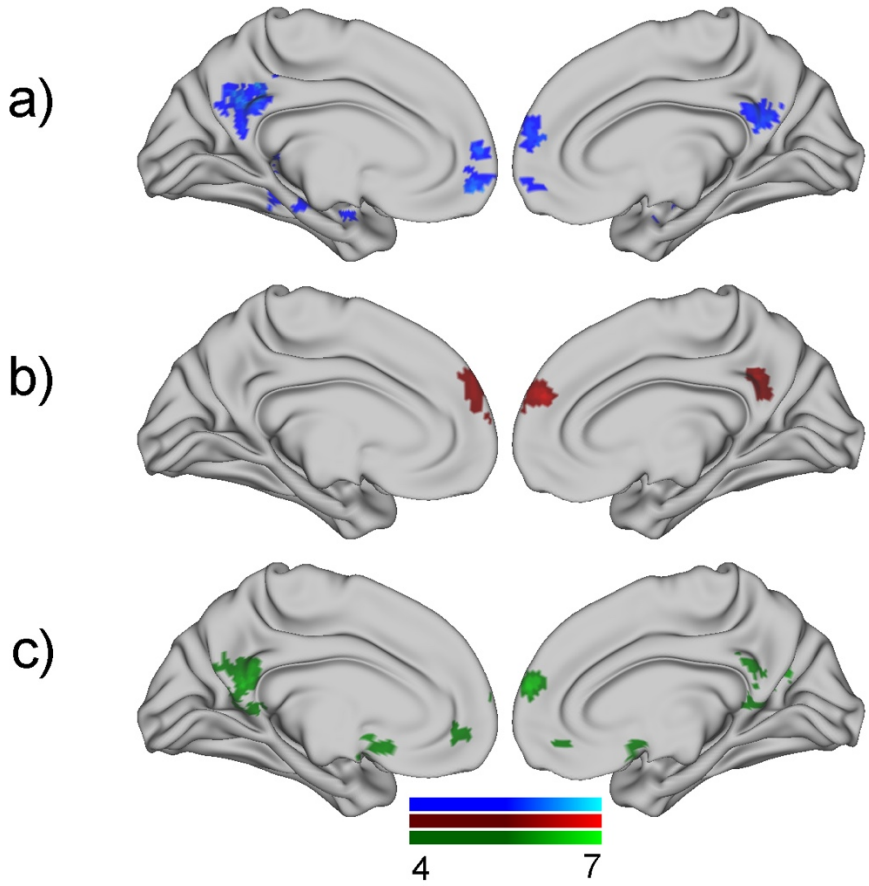


Figure 3.8. Group-level whole-brain maps for the contrast emotional vocalisations > neutral vocalisations. Shown on the medial surface of the two hemispheres. Blue activation maps (a) represent the language typical right-handed group; red activation maps (b) the language typical non-right-handed group; and green activation maps (c) the language atypical group. The coloured bars represent t-values.

LI values for each group can be seen in Figure 3.9, and a scatterplot of emotional vocalisations and verbal fluency LI values for each participant, grouped by handedness, can be found in Appendix D. To examine if the groups, on average, were lateralised for emotional vocalisations when compared to neutral vocalisations a one sample t-test against 0 was performed. None of the groups were found to be significantly lateralised (language typical right-handers, $p = .401$; language typical non-right-handers, $p = .249$; atypicals, $p = .267$). A one-way between subjects ANOVA was carried out to examine if average LI values differed between the groups, but no significant difference was found ($p = .612$).

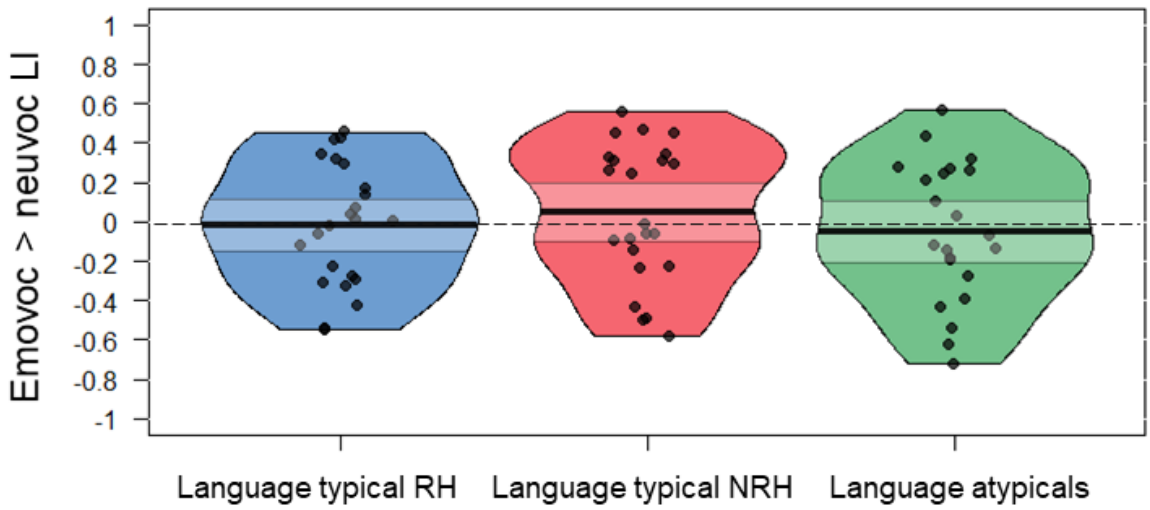


Figure 3.9. Pirate plot showing distributions of emotional vocalisation LI values for each of the language defined groups. Values were derived from the contrast emotional vocalisations > neutral vocalisations. The bold line indicates the mean and the highlighted area the 95% confidence intervals. The lack of asymmetry in this contrast is noteworthy.

The proportions of right and typical hemispheric processing in each of the groups can be seen in Figure 3.12. Binomial tests against 50% were carried out, and it was found that none of the groups had significant group level biases towards one hemisphere, language typical right-handers (right hemisphere) = .48, p = 1, language typical non-right-handers (right hemisphere) = .52, p = 1, language atypicals (left hemisphere) = .45, p = .832. A z-test found that there was no significant difference in the proportion of typical (right) prosody processing in language typical right-handers (11/23 = .48), 95% CI [.29, .67] and language typical non-right-handers (12/23 = .52), 95% CI [.33, .71], z = -0.29, p = .772. To examine if there was a difference in the complementary patterns found for language and emotional vocalisations in the two language typical groups with the language atypical group, z-tests between proportion of right hemisphere processing in the typical groups and left hemisphere processing in the atypical group was compared. There was no significant difference between language atypicals (10/22 = .45), 95% CI [.27, .65], and language typical right-handers z = 0.16, p = .873, or between language atypicals and language typical non-right-handers, z = 0.45, p = .653.

The activation patterns when comparing emotional vocalisations with neutral vocalisations were odd in two different ways. Firstly, they were not asymmetrical for any of the groups. Secondly, activation patterns seen in the groups were in cortical and subcortical medial areas not comparable with those reported in previous literature. Therefore, emotional vocalisations were explored using a second contrast. The other comparable condition, which uses the human vocal tract but does not contain emotional or linguistic information, was the

nonword stimuli that were originally intended as a control for words. This contrast was not planned.

3.3.3.2 Emotional vocalisations > non-words.

To examine lateralisation of emotional vocalisations using a different control contrast, neutral non-words were used as the control condition. Significant activation at a threshold of $p < .001$ with FWE-correction at the cluster level was only found for the language typical right-handers and the language atypicals. Anatomical regions showing significant activation for these two groups are reported in Table 3.6 and illustrated in Figure 3.10

Table 3.6

Statistics of whole-brain analysis for the contrast emotional vocalisations > non-words for language typical right-handers and language atypicals

		MNI coordinates (peak voxel)				*Cluster*
Group	Anatomical definition	*x*	*y*	*z*	*t-value*	*size*
Language typical RH	Right superior temporal gyrus	54	-10	2	9.12	361
	Right superior temporal gyrus	42	2	-22	8.13	
	Right middle temporal gyrus	54	-1	-22	6.54	
	Right inferior frontal gyrus, pars triangularis	51	26	-1	7.47	130
	Right inferior frontal gyrus, pars triangularis	54	32	8	5.88	
	Right superior frontal gyrus, medial part	6	53	38	6.17	71
	Right superior frontal gyrus, medial part	9	59	26	4.91	
	Left superior frontal gyrus, medial part	-6	59	32	4.07	
	Left angular gyrus	-54	-67	26	5.88	42
	Left middle occipital gyrus	-42	-79	32	4.20	
	Left inferior frontal gyrus, pars orbitalis	-42	26	-16	5.03	39
	Left superior temporal gyrus	-36	17	-25	4.84	
	Right inferior frontal gyrus, pars triangularis	51	17	20	4.76	51
	Left amygdala	-24	-7	-16	4.69	41
	Left amygdala	-15	-1	-16	4.19	
Language atypicals	Left superior temporal gyrus	-48	-13	2	5.91	52
	Left superior temporal gyrus	-51	-4	-7	4.31	
	Left middle temporal gyrus	-54	-10	-16	3.76	

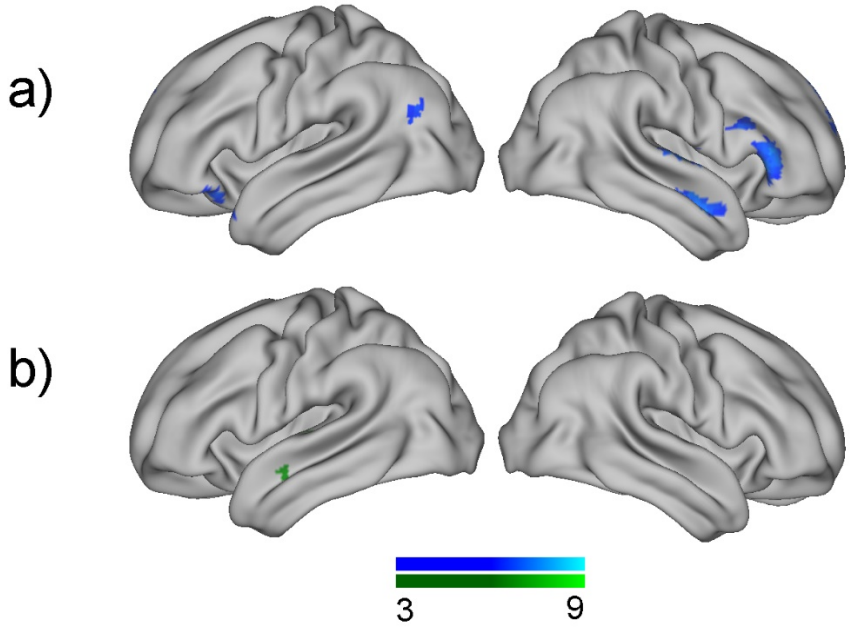


Figure 3.10. Group-level whole-brain maps for the contrast emotional vocalisations > non-words. Blue activation maps (a) represent the language typical right-handed group, and green activation maps (b) the language atypical group. The language typical non-right-handed group did not show any activation above the statistical threshold. The coloured bars represent t-values.

LI values for each group can be seen in Figure 3.11, and a scatterplot of emotional vocalisations and verbal fluency LI values for each participant, grouped by handedness, can be found in Appendix D. To examine if the groups were lateralised, on average, for emotional vocalisations when contrasted with non-words a one sample t-test against 0 was performed. It was found that language typical right-handers (M = -0.25, SD = 0.36) were significantly right lateralised, $t(22) = -3.12$, $p = .001$. Language typical non-right-handers (M = -0.05, SD = 0.42) were not significantly lateralised, $t(22) = -0.58$, $p = .283$. The atypical group (M = 0.25, SD = 0.39) was, on average, significantly left lateralised for emotional vocalisations, $t(21) = 3.07$, $p = .003$. A one-way between subjects ANOVA found a significant difference in mean LI values between the groups, $F(2, 65) = 9.40$, $p < .001$, $\eta^2 = .22$. Post-hoc tests using Bonferroni found a difference between typical right-handers and atypicals ($p < .001$, $d = 1.34$) and typical non-right-handers and atypicals ($p = .033$, $d = 0.75$). There was no significant difference between typical right-handers and typical non-right-handers ($p = .280$).

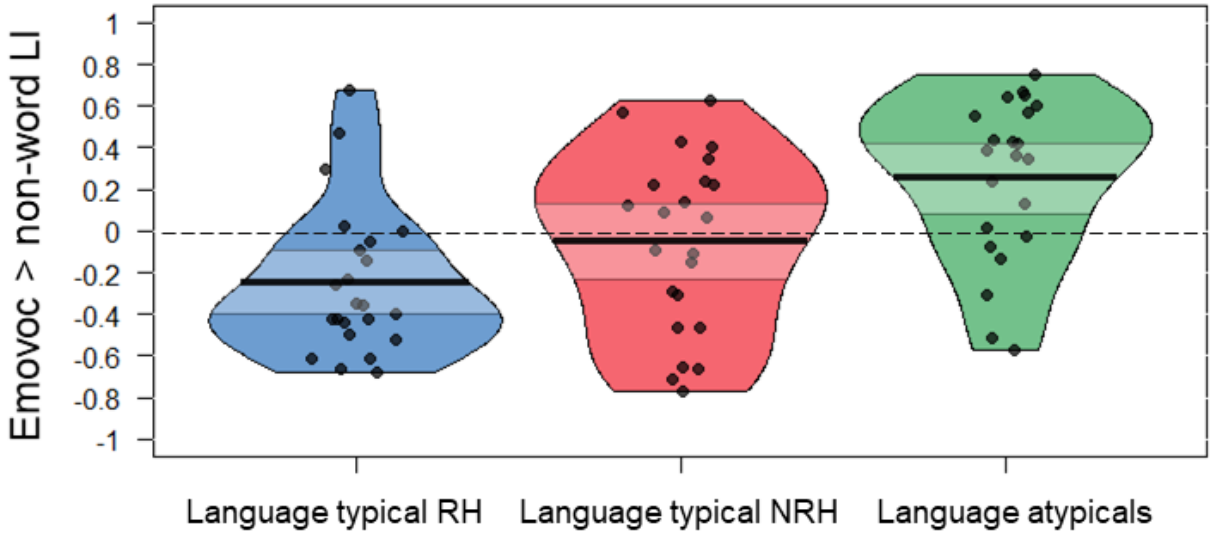


Figure 3.11. Pirate plot showing distributions of individual emotional vocalisation LI values, for the contrast emotional vocalisations > non-words, for each of the groups. The bold line indicates the mean and the highlighted area the 95% confidence intervals.

The proportion of individuals with *typical* hemispheric processing in each group can be seen in Figure 3.12, and was compared against .50 using binomial tests. The proportion of right hemisphere processing in language typical right-handers (.78) was significantly higher than .50, p = .011. The proportion of right hemisphere processing in language typical non-right-handers (.48) was not significant different, p = 1. The proportion of left hemisphere processing in language atypicals *of .73* was not significantly different, p = .052.

A z-test was used to compare if there were differences in the proportion of participants with right hemisphere LI values in the different groups. There was a significant difference in the proportion of individuals who had typical LI values for language typical right-handers (18/23 = .78, 95% CI .58, .90) and typical non-right-handers: (11/23 = .48), 95% CI [.29, .67], z = 2.14, p = .032, 95% CI of the difference (-.30) did not overlap with zero [-0.53, -0.03]. To examine if there was a difference in the complementary patterns found for language and emotional vocalisations in the two language typical groups with the language atypical group, z-tests between proportion of right hemisphere processing in the typical groups and left hemisphere processing in the atypical group was compared. There was no significant difference between language typical right-handers and atypicals (16/22 = .73), 95% CI [.52, .87], z = 0.43, p = .667, and there was no significant difference between language typical non-right-handers and atypicals, z = -1.70, p = .089.

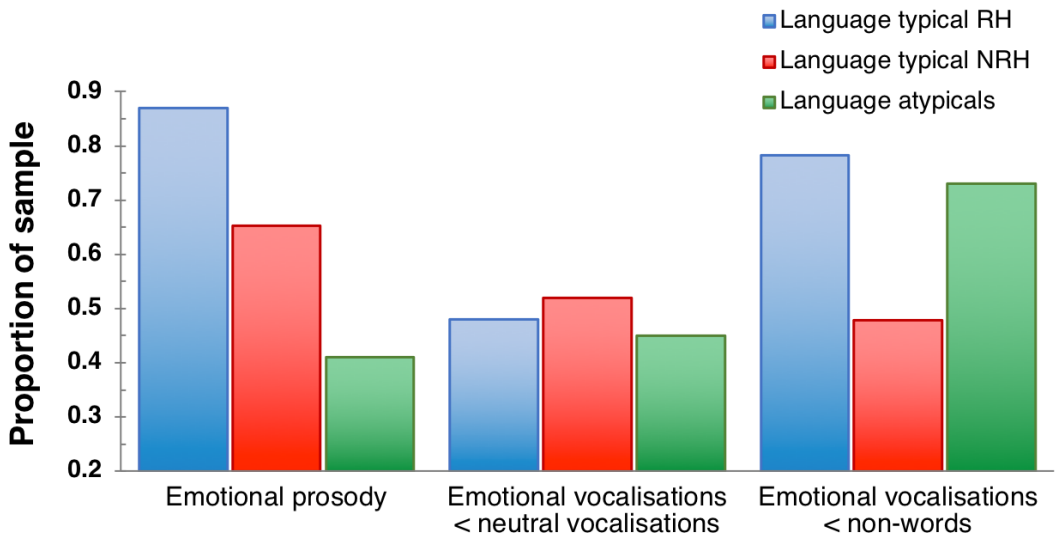


Figure 3.12. The proportion of each group with complementary hemispheric patterns of dominance with language for emotional prosody and the two emotional vocalisation contrasts. RH = right=handers, NRH = non-right-handers.

3.3.4 Neutral faces

Significant activation at a threshold of $p < .001$ with FWE-correction at the cluster level for neutral faces was only found for the language typical right-handers and the language atypicals. The significant activation in these two groups are reported in Table 3.7 and illustrated in Figure 3.13.

Table 3.7

Statistics of whole-brain analysis for the contrast neutral faces > control for all three language/handedness defined groups

Group	Anatomical definition	MNI coordinates (peak voxel) *x*	*y*	*z*	*t-value*	*Cluster size*
Language typical RH	Right amygdala	18	-10	-16	9.14	231
	Right hippocampus	33	-22	-10	5.86	
	Right amygdala	27	-4	-22	4.99	
	Left hippocampus	-21	-16	-16	8.77	276
	Left Amygdala	-30	-1	-25	5.93	
	Left caudate nucleus	0	11	-13	5.80	
	Right inferior frontal gyrus, pars triangularis	45	23	20	7.30	126
	Right inferior frontal gyrus, pars opercularis	39	14	26	6.22	
	Right superior temporal gyrus	60	-46	11	7.20	303
	Right superior temporal gyrus	51	-49	11	6.18	
	Right middle temporal gyrus	48	-61	17	5.19	
Language atypicals	Left middle temporal gyrus	-45	-70	14	8.19	241
	Left middle temporal gyrus	-48	-52	8	7.67	
	Left middle temporal gyrus	-60	-49	-4	5.31	
	Right amygdala	21	-7	-16	7.28	53
	Left amygdala	-24	-13	-13	5.77	48

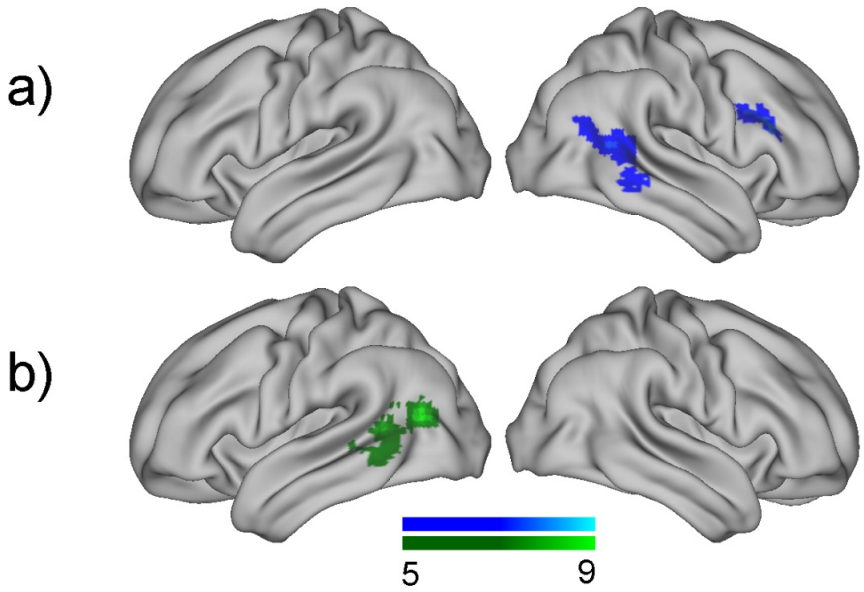


Figure 3.13. Group-level whole-brain activation maps for the contrast neutral faces > control. Blue activation maps (a) represent the language typical right-handed group, and green activation map (b) the language atypical group. The language typical non-right-handed group did not show any activation above the statistical threshold. The coloured bars represent t-values.

LI values for each group can be seen in Figure 3.14, and a scatterplot of neutral face and verbal fluency LI values for each participant, grouped by handedness, can be found in Appendix D. To examine if the groups, on average, were lateralised for neutral faces, a one sample t-test against 0 was performed. It was found that language typical right-handers (M = -0.32, SD = 0.33) were significantly right lateralised, $t(21) = -4.48$, $p < .001$, the language typical non-right-handers were also significantly right lateralised (M = -0.31, SD = 0.34), $t(22) = -4.41$, $p < .001$. The atypical group was, on average, significantly left lateralised for neutral faces (M = 0.17, SD = 0.46), $t(21) = 1.75$, $p = .048$**.** A one-way between subjects ANOVA found a significant difference in mean LI values between the groups, $F(2, 64) = 12.01$, $p < .001$. $\eta^2 = .27$. Post hoc tests using Bonferroni revealed that the difference between language typical right-handed LI values and atypical LI values was significant ($p < .001$, $d = 1.22$), the difference between language typical non-right-handed LI values and atypical LI values was significant ($p < .001$, $d = 1.19$). No significant difference was found between the two language typically lateralised groups ($p = 1$).

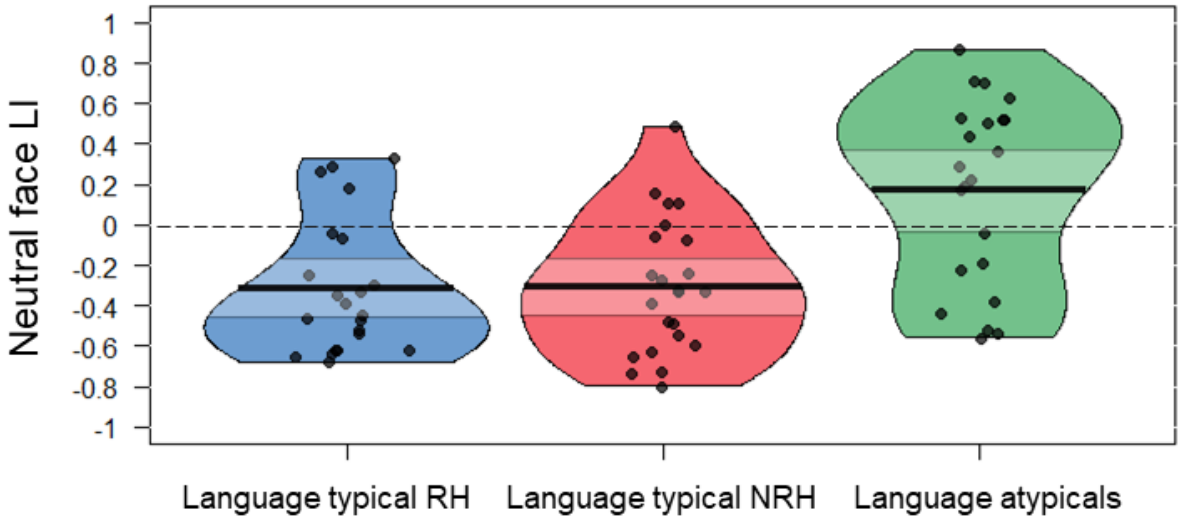


Figure 3.14. Pirate plot showing distributions of individual neutral face LI values for each of the groups.

The proportion of individuals with *typical* hemispheric processing in each group can be seen in Figure 3.19, and was compared against .50 using binomial tests. The proportion of right hemisphere processing in language typical right-handers (.82) was significantly higher, $p = .004$. The proportion of right hemisphere processing in language typical non-right-handers (.83) was significantly higher, $p = .003$. The proportion of left hemisphere processing in language atypicals of .64 was not significantly different, $p = .286$.

A z-test was used to compare if there were differences in the number of participants with right hemisphere dominance in the different groups. There was no significant difference between language typical right-handers (18/22 = .82), 95% CI [.62, .93], and language typical non-right-handers (19/23 = .83), 95% CI [.63, .93], z = -0.07, p = .944). To examine if there was a difference in the complementary patterns found for language and neutral faces in the two language typical groups with the language atypical group, z-tests between proportion of right hemisphere processing in the typical groups and left hemisphere processing in the atypical group was compared. It was found that the proportion of language typical right-handed participants with a right hemisphere dominance was not significantly higher than that of the language atypicals (14/22 = .64), 95% CI [.43, .80], z = 1.35, p = .177, 95% CI of the difference (-.18) overlapped with zero [-0.42, 0.08]. The proportion of right hemisphere processing in language typical non-right-handers was also not significantly higher compared to language atypicals z = 1.44, p = .150, 95% CI of the difference (-.19) overlapped with zero [-0.42, 0.07].

3.3.5 Emotional faces

Anatomical regions showing significant activation for neutral face processing in the three groups are reported in Table 3.8 and illustrated in Figure 3.15 at a threshold of $p < .001$ with FWE-correction at the cluster level.

Table 3.8

Statistics of whole-brain analysis for the contrast emotional faces > control for all three language/handedness defined groups

Group	Anatomical definition	MNI coordinates (peak voxel) *x*	*y*	*z*	*t-value*	*Cluster size*
Language typical RH	Right amygdala	18	-7	-16	8.34	181
	Right superior temporal gyrus	36	5	-28	5.32	
	Right hippocampus	33	-22	-10	4.63	
	Right superior temporal gyrus	63	-46	11	7.28	170
	Right middle temporal gyrus	51	-37	-1	5.15	
	Right superior temporal gyrus	51	-46	14	4.94	
	Left amygdala	-18	-10	-16	6.38	87
	Left globus pallidus	-21	-7	-7	5.30	
	Right inferior frontal gyrus, pars triangularis	45	23	20	6.20	130
	Right inferior frontal gyrus, pars opercularis	48	14	26	5.18	
	Right inferior frontal gyrus, pars triangularis	36	14	23	5.02	
	Right middle temporal gyrus	48	-7	-19	5.57	44
	Right middle temporal gyrus	48	-19	-10	5.42	
	Precuneus	0	-64	29	5.54	90
	Left precuneus	-6	-55	38	5.36	
Language typical NRH	Right inferior frontal gyrus, pars triangularis	48	17	20	7.33	133
	Right inferior frontal gyrus, pars triangularis	54	26	17	5.33	
	Right inferior frontal gyrus, pars triangularis	54	29	5	4.43	
	Right superior temporal gyrus superior	54	-49	11	6.07	290
	Right superior temporal gyrus, superior	63	-49	14	5.54	
	Right superior temporal gyrus, superor	48	-40	5	5.49	
	Left inferior frontal gyrus, pars triangularis	-39	11	26	5.89	54
	Left inferior frontal gyrus, pars triangularis	-45	17	20	4.82	
	Left superior temporal gyrus	-45	-64	20	4.61	93
	Left middle temporal gyrus	-57	-55	5	4.28	
	Left middle temporal gyrus	-48	-52	5	4.21	
Language atypicals	Right amygdala	21	-7	-16	8.00	50
	Right amygdala	30	-4	-19	5.00	
	Left amygdala	-21	-10	-13	7.53	71
	Left amygdala	-27	-4	-22	5.55	
	Left middle temporal gyrus	-42	-70	14	7.13	379
	Left middle temporal gyrus	-54	-70	11	6.56	
	Left middle temporal gyrus	-45	-52	8	5.92	
	Right middle temporal gyrus	57	-46	2	6.44	155
	Right middle temporal gyrus	57	-61	8	5.28	
	Right superior temporal gyrus	60	-55	17	5.08	
	Right inferior frontal gyrus, pars triangularis	51	23	23	5.15	46
	Left inferior frontal gyrus, pars triangularis	-45	17	23	5.11	114
	Left precentral gyrus	-45	8	32	4.70	
	Left inferior frontal gyrus, pars opercularis	-54	8	17	4.26	

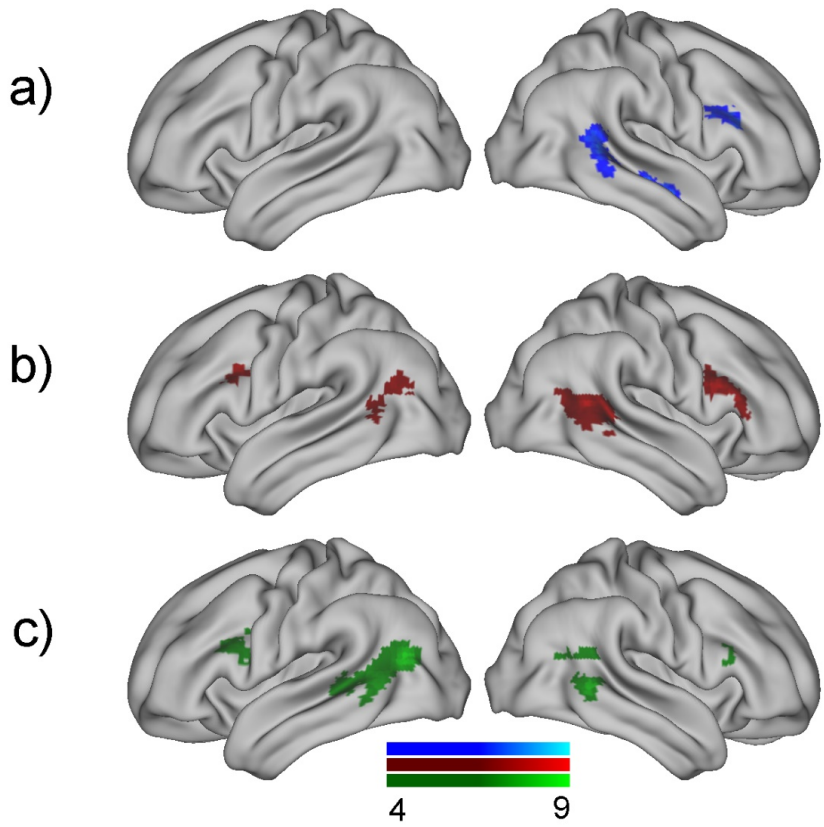


Figure 3.15. Group-level whole-brain maps for the contrast emotional faces > control. Blue activation maps (a) represent the language typical right-handed group; red activation maps (b) the language typical non-right-handed group; and green activation maps (c) the language atypical group. The coloured bars represent t-values.

LI values for each group can be seen in Figure 3.16, and a scatterplot of emotional face and verbal fluency LI values for each participant, grouped by handedness, can be found in Appendix D. To examine if the groups, on average, were lateralised for emotional faces a one sample t-test against 0 was performed. It was found that language typical right-handers were significantly right lateralised (M = -0.31, SD = 0.37), $t(21)$ = -3.89, $p < .001$. Language typical non-right-handers were significantly right lateralised (M = -0.20, SD = 0.44), $t(22)$ = -2.16, p = .021. The atypical group was significantly left lateralised for emotional faces (M = 0.22, SD = 0.49), $t(21)$ = 2.09, p = .025.

A one-way between subjects ANOVA found that mean LI values for emotional faces differed significantly between the groups, $F(2, 64) = 8.89$, $p < .001$, $\eta^2 = .22$. Post hoc tests using Bonferroni revealed that the difference between typical right-handed LI values and atypical LI values was significant (p = .001, d = 1.21). The difference between typical non-right-handed LI values and atypical LI values was significant (p = .007, d = 0.89). The

difference between typical right-handers and typical non-right-handers was not significant (p = 1).

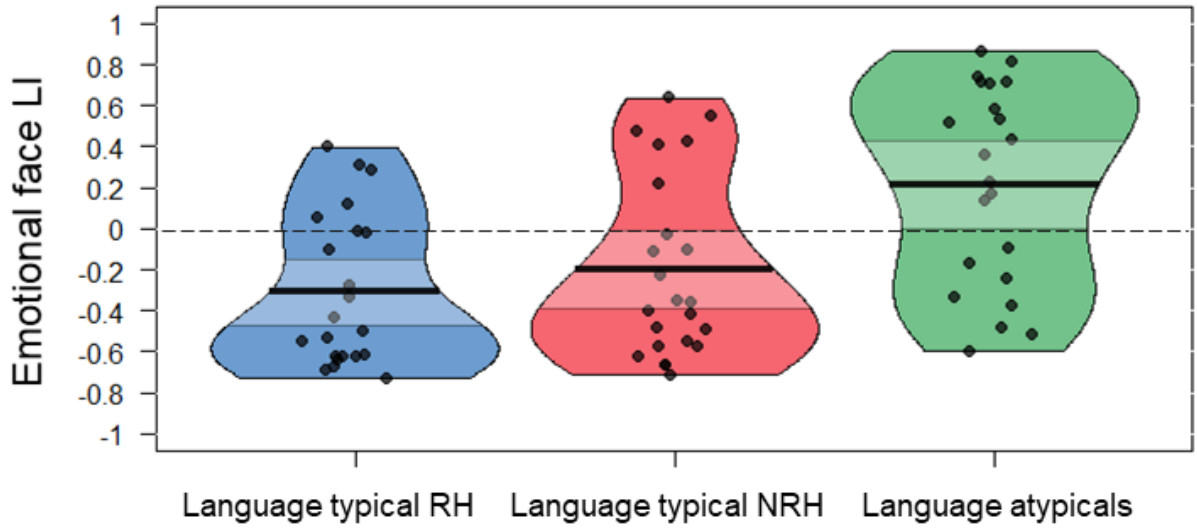


Figure 3.16. Pirate plot showing distributions of individual emotional face LI values for each of the groups. The bold line indicates the mean and the highlighted areas the 95% confidence intervals.

The proportion of individuals with *typical* hemispheric processing in each group can be seen in Figure 3.19, and was compared against .50 using binomial tests. The proportion of right hemisphere processing in language typical right-handers (.77) was significantly higher than .50, p = .017. The proportion of right hemisphere processing in language typical non-right-handers (.74) was significantly higher, p = .035. The proportion of left hemisphere processing in language atypicals of .64 was not significantly different, p = .286.

A z-test was used to compare if there were differences in the number of participants with right hemisphere dominance in the different groups. There was no significant difference between language typical right-handers (17/22 = .73, 95% CI .52, .87) and language typical non-right-handers (17/23 = .71, 95% CI .50, .86), z = 0.26, p = .795. To examine if there was a difference in the complementary patterns found for language and emotional faces in the two language typical groups with the language atypical group, z-tests between proportion of right hemisphere processing in the typical groups and left hemisphere processing in the atypical group was compared. It was found that the proportion of language typical participants with a right hemisphere dominance was not significantly different to language atypicals (14/22 = .64, 95% CI .43, .80), z = 0.99, p = .322. It was also found that the proportion of language typical

participants with a right hemisphere dominance was not significantly different to language atypicals, $z = 0.74$, $p = .459$.

3.3.7 Bodies

Anatomical regions showing significant activation for body processing in the three groups are reported in Table 3.9 and illustrated in Figure 3.17, and at a threshold of $p < .001$ with FWE-correction at the cluster level.

Table 3.9

Whole-brain analysis for the contrast bodies > chairs for all three language/hand groups

		MNI coordinates (peak voxel)				*Cluster*
Group	Anatomical definition	*x*	*y*	*z*	*t-value*	*size*
Language typical RH	Right middle temporal gyrus	48	-61	2	7.89	286
	Right inferior temporal gyrus	48	-70	-1	7.35	
	Right superior temporal gyrus	39	-55	11	6.19	
	Right fusiform gyrus	45	-46	-19	6.01	48
	Right middle temporal gyrus	45	-46	-4	3.72	
Language typical NRH	Left middle occipital gyrus	-48	-73	14	7.99	234
	Left middle temporal gyrus	-51	-73	5	7.50	
	Left middle temporal gyrus	-39	-61	11	6.10	
	Right middle temporal gyrus	54	-64	-1	7.59	392
	Right middle temporal gyrus	48	-64	11	6.96	
	Right middle temporal gyrus	60	-55	-4	5.70	
	Left fusiform gyrus	-42	-46	-22	6.57	47
	Right fusiform gyrus	42	-49	-19	5.81	64
	Right inferior frontal gyrus, pars opercularis	51	8	26	5.15	167
	Right precentral gyrus	39	-4	41	4.45	
	Right precentral gyrus	48	-1	38	4.05	
Language atypicals	Left middle occipital gyrus	-51	-76	2	8.34	530
	Left middle temporal gyrus	-51	-70	8	7.23	
	Left fusiform gyrus	-45	-55	-22	6.95	
	Right hippocampus	15	-7	-10	7.59	45
	Right caudate nucleus	9	5	-13	4.55	
	Right middle occipital gyrus	51	-70	2	7.02	173
	Right middle temporal gyrus	57	-58	8	5.82	
	Right superior temporal gyrus	51	-46	17	4.77	
	Left precuneus	-18	-55	44	6.32	42
	Left superior parietal lobule	-30	-61	44	4.34	
	Left parietal lobe	-27	-55	35	4.21	
	Right fusiform gyrus	42	-52	-19	6.28	63
	Right fusiform gyrus	42	-43	-19	6.03	
	Right inferior frontal gyrus, pars triangularis	36	17	20	5.30	41
	Right middle frontal gyrus	33	26	20	4.34	
	Right middle frontal gyrus	39	11	29	3.90	
	Right inferior frontal gyrus, pars triangularis	51	26	23	5.23	44

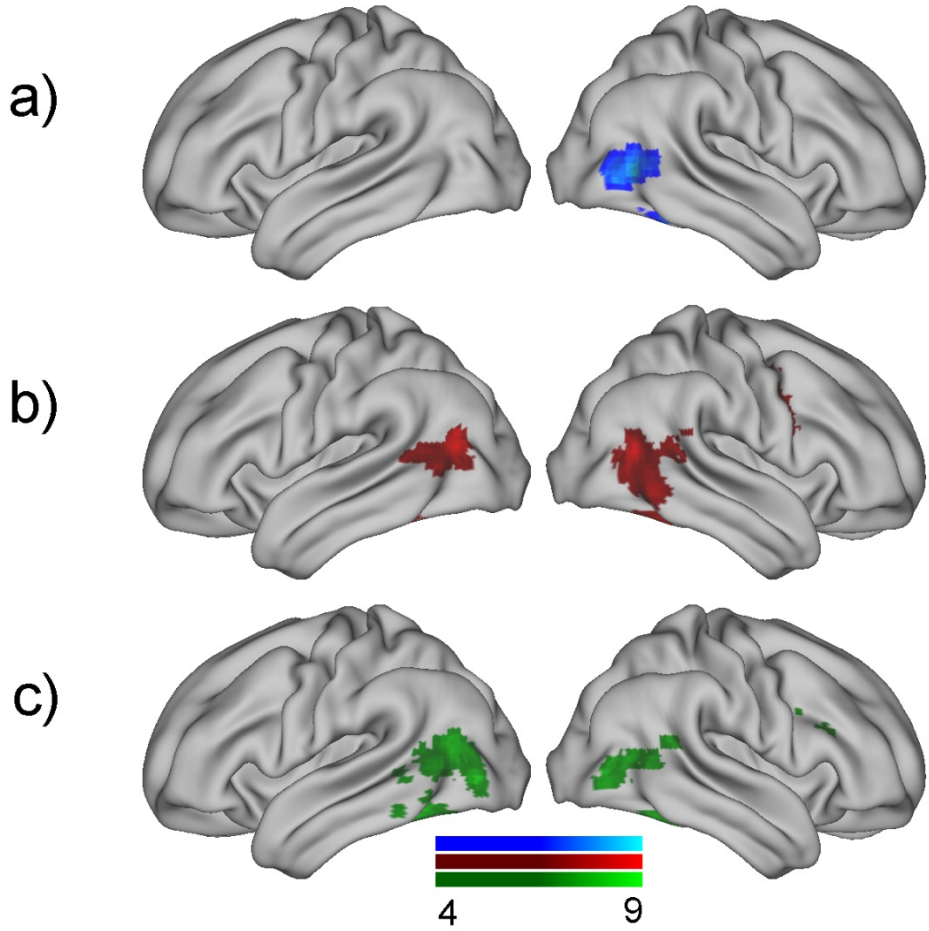


Figure 3.17. Group-level whole-brain maps for the contrast bodies > chairs. Blue activation maps (a) represent the language typical right-handed group, red activation maps (b) the language typical non-right-handers, and green activation maps (c) the language atypical group. The coloured bars represent t-values.

LI values for each group can be seen in Figure 3.18, and a scatterplot of body and verbal fluency LI values for each participant, grouped by handedness, can be found in Appendix D. To examine if the groups, on average, were lateralised for bodies a one sample t-test against 0 was performed. It was found that language typical right-handers (M = -0.38, SD = 0.32) were significantly right lateralised, $t(22) = -5.72$, $p < .001$. The language typical non-right-handers (M = -0.11, SD = 0.34) were not significantly lateralised, $t(22) = -1.59$, $p = .064$, and the language atypical group (M = 0.08, SD = 0.40) was not significantly lateralised, $t(21) = 0.97$, $p = .171$.

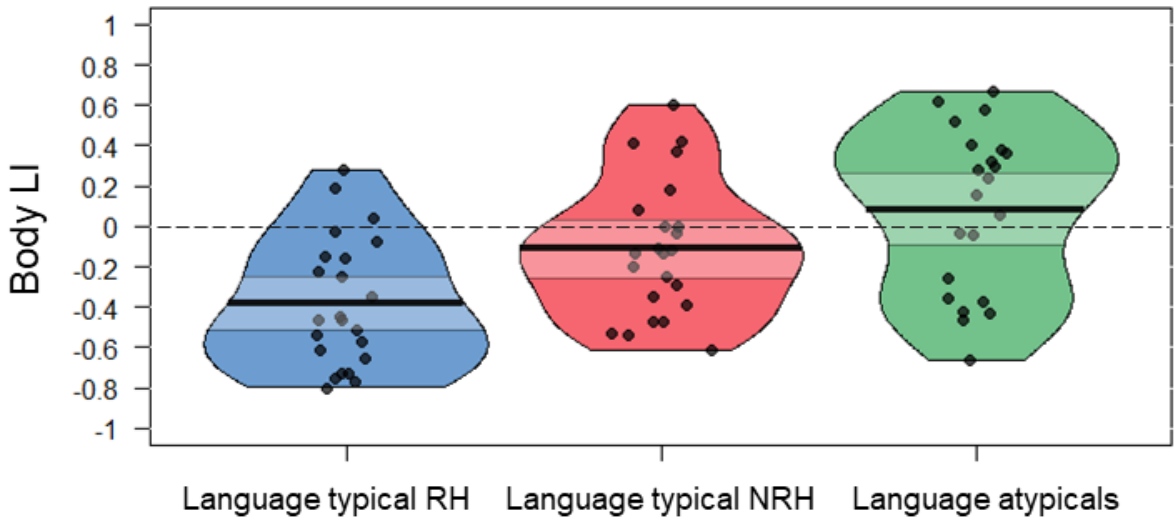


Figure 3.18. Pirate plot showing distributions of individual body LI values for each of the groups. The bold line indicates the mean and the highlighted areas the 95% confidence intervals.

A one-way between subjects ANOVA found that mean LI values in the groups were significantly different, $F(2, 65) = 9.75$, $p < .001$. $\eta^2 = .23$. Post hoc tests using Bonferroni revealed that the difference between right-handed LI values and atypical LI values was significant ($p < .001$, $d = 1.27$). The difference between typical right-handers and typical non-right-handers was significant ($p = .037$) $d = 0.82$. The difference between typical non-right-handers and atypicals was not significant ($p = .207$).

The proportion of individuals with *typical* hemispheric processing in each group can be seen in Figure 3.19, and was compared against .50 using binomial tests. The proportion of right hemisphere processing in language typical right-handers (.87) was significantly higher, $p < .001$. The proportion of right hemisphere processing in language typical non-right-handers (.70) was not significantly higher, $p = .093$. The proportion of left hemisphere processing in language atypicals of .59 was not significantly different, $p = .523$.

To compare if there were differences in the number of participants with right hemisphere dominance in the different groups, a z-test was used. There was no significant difference in the proportion of individuals who processed bodies in the right hemisphere between language typical right-handers (20/23 = .87) 95% CI [.68, .96] and language typical non-right-handers (16/23 = .70), 95% CI [.49, .84], $z = 1.43$, $p = .153$. To examine if there was a difference in the complementary patterns found for language and bodies in the two language typical groups with the language atypical group, z-tests between proportion of right hemisphere processing in the typical groups and left hemisphere processing in the atypical group was compared.

There was a significant difference between language typical right-handers and atypicals (13/22 = .59), 95% CI .39, .77), $z = 2.11$, $p < .035$, 95% CI of the difference (-0.46) did not overlap with zero [-0.50, -0.02]. There was no significant difference between language typical non-right-handers and atypicals, $z = 0.73$, $p = .465$.

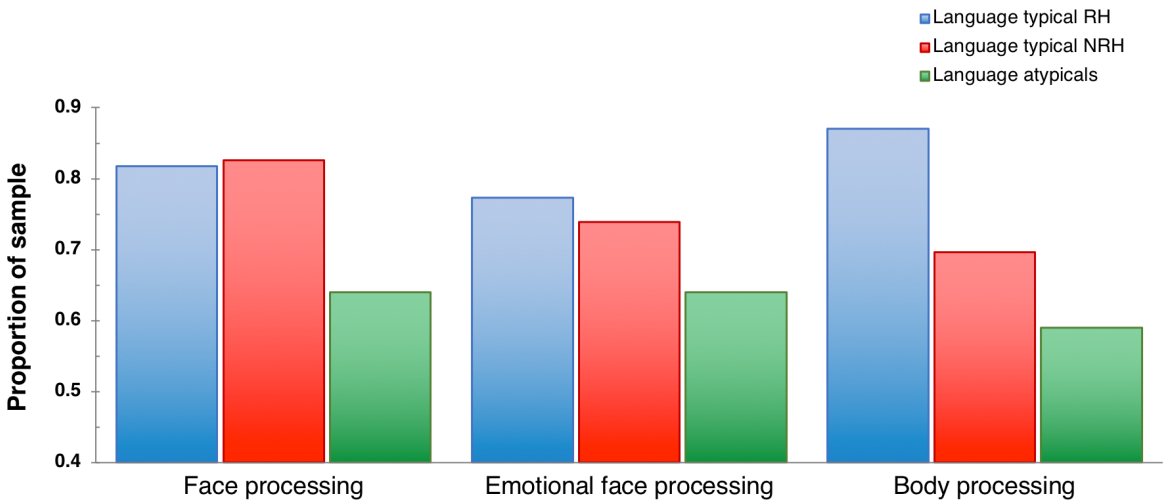


Figure 3.19. The proportion of each group displaying complementary hemispheric dominance with language for each of the visual tasks. RH = right-handers, NRH = non-right-handers. A consistent reduction of a complementary pattern can be seen for the atypical group in each of the tasks. The reduction in rates of complementarity for language typical non-right-handers as compared to their right-handed counterparts is also noteworthy.

3.3.8 Interim conclusion

The results presented does not support complementarity of these functions with language in non-right-handed participants, unlike claims by a recent study by Cai et al. (2013). However, Cai and colleagues used a fairy strict LI cut-off of +0.50 and -0.45 for inclusion in the study. Perhaps individuals that are more strongly lateralised are more likely to show complementary patterns. This was examined below.

3.3.9 Using different cut-offs

There is currently no agreed upon cut-off of what constitutes as lateralised when examining hemispheric asymmetries, and whether a bilateral category should be included or not. Some authors opt to use zero as the boundary, which is the approach used for all other analyses in this chapter. However, LI cut-offs vary, and stringent ones as excluding LI values of +/- > 0.6 have been used (e.g. Van der Haegen et al., 2013). Therefore, the influence of LI cut-off on percentages of *complementarity* was examined (right hemisphere processing in the

two language typical groups and left hemisphere processing in the language atypical group). In Table 3.10, the percentage of individuals with LIs complementary to that of their language function is outlined using different cut-offs, together with the number of individuals that was included in the group at the specific cut-off. As expected, there is a general trend towards increased complementarity at more stringent cut-offs.

Table 3.10

Complementarity of each 'right hemisphere' tasks with language, as a function of different cut-offs. Complementarity generally increases with higher thresholds. Interestingly, emotional prosody and vocalisations, oddly, tend to show decreased complementarity with increasing cut-off bandwidth. Bodies and faces tend to show the expected pattern of increased complementarity with higher cut-offs

		LI cut-off				
		0	0.1	0.2	0.3	0.4
Bodies	**Typical RH**	87% (20/23)	90% (18/20)	94% (15/16)	100% (13/13)	100% (12/12)
	Typical NRH	70% (16/23)	74% (14/19)	71% (10/14)	70% (7/10)	67% (4/6)
	Atypicals	59% (13/22)	67% (12/18)	75% (12/16)	75% (9/12)	71% (5/7)
Emotional vocalisations < non-words	**Typical RH**	78% (18/23)	84% (16/19)	82% (14/17)	80% (12/15)	83% (10/12)
	Typical NRH	48% (11/23)	50% (10/20)	50% (8/16)	50% (5/10)	57% (4/7)
	Atypicals	73% (16/22)	79% (15/19)	82% (14/17)	80% (12/15)	80% (8/10)
Emotional prosody	**Typical RH**	87% (20/23)	85% (17/20)	82% (14/17)	75% (9/12)	63% (5/8)
	Typical NRH	65% (15/23)	73% (11/15)	80% (8/10)	78% (7/9)	100% (5/5)
	Atypicals	41% (9/22)	40% (8/20)	41% (7/17)	42% (5/12)	50% (3/6)
Neutral faces	**Typical RH**	82% (18/22)	80% (16/20)	83% (15/18)	93% (14/15)	100% (10/10)
	Typical NRH	83% (19/23)	80% (16/20)	94% (16/17)	92% (12/13)	88% (7/8)
	Atypicals	64% (14/22)	70% (14/20)	75% (12/16)	77% (10/13)	82% (9/11)
Emotional faces	**Typical RH**	77% (17/22)	79% (15/19)	81% (13/16)	86% (12/14)	92% (11/12)
	Typical NRH	74% (17/23)	73% (16/22)	70% (14/20)	69% (11/16)	64% (9/14)
	Atypicals	64% (14/22)	70% (14/20)	75% (12/16)	85% (11/13)	90% (9/10)

3.3.9 Hemispheric patterns in individuals

Lateralisation patterns found amongst the participants in the study may be worth pursuing, but with some caution with the modest sample size reported here. Hemispheric dominance for fluency, neutral faces, bodies, emotional prosody and emotional vocalisations > non-words were included, and the different combinations of hemispheric patterns found in individuals were investigated. It can be seen that the 'traditional' pattern of hemispheric dominance (with language in the left hemisphere and the other asymmetries in the right hemisphere) is also the most common pattern, with 17 of participants exhibiting this pattern. The second most common pattern, found in 10 individuals is with language and emotional vocalisations processed in the left hemisphere, and faces, bodies, and emotional prosody in the right hemisphere. Amongst language atypical individuals, two patterns were seen most frequently; the reversed 'anti-localising' asymmetry was not as common as expected, but was the joint most common one and seen in four individuals. In a different four individuals, language, bodies, and emotional prosody was processed in the right hemisphere, and faces and emotional vocalisations in the left hemisphere. In total, 24 different combinations of asymmetry patterns were seen in this dataset.

Table 3.11

Lateralisation patterns found amongst the participants in the study. Hemispheric dominance for fluency, neutral faces, bodies, emotional prosody (emopro) and emotional vocalisations > non-words (emovoc) were included

Pattern	Fluency	Face	Body	Emopro	Emovoc	% (n)	Handedness
Traditional	**L**	**R**	**R**	**R**	**R**	**25.37% (17)**	**L = 4, R = 13**
Reversed	**R**	**L**	**L**	**L**	**L**	**5.97% (4)**	**L = 3, R = 1**
Right hemispheric	**R**	**R**	**R**	**R**	**R**	**2.99% (2)**	**L = 2**
Other patterns	**L**	**R**	**R**	**R**	**L**	**14.93% (10)**	**L = 8, R = 2**
	L	**R**	**R**	**L**	**R**	**1.49% (1)**	**L = 1**
	L	**R**	**R**	**L**	**L**	**5.97% (4)**	**L = 2, R = 2**
	L	**R**	**L**	**R**	**R**	**1.49% (1)**	**L = 1**
	L	**R**	**L**	**R**	**L**	**1.49% (1)**	**L = 1**
	L	**R**	**L**	**L**	**R**	**4.48% (3)**	**L = 2, R = 1**
	L	**L**	**R**	**R**	**R**	**1.49% (1)**	**R = 1**
	L	**L**	**R**	**R**	**L**	**1.49% (1)**	**R = 1**
	L	**L**	**R**	**L**	**R**	**1.49% (1)**	**L = 1**
	L	**L**	**L**	**R**	**R**	**2.99% (2)**	**R = 2**
	L	**L**	**L**	**R**	**L**	**1.49% (1)**	**L = 1**
	L	**L**	**L**	**L**	**R**	**2.99% (2)**	**L = 2**
	R	**L**	**L**	**L**	**R**	**1.49% (1)**	**L = 1**
	R	**L**	**L**	**R**	**L**	**5.97% (4)**	**L = 4**
	R	**L**	**L**	**R**	**R**	**1.49% (1)**	**L = 1**
	R	**L**	**R**	**R**	**L**	**5.97% (4)**	**L = 3, R = 1**
	R	**R**	**L**	**L**	**L**	**1.49% (1)**	**L = 1**
	R	**R**	**L**	**R**	**L**	**1.49% (1)**	**L = 1**
	R	**R**	**L**	**R**	**R**	**1.49% (1)**	**L = 1**
	R	**R**	**R**	**L**	**L**	**2.99% (2)**	**L = 2**
	R	**R**	**R**	**L**	**R**	**1.49% (1)**	**L = 1**
Left lateralised	45	22	23	20	33		
Right lateralised	22	45	44	47	34		

3.3.10 Depth of asymmetry based on "typical" and "atypical" processing as a function of handedness

One of the longer-term goals of this type of research would be to quantify asymmetries in larger groups of people who have typical and atypical lateralisation for the function of interest. For example, t-maps could be statistically compared to examine the possibility of any subtle difference in functional organisation in, for example, left hemisphere dominant face individuals compared with their right hemisphere dominant counterparts. In addition, some interesting questions related to handedness and each asymmetry could also be explored. As a first pass, acknowledging the limited sample sizes in some instances, mean LI values for typical and atypical hemispheric specialisation were calculated as a function of handedness group. These mean LI values were compared for the two handedness groups using two-tailed independent samples t-tests to see if the groups differed. Mean LI values can be seen below in Figure 3.20 for individuals with right hemisphere (typical) dominance and Figure 3.21 for individuals with left hemisphere (atypical) dominance. One caveat to these analyses is the rather small number of individuals who are atypically lateralised and right-handed, so those means in particular must be considered tentative.

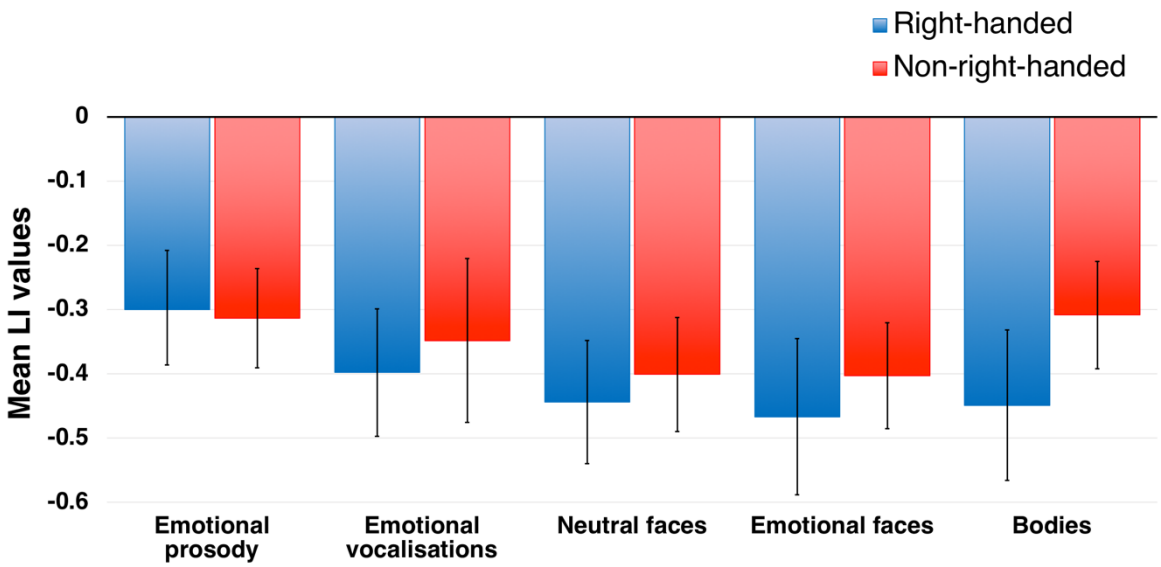


Figure 3.20. Average LI values for right-handers and non-right-handers that were classified as *being right hemisphere dominant* (i.e. typical for each function, LI < 0) for the five different tasks. Errors bars = 95% CIs. A general trend in a reduction in mean LI values for non-right-handers can be seen for most measures, but was only significantly reduced for bodies.

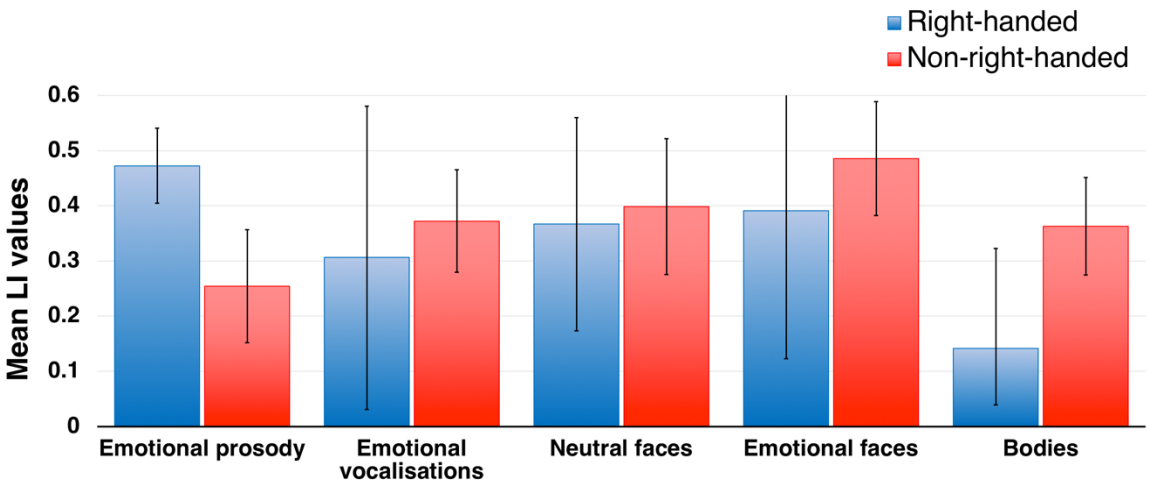


Figure 3.21. Average LI values for right-handers and non-right-handers that were classified as *having left hemisphere dominance* (i.e. atypical for each function, LI > 0) for the five different tasks. Errors bars = 95% CIs. The only significant differences were seen for emotional prosody and bodies. However, these should be interpreted with caution due to the low participant numbers (only 4 participants in both right-handed groups).

3.3.10.1 Emotional prosody.

Out of participants who were right hemisphere lateralised, mean LIs for right-handed (M = -.30, SD = 0.19, n = 21) and non-right-handed (M = -.31, SD = 0.20, n = 27) groups did not significantly differ, $t(46) = -0.16$, $p = .871$. Of those who were left hemisphere lateralised, mean LI values for right-handed (M = .47, SD = 0.04, n = 4) and non-right-handed (M = .25, SD = 0.19, n = 16) were significantly different, $t(18) = 4.14$, $p = .001$, $d = 1.60$.

3.3.10.2 Emotional vocalisations > non-words.

Out of participants who were right hemisphere lateralised, right-handed (M = -.40, SD = 0.19, n = 18) and non-right-handed (M = -.37, SD = 0.25, n = 17) mean LIs did not significantly differ, $t(33) = -0.39$, $p = .701$. Of those who were left hemisphere lateralised, mean LIs for right-handed (M = .31, SD = 0.24, n = 7) and non-right-handed (M = .38, SD = 0.22, n = 26) groups did not significantly differ, $t(8.85) = -0.71$, $p = .494$.

3.3.10.3 Neutral faces.

Of participants who were right hemisphere lateralised for faces, groups of right-handed (M = -.44, SD = 0.19, n = 18) and non-right-handed (M = -.40, SD = 0.22, n = 27) participants did not significantly differ, $t(43) = -0.67$, $p = .507$. Mean LI for right-handed (M = .37, SD =

0.18, n = 6) and non-right-handed (*M* = .40, *SD* = 0.23, n = 16) left lateralised groups did not significantly differ, *t*(20) = -0.30, *p* = .764.

3.3.10.4 Emotional faces.

Out of participants who were right hemisphere lateralised, right-handed (*M* = -.47, *SD* = 0.24, n = 17) and non-right-handed (*M* = -.40, *SD* = 0.20, n = 25) mean LI did not significantly differ, *t*(40) = -0.94, *p* = .352. Of those who were left hemisphere lateralised, mean LIs for right-handed (*M* = .39, *SD* = 0.29, n = 7) and non-right-handed (*M* = .49, *SD* = 0.21, n = 18) groups did not significantly differ, *t*(23) = -0.91, *p* = .371.

3.3.10.5 Body processing.

Of those right lateralised for bodies, mean LI values for groups of right-handers (*M* = -.45, *SD* = 0.24, n = 21) and non-right-handers (*M* = -.31, *SD* = 0.20, n = 24) were significantly different, *t*(43) = -2.20, *p* = .034, *d* = 0.63. Of those who were left hemisphere lateralised, LI values for right-handers (*M* = .14, *SD* = 0.11, n = 4) and non-right-handers (*M* = .36, *SD* = 0.18, n = 19) were significantly different, *t*(21) = -2.29, *p* = .033, *d* = 1.47.

3.4 Discussion

The aim of this set of studies was to examine the relationship between handedness and language dominance for several asymmetries that have been reported in the previous literature to depend more on the right cerebral hemisphere (in groups of right-handed participants at least). Of specific interest was the breadth and depth of the right hemisphere asymmetry in in language dominance groups, subdivided by handedness for language typicals. Of crucial importance was the recruitment of individuals with language lateralised to the atypical, right, hemisphere to examine if these individuals had reversed asymmetries for what are typically right hemispheric functions, as predicted by complementary accounts of hemispheric asymmetries. The results presented in this chapter are novel, and first of their kind in many ways, which makes comparisons with extant literature more challenging.

The first, and perhaps most crucial detail to note about these data is that all three groups were matched in terms of mean lateralisation for verbal fluency. Language atypical participants were not just bilateral or less lateralised individuals - they showed as strong activation patterns as language typicals. This finding was seen without the use of any sort of bilateral or excluded category (which could be used to filter cases from one group or the other), which is surprisingly common in the literature. *This 'symmetry' means that any differences*

between the groups on other measures cannot easily be explained by different degrees of language specialisation.

The findings in this chapter support the group-level right hemisphere dominance often reported for emotional prosody in language-typical right-handed participants. Both language typical right-handers and non-right-handers were, on average, right lateralised for emotional prosody. The atypical group was not lateralised in any direction. However, when comparing mean LI values, no differences were found between the groups. Most language typical right-handers were found to process emotional prosody in the 'non-language' hemisphere (.87), and this proportion was higher than expected by chance. Neither language typical non-right-handers and language atypicals had proportions that were different from chance. Furthermore, the .87 of emotional prosody in the non-language hemisphere for language typical right-handers was considerably higher than left hemisphere processing of emotional prosody seen in language atypical participants (.41). There were no differences between the language atypical group or the language typical non-right-handers (.65). Overall, these results suggest that the right hemisphere processing of emotional prosody is reduced in the language atypical sample, but not reversed to the opposite hemisphere. Such data are the first of many in this chapter that are hard to reconcile with complementarity of language and emotional prosody.

The findings from emotional vocalisations were more surprising. Initially, when compared with neutral vocalisations, none of the groups were found to, on average, be lateralised for the contrast. This bilaterality was furthermore reflected in proportional estimates of hemispheric processing, with approximately half of the participants processing emotional vocalisations in the right hemisphere, and half in the left hemisphere. However, when investigating the average group activation maps from these groups, they significantly deviated from other activation patterns reported in the literature. Because of these differences, emotional vocalisations were compared against another neutral contrast, non-words, which were chosen to minimise the linguistic processing that would normally accompany words.

The emotional vocalisation > non-word contrast yielded activation patterns in the STG and amygdala consistent with previous reports (Bestelmeyer et al., 2014; Cervolo et al., 2016; Fecteau et al., 2007; Joly, 2012; Meyer et al., 2005; Phillips et al., 1998). Therefore, it is more likely that the surprising results obtained when contrasted with neutral vocalisations were linked to the control used. Why this was the case remains unclear. Fecteau and colleagues (2007) previously contrasted emotional vocalisations with neutral vocalisations, such as coughs and throat clearings, and reported activity in areas such as the STG, STS, amygdala, and primary auditory cortex, so in theory the original contrast was appropriate.

When emotional vocalisations were examined using this second, unplanned contrast, language typical right-handers were, on average, found to be right lateralised. Language typical non-right-handers were not lateralised for emotional vocalisations when contrasted with non-words, although the average LI was not significantly reduced compared to the right lateralised language typical right-handers. Language atypicals were, on average, left lateralised, but this was not reflected in the breadth of the bias, as a majority was not lateralised to the left hemisphere.

Language typical right-handers and non-right-handers were, on average, right lateralised for neutral face processing to a similar depth. The language atypical group was, on average, left lateralised. The depth of asymmetry seen in the LI values provide some of the strongest support for complementarity with averages, but the underlying proportions tell a slightly less convincing story. Approximately .82 of both language typical groups and .64 of language atypical participants showed a complementary relationship with language processing. This percentage of left hemisphere processing was not significantly different from 50% in this sample of atypical participants. These results are similar to the one study that proportions of hemispheric dominance can be calculated from. It can be deduced from Badzakova-Trajkov et al. (2010) supplementary data that 96% of their language typical right-handers and 77% of their language typical non-right-handers were right hemisphere dominant for faces. In their sample of atypicals, only 44% showed a complementary relationship, which is slightly lower that is seen in the current study.

The result does not support current crowding hypotheses that specifically theorise that face processing and language processing are linked (Behrmann & Plaut, 2015; Dehaene et al., 2010). Of course, it should be noted that this may also depend on the tasks used. The current incarnations of the crowding hypotheses between faces and language is about reading and asymmetry in the vWFA. In this instance, verbal fluency tested here is a proxy for any language-related asymmetry. In fact, Van der Haegen, Cai, and Brysbaert (2012) found congruency of 100% in non-right-handed language atypicals as defined by one block of verbal fluency, with vWFA asymmetry. Having said that, their participants were defined as atypical based on LI values of greater than -0.5. The analysis in this chapter do suggest that complementarity, of at least verbal fluency and faces, goes up if a stricter cut-off is applied to the data. Of course, this does not mean that less lateralised individuals should be disregarded, as these people are important for such theoretical questions. The choice of not having a cut-off or using a bilateral category is something that was discussed extensively before the start of data collection. As reviewed in Chapter 1, the boundaries to what classifies as 'bilateral' are difficult to justify and are not well agreed upon in the literature. Furthermore, test-retest with

fMRI LI data is rare. Therefore, it is difficult to know how stable these LI values are from session to session. It would not be unreasonable to expect more noise around 0, for weakly lateralised individuals. However, Jansen et al. (2006) found that if a bilateral category was used (± .2), participants who were classified as bilateral by one calculation, was often not by a different calculation of LIs, or reproducible in a second session. It would perhaps be more appropriate to classify participants in more data driven ways. For example, test-retest could be used to classify individuals as consistently lateralised or not. Alternatively, the boundaries for categorical misclassification rates could be defined. In other words, identify how often individuals with single session LI values of, for example, ± 0.1 would be misclassified in a second session or run.

Interestingly, asymmetries for emotional face processing were very similar to that of neutral face processing. It was proposed that the emotional expressions would have had additive effects, as both face processing and emotional processing have been linked with the right hemisphere. Again, the two language typical groups were, on average right lateralised, and the atypical group, on average, left lateralised in the task. The breadth of asymmetry for emotional faces was also nearly identical to that seen in neutral faces. Perhaps there are not large differences in how these neutral and emotional static images are processed, in terms of asymmetry at least. For example, Carvajal et al. (2013) argue that neutral expressions are usually assigned some emotional significance. This could be why differences between the two conditions are not seen.

Language typical right-handers were, on average, right lateralised for body perception. The other two groups were not lateralised, on average. A large proportion (.87) of right-handers had more activation in the non-language hemisphere for body perception, and this was statistically higher than 50. Language typical non-right-handers (.70) and language atypicals (.59) did not have a significant breadth for body processing. This pattern suggests the intriguing possibility of handedness moderating the effect of body dominance (interest in such patterns is also facilitated by the equivalence of all three groups on their depth of language asymmetry). This possibility is further substantiated by the fact that the handedness groups, regardless of language dominance, differed in mean LI values even when they were categorised as right hemisphere body dominant or left hemisphere body dominant. Body typical right-handers were, on average, more strongly lateralised than non-right-handers. Also noteworthy was that body atypical non-right-handers were, on average, more strongly lateralised than the right-handed group, although keeping in mind that this right-handed group only consisted of four individuals.

This weakened asymmetry in body processing in non-right-handers is consistent with the results from Willems et al. (2010), who found that such participants were bilateral on average when measuring EBA activation, in comparison to right-handers who were right lateralised, as in the current study. Willems et al. (2010) did, however, also find that FFA was not lateralised in their sample of non-right-handed participants. Although FFA specifically was not measured in this study, non-right-handers were, on average, right lateralised for the whole-brain activation pattern. One difference between the studies is that Willems and colleagues (2010) used a threshold dependent measure of activity, whilst a threshold-independent approach was utilised here. Bukowski et al. (2013) also found that FFA was activated bilaterally for non-right-handed participants, but that this difference was not apparent when comparing the whole-brain, as OFA and pSTS were right lateralised. If ROIs had been used to target the different core face networks areas, then perhaps differences may have been found on a regional level between the groups.

In summary, most right-handers were right lateralised in their breadth of prosody processing, face processing, emotional face processing, and body processing. It was also to an extent observed for emotional vocalisations (depending on the subtraction condition). This was also apparent in average LI values, as right-handed participants showed group-level right hemisphere biases for each of the tasks. Language typical non-right-handers were also right-lateralised, on average, for emotional prosody processing, face processing and emotional face processing. The only two tasks language typical non-right-handers were not lateralised for, as groups, were for emotional vocalisations and body processing. Language atypicals were left lateralised, on average, for face processing, emotional face processing and emotional vocalisations when contrasted with non-words. Language atypicals were, however, in terms of breadth of asymmetry, not lateralised for any of the measured contrasts.

Overall, the results do not support complementarity of functions when both language typical and language atypical participants are included. This is different from conclusions by Cai et al. (2013) who found strong support for complementary of functions for a verbal fluency task and a landmark task. They found that *all* atypically lateralised individuals were left hemisphere lateralised in their spatial task, and 15 out of 16 language typicals were right hemisphere lateralised. Of course, one caveat is that they only included participants who had LIs of > 0.5 or < 0.45. Instead, the strongest support for complementarity with language processing in the current dataset came from the group of language typically lateralised right-handers. Interestingly, the highest rates of complementarity in language typical right-handers alone was seen for emotional prosody and bodies. Rates of right hemisphere processing in typical non-right-handers were significantly reduced in both of these contrasts. It should be

noted that the 95% confidence intervals did not overlap with zero for emotional prosody processing but did so for body processing. Nevertheless, these results suggest that *non-right-handers are more variable in their lateralisation patterns in a way that is independent from language*.

These sorts of data might be relevant for ideas gleaned from the handedness literature, where similar genetic theories of human handedness have been proposed (e.g. McManus 1999; Annett, 2002). For example, McManus (1999) proposed a two-allele gene, with a dextral (D) allele specifying right-handedness and a chance (C) allele that does not specify the direction of handedness, and instead leaves it to chance. In accordance with this theory, DD individuals would be right-handed; 75% of DC right-handed and 25% non-right-handed. CC phenotypes would be divided equally between the two handedness groups. By cataloguing multiple asymmetries in large numbers of individuals, the most common phenotype(s) of cerebral patterns might be identifiable. According to this kind of model, some subset of individuals have handedness and different cerebral asymmetries randomly determined (subject to crowding constraints at some of the more extreme ends of the random distribution).

Of course, one limitation is that the sample sizes here are small for proportional analyses, and this is particularly true considering the skewed nature of the data. This is reflected in the rather large confidence intervals that accompanies each proportional difference. Nonetheless, by accumulating data from more participants, this is an extremely useful analysis for determining constructs/processes that really differentiate right-handers and non-right-handers in terms of proportional properties. Furthermore, only associations between language asymmetry and each of the other functions were investigated as part of this chapter. This direction of travel was largely influenced by history. In terms of handedness and cerebral asymmetries, language asymmetry came first and is in some sense, at least implicitly, seen as the 'mother' of all cerebral asymmetries. In fact, models of human evolution often link bipedalism to freeing up the hands for tool use as well as gestural communication (e.g. Arbib et al., 2008). Michael Corballis in turn links these ideas to human right-handedness (Coballis, 1991).

It is clear from the presented set of studies that any claim of complementary specialisation is incomplete unless it has been evaluated using both typically and atypically lateralised individuals. Saying that, finding atypically lateralised individuals *has been a challenge*. Most efforts by others to include at least a few atypically lateralised individuals in their samples have consisted of scanning large numbers of non-right-handed individuals, a costly enterprise. As seen in this chapter, atypically lateralised individuals (not only for language processing) are valuable for several theoretical questions. Being able to identify likely atypical candidates

before (or without) scanning, using simple behavioural measures, would open doors to make these investigations able to be carried out on a larger scale. If hemispheric dominance can be determined using short behavioural predictors is examined in the next, and final empirical chapter.

CHAPTER 4

Behavioural predictors of functional cerebral asymmetries

4.1.1 Introduction

Behavioral responses on perceptual asymmetry tasks, should, at least, weakly relate to an individual's brain lateralisation. It is however sensible to suggest, considering the varied results obtained from different measures that are supposed to be linked to at least similar constructs, that some tasks may be better at predicting brain asymmetries than others. As such, fMRI data can be used for evaluating how well these behavioural measures predict underlying cerebral asymmetry. With the development of more robust techniques to examine neuroimaging data from individual participants, these questions are now possible to examine.

Surprisingly, studies examining associations between perceptual measures of asymmetry with data from neuroimaging, or other more direct techniques, are relatively rare. One of these studies was conducted by Yovel, Tambini, and Brandman (2008). They scanned 17 right-handed participants on a face localiser and asked the same participants to complete a chimeric face task outside of the scanner. They used a ROI approach to identify face-selective activations in the right and left FFA and OFA, and compared the lateralisation of these with the biases obtained in the chimeric face task. They found a significant positive correlation between the asymmetry of the FFA volume and the behavioural visual-field asymmetry (r = .49, see Figure 4.1), but no correlation between the asymmetry of the OFA and the behavioural measure (r = .15). This paper suggests that the magnitude of right hemisphere FFA activation, at least, correlate with visual field superiority in a perceptual face task.

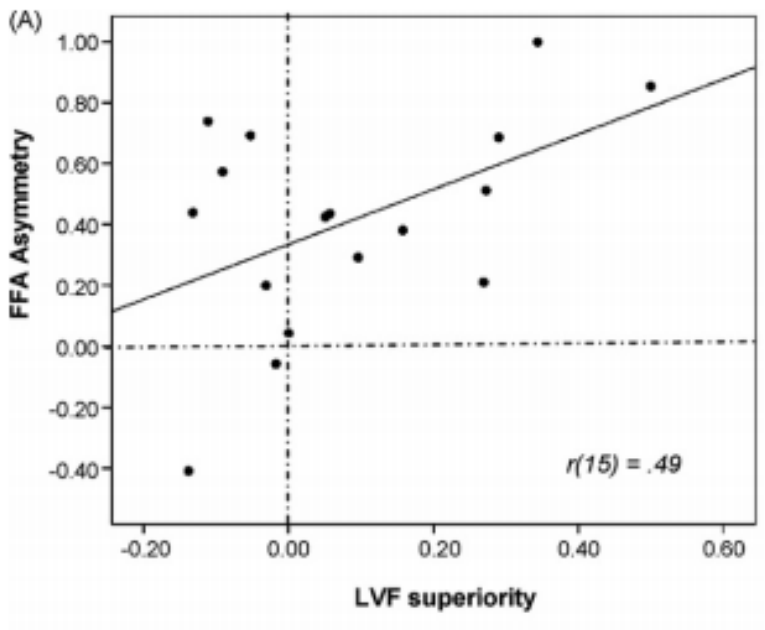


Figure 4.1. Scatterplot of FFA and VHF asymmetry from Yovel et al. (2008). A positive value for FFA indicates larger activation in the right hemisphere. All nine subjects who showed a left side bias had a larger right than left FFA, but only two of seven individuals with a RFA had larger activation in left, as compared to right, FFA.

There have been a few attempts (all from the same research group) to relate behavioural measures of asymmetry to hemispheric dominance for language. In the first paper of the series, Hunter and Bryesbaert (2008) used a bilateral VHF picture naming task and a bilateral VHF word naming task to examine how well these tests would predict hemispheric processing of language as assessed using a verbal fluency task in a fMRI experiment. They recruited 26 non-right-handed participants (as non-right-handed individuals are more likely to have varied language dominance) for the behavioural part of the experiment. They selected 10 out of these participants for inclusion in the fMRI experiment; 6 with consistent RFAs in both tasks, 2 with no clear advantage, and 2 with LFAs in both behavioural tasks. Both participants with no clear advantage had a LFA in the words task, but no advantage in the picture task. They found strong positive correlations (picture naming: $r = 0.77$; word naming: $r = 0.63$) between LIs from each perceptual task with fMRI LIs. More importantly, all participants with a strong RFA were left hemisphere dominant as assessed with fMRI, and both participant with a strong LFA were right hemisphere dominant. Out of the two weakly lateralised individuals, one was right hemisphere dominant and one left hemisphere dominant (LI values: -0.19 and +0.37 respectively), but both were classified as bilateral by the authors.

One issue with this study is its very small sample size. Therefore, the usefulness of these same two perceptual tests in predicting asymmetries was examined in a larger cohort of non-

right-handers by Van der Haegen and colleagues (2011). They recruited 250 participants for the perceptual tests, and invited 50 back to be scanned. Of these participants, 20 had a LVF advantage of at least 10ms in both the picture and word naming task. Fourteen participants had RFAs, with LIs of more than 10ms favouring the RVF, in both tasks. The remaining 16 participants had either had no advantage (< 10ms), or an advantage on one task but not the other. They used the LI toolbox (Wilke & Lidzba, 2007) to examine lateralisation patterns in ROIs of Broca's area, (pars opercularis and pars triangularis) as 'these showed the highest correlations with the VHF data' (Van der Haegen et al., 2001, pp. 2884). As in Hunter and Bryesbaert (2008), they found positive correlations between the picture naming task (r = .65) and word naming task (r = .64) with the fMRI data (see Figure 4.2). Importantly, of the 20 participants with consistent LVF advantages scanned, 16 turned out to have atypical dominance (80%, 95% CIs 58%, 92%). The classification was more successful for individuals with consistent visual field advantages for both tasks (when only these individuals were assessed, correlations were increased, picture: r = 0.76; word: r = 0.74), suggesting that perhaps combining tasks can predict language lateralisation more reliably then a single test on its own.

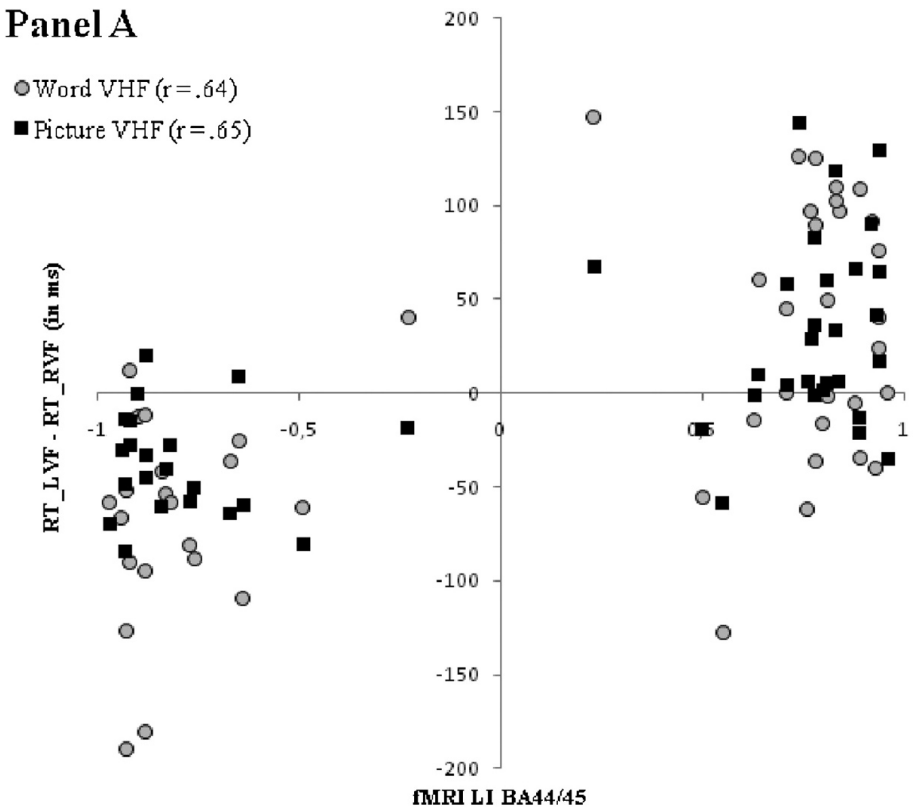


Figure 4.2. Correlation between LIs on the VHF tasks and LIs on the fMRI task from Van der Haegen et al. (2011). LI values from fMRI were based on the activation in Brodmann area 44 and 45 (Broca's area) in the verbal fluency task (*x*-axis). Perceptual measures are RT differences in the picture and word VHF task (*y*-axis) (two data points per participant are plotted), for all participants but one (*N* = 49).

Lastly, Van der Haegen, Westerhausen, Hugdahl, and Brysbaert (2013) examined if left hemisphere dominant individuals, as assessed with fMRI, had significant REAs and right hemisphere dominant individuals had significant LEAs in a CV dichotic listening task. They recruited 41 non-right-handed participants, 31 who had taken part in the previous VHF study. The 31 participants from the previous study were not chosen based on any criteria, and all participants from Van der Haegen et al. (2011) were asked to take part in the dichotic listening task. The additional 10 participants were recruited to increase participant numbers. They also recruited an additional sample of 22 right-handers. Van der Haegen et al. (2011) found that those that were left hemisphere dominant on the language task were, on average, right ear biased on the CV dichotic listening task, and those who were right hemisphere dominant were, on average, biased towards the left ear. Data from individual participants was not reported, but can be deduced from a scatterplot provided in the paper. It should be noted that this paper only included participants with a LI value of +/- 0.6 for verbal fluency in the analysis, and it is

not clear if or how many participants were excluded if they fell below this value. Twelve of the 16 right hemisphere dominant individuals had a LEA (75%, 95% CIs 51%, 90%). Out of individuals who were left hemisphere dominant, 32 of 43 had a REA (74%, 95% CI 60%, 85%). Unfortunately, the authors did not compare the results from the DL task and the VHF task for the 31 participants who took part in both.

There are currently no studies with multiple perceptual predictors of neuroimaging data, these two VHF language tasks aside. This absence is somewhat understandable, as there are currently no models of what asymmetries relate to one another. There are currently two extreme options from the literature; either all functions are yoked to language, or all functions lateralise independently and just happen to be skewed towards one hemisphere over the other (Bryden, 1990; Bryden & Allard, 1981; Bryden et al., 1983). Of course, the reality might fall in between these two options; a subset of functions might relate to one another in a complementary fashion. Therefore, perhaps a test of attentional asymmetry might help predict asymmetries in face of body processing, if these functions share variance in some sense.

When dealing with these kinds of data, skew is a problem, as a considerable majority are typically lateralised, for language at least. Most studies that have attempted to identify individuals with atypical profiles (or determine relationships between lateralised functions), for language, have recruited a large number of participants in order to include at least a few individuals with atypical dominance (Allendorfer et al., 2016; Häberling et al., 2016; Króliczak, Piper & Frey, 2016; Mazoyer et al., 2016; Tzourio-Mazoyer et al., 2015; Van der Haegen et al., 2011). These studies are quite expensive to run, given the costs of neuroimaging, as well as the time it takes to recruit large numbers of non-right-handers who are relatively rare (for a review of the unfortunate exclusion of non-right-handers from psychology and neuroscience, see Willems et al., 2014).

Given the costs involved with the use of fMRI, *the development of a behavioural battery with predictive qualities could provide researchers with a means to identify individuals with likely atypically lateralised profiles before scanning*. Thus, to conclude the empirical work of this thesis, this chapter aims to quantify the potential value of the behavioural measures used to date as predictors of five different fMRI-derived asymmetries. The specific aim was to examine if combinations of behavioural measures from the perceptual asymmetry battery of tests can help predict typical and atypical lateralisation for the some of the specialisations described in Chapter 3.

4.1.2 Multivariate techniques to predict categorical data

Discriminant analysis (DA) and logistic regression (LR) and are two multivariate techniques used to examine categorical dependent variables. Both techniques are used to predict group membership reliably from a set of independent variables, but work in different ways and require different assumptions.

The primary goal of discriminant analysis is to interpret patterns of differences amongst predictors as a whole to understand the dimension(s) along which groups differ, and to find n - 1 (n = number of groups) classification functions to predict group membership. DA uses the F statistic derived from measures of central tendency. As such, it is used to interpret patterns of differences amongst the predictors as a whole to identify key differences between the groups. DA creates a linear combination of independent variables to maximize group differences to develop a model which classifies cases at a better rate than chance alone.

The second technique that can be used is logistic regression. LR is a form of regression for dichotomous dependent variables. It overcomes the regression assumption of observed data having a linear relationship through a logarithmic transformation, which is a way of expressing a non-linear relationship in a linear way (Berry & Fieldman, 1985). LR predicts the probability of group membership in relation to several variables. The LR analysis is based on calculating the odds of the outcome, as the ratio of the probability of having the outcome divided by the probability of not having it. LR is popular as it is a flexible technique; predictors do not need to be normally distributed, related to the dependent variable in a linear fashion, or of equal variance within each group.

4.1.3 Comparing DA and LR

Many chose LR over DA because it is not as rigid in its assumptions, and easy to interpret. There are a range of assumptions that needs to be met before conduction a DA. The data for the variables must be multivariate normally distributed. Since each of the predictor variables must have an equal chance of contributing to the function at the inception, DA is sensitive to violations of homogeneity of the variance-covariance matrices. Satisfying this assumption is especially important if classification is an important goal of the analysis and when sample sizes are unequal or small. In order to obtain an effective discriminant function, the variables used to predict group membership should not be highly correlated with each other. Each variable must be independent of each other so the analysis will be able to distinguish the relative importance of each predictor. As DA is sensitive to measures of central tendency, it is highly sensitive to outliers. Violations of the multivariate normal distribution are acceptable as long as the distribution is skewed rather than subjected to outliers.

For LR there is no formal requirement for multivariate normality, homoscedasticity, or linearity of the independent variables within each category of the dependent variable, although satisfying these conditions may enhance power (Tabachnick & Fidell, 2014). Predictors can also be a mix of categorical and continuous independent variables, whilst DA traditionally only uses continuous variables as the predictor variables. LR is especially useful when the distribution of responses for the dependent variable is expected to be nonlinear with one or more of the independent variables. LR is, however, sensitive to multicollinearity (high correlations among predictor variables). Another of the disadvantages of LR is its need for very large sample sizes. When the data set is small, the analysis becomes unstable and LR may give misleading results for samples under 100 (Pampel, 2000). More independent variables also require more cases, and a minimum of 50 cases per independent variable is recommended (Wright, 1995). Furthermore, imbalances in group sizes demand larger number of cases in each category. DA usually has no problem with unequal samples if the size of the smallest group exceeds the number of predictor variables (Stevens, 2002). However, highly unequal sample sizes are better handled by LR than DA is the sample size is sufficiently large (Tabachnick & Fidell, 2001). Overall, the two techniques often reveal similar patterns in the data, however, when assumptions are met, discriminant analysis may be more powerful (Spicer, 2005).

For the current study, DA was chosen as the participant numbers available for inclusion were small. Discriminatory analyses were carried out to examine which variables best differentiate right hemisphere and left hemisphere dominance for verbal fluency, neutral face processing, emotional prosody processing, emotional vocalisation processing, and body processing, respectively.

4.2 Methods

4.2.1 Participants

The sample consisted of 63 individuals who took part in the fMRI and behavioural experiments, 23 were right-handed and 40 non-right-handed. The mean age of the sample was 23.84 (*SD* = 6.25), and average WHQ 28.22 (*SD* = 1.83) for right-handers, and -23.03 (*SD* = 11.92) for non-right-handers.

4.2.2 Stimuli/materials and procedures

4.2.2.1 Group variables.

The grouping variables for the different analyses were derived from the fMRI data described in more detail in Chapter 3. Participants were either categorised into a right hemisphere dominant group or a left hemisphere dominant group, based on LI values from the associated neuroimaging contrast. A cut-off of 0 was used for this categorisation; all participants < 0 were categorised into the right hemisphere group, and all LI > 0 into the left hemisphere group. The grouping variables that were used for separate analyses, and the associated contrasts used to calculate these, can be seen in Table 4.1.

Table 4.1

fMRI contrasts used to group participants as either left hemisphere dominant or right hemisphere dominant for the different analyses

Grouping variable	fMRI contrast
Language	Verbal fluency > control
Faces	Neutral faces > flowers, butterflies
Bodies	Bodies > chairs
Emotional prosody	Emotional prosody > neutral prosody
Emotional vocalisations	Emotional vocalisations > non-words

4.2.2.2 Predictor variables.

A subset of the behavioural measures described in Chapter 2 were included as predictors for each of the analyses. The criterion for inclusion was that all perceptual tests scores were available for each of the scanned participants. The values from each perceptual test was expressed as an LI, where a negative score indicates a left field/ear advantage, and a positive score indicates a right field/ear advantage. The following behavioral measures were included as predictors:

Chimeric faces 2.0: a chimeric face task where the score indicates bias to the side of the face participants found more emotionally expressive;

Colourscales: a task where participants made judgments about coloured bars. The score reflects the side bias participants had in the task;

CV dichotic listening: a dichotic listening task were participants reported back one out of two syllables that were presented to the left and right ear simultaneously. The score represents the ear bias participants had in the task;

EmoDL short: a dichotic listening task where participants reported back one out of two emotional tones presented to the left and right ear simultaneously. The score represents the ear participants reported more emotional tones from;

Lateral naming: a lateralised naming task were participants were asked to name words presented in their left or right visual fields. The score represents the visual field a participant was more accurate at reporting back the word from;

VHF face categorisation: a visual half field task were participants decided if faces presented to their right or left visual fields were male or female. The score reflects the reaction time biases participants had to one visual field over the other;

VHF word categorisation: a visual half field task were participants decided if words presented to their right or left visual fields were animal words or vegetable/fruits. The score reflects the reaction times biases participants had to one field over the other.

The detailed behavioural test descriptions and procedures can be found in Chapter 2.

4.2.3 Data analysis

As these analyses were exploratory, all variables were inputted into the model simultaneously. It was tempting to assume that the domain-relevant perceptual task for each functional asymmetry would be the mostly highly weighted predictor in any or all of the obtained equations. In fact, error-related variance in another perceptual task could just as

easily aid in prediction, assuming either reciprocal arrangements between those two domains, or perhaps independent sources of noise for the two perceptual tests.

4.3 Results

Table 4.2

Mean LI values for each grouping variable as function of dominance category, and independent t-tests comparing absolute LI values between the two groups. It was found that the two dominance groups for each of the grouping values were matched in terms of lateralisation values. It can also be observed that all functions were, on average, moderately to strongly lateralised

Dominance	**Left hemisphere group**	**Right hemisphere group**	**Comparison of absolute scores**
Fluency	.64 (0.17)	-.58 (0.22)	$t(61) = -1.27$, $p = .210$
Neutral faces	.38 (0.22)	-.40 (0.21)	$t(60) = 021$, $p = .832$
Bodies	.32 (0.19)	-.38 (0.23)	$t(61) = 0.99$, $p = .328$
Emotional prosody	.29 (0.20)	-.31 (0.19)	$t(61) = 0.21$, $p = .833$
Emotional vocalisations	.36 (0.23)	-.37 (0.21)	$t(61) = 0.27$, $p = .789$

4.3.1 Language dominance

Out of the 63 individuals who took part in both studies, 43 were categorised as left hemisphere dominant for language processing, and 20 as right hemisphere dominant. Table 4.3 shows the average LI scores for each of the predictors and each hemispheric group, and the main effect of hemisphere on LI values using univariate ANOVAs. Histograms for each predictor and hemispheric group can be seen in Appendix E. A discriminant analysis was used to determine the linear combination of predictor variables that best classified the cases into the two groups. The discriminant analysis showed that Wilks' lambda, as a test of discriminant function, was significant, $\lambda = .62$; $\chi^2 (7) = 27.89$, $p < .001$, with an R^2 canonical = .62 (79% of variance explained by the model). Table 4.3 also shows the standardised canonical coefficients and the structure weights. Four of the seven variables contributed to the multivariate effect based on standardised canonical coefficients (indicated by a value of > .3, Tabachnick & Fidell, 2014). The following four variables were found to be determinants of hemispheric dominance for language: CV dichotic listening (.62), chimeric faces 2.0 (-.49), lateral naming (.35), and emoDL short (-.33).

Table 4.3

Predictors, standardised coefficients, structure weights, means and ANOVA results for the discriminant analysis. The standardised coefficients indicate the relative importance of the predictor variables in predicting the dependent. The structure matrix shows the magnitude of correlations between each measure and the discriminant function

Predictor variable	Standardised coefficient loading	Structure matrix	F ratio	Left hemisphere mean LI (SD)	Right hemisphere mean LI (SD)
Chimeric Faces 2.0	-.49	-.57	12.28**	-23.93 (41.54)	14.17 (36.98)
Colourscales	.06	-.09	0.30	-20.35 (38.67)	-14.25 (47.00)
CV dichotic Listening	.62	.70	18.46***	19.47 (30.68)	-18.99 (37.87)
EmoDL short	-.33	-.32	3.83	-17.15 (30.31)	-0.66 (32.91)
Lateral Naming	.35	.38	5.57*	0.17 (0.17)	0.04 (0.26)
VHF Face task	.13	.13	0.68	-0.94 (6.74)	-2.41 (6.21)
VHF Word task	.17	.21	1.74	3.60 (7.15)	1.17 (6.01)

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 4.4 summarises the group membership results of the classification routine. The overall correct classifications of hemispheric dominance from the model was 81%. Of the variables investigated, CV dichotic listening was the most discriminating and colourscales the least.

Table 4.4

Classification results of the discriminant analysis for language dominance

Group	Number of cases	Correctly classified, n (%)	Misclassified, n (%)
Left hemisphere	43	39 (90.7)	4 (9.3)
Right hemisphere	20	12 (60.0)	8 (40.0)

4.3.2 Neutral face dominance

For this task, data from 62 participants was available as one right-handed female did not take part in the face localiser experiment. Out of the 62 individuals, 41 were categorised as right hemisphere dominant for neutral face processing, and 21 as left hemisphere dominant. Table 4.5 describes the average scores for each of the predictors and each group, and the main effect of hemisphere on LI values using univariate ANOVAs. Histograms for each

predictor and hemispheric group can be seen in Appendix E. A discriminant analysis was used to determine the linear combination of predictor variables that best classified the cases into the two groups. The discriminant analysis showed that Wilks' lambda, as a test of discriminant function, was significant, $\lambda = .58$; $\chi^2(7) = 30.65$, $p < .001$, with an R^2 canonical = .65 (80.62% of variance explained by model). Table 4.5 also shows the standardised canonical coefficients and the structure weights, revealing that three of the seven variables contributed to the multivariate effect. The following three variables were found to be determinants of hemispheric dominance for neutral faces: CV dichotic listening (-.85), emoDL short (.71), VHF words categorisation (.42).

Table 4.5

Predictors, standardised coefficients, structure weights, means and ANOVA results from the discriminant analysis of face dominance

Predictor variable	Standardised coefficient loading	Structure matrix	F ratio	Left hemisphere mean LI (SD)	Right hemisphere mean LI (SD)
Chimeric Faces 2.0	.18	.48	10.01**	11.71 (46.05)	-22.97 (37.97)
Colourscales	-.01	.10	0.45	-13.10 (40.26)	-20.61 (42.31)
CV dichotic Listening	-.85	-.47	9.69**	-11.36 (37.59)	17.83 (33.55)
EmoDL short	.71	.57	13.81***	7.53 (30.20)	-21.51 (28.59)
Lateral Naming	.16	.03	0.04	0.14 (0.22)	0.13 (0.21)
VHF Face task	.28	.24	2.58	0.47 (5.43)	-2.35 (7.02)
VHF Word task	.42	.14	0.80	3.60 (7.07)	2.02 (6.30)

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 4.6 summarises the group membership results of the classification routine. The overall correct classifications of hemispheric dominance from the model was 82.3%. Of the variables investigated, CV dichotic listening was the most discriminating and colourscales the least.

Table 4.6

Classification results of the discriminant analysis for face dominance

Group	Number of cases	Correctly classified, n (%)	Misclassified, n (%)
Right hemisphere	41	39 (95.1)	2 (4.9)
Left hemisphere	21	12 (57.1)	9 (42.9)

4.3.3 Body dominance

Out of the 63 individuals who took part in the study, 40 were categorised as right hemisphere dominant for body processing, and 23 as left hemisphere dominant. Table 4.7 describes the average scores for each of the predictors and each group, and the main effect of hemisphere on LI values using univariate ANOVAs. Histograms for each predictor and hemispheric group can be seen in Appendix E. A discriminant analysis was used to determine the linear combination of predictor variables that best classified the cases into the two groups. The discriminant analysis showed that Wilks' lambda, as a test of discriminant function, was significant, $\lambda = .61$; χ^2 (7) = 28.85, $p < .001$, with an R^2 canonical = .63 (79.37% of variance explained by model). Table 4.7 also shows the standardised canonical coefficients and the structure weights, revealing that two of the seven variables contributed to the multivariate effect. The following two variables were found to be determinants of hemispheric dominance of body processing: CV dichotic listening (-.88), and emoDL short (.54).

Table 4.7

Predictors, standardised coefficients, structure weights, means and ANOVA results from the discriminant analysis of body dominance

Predictor variable	Standardised coefficient loading	Structure matrix	F ratio	Left hemisphere mean LI (SD)	Right hemisphere mean LI (SD)
Chimeric Faces 2.0	.18	.45	8.16**	7.79 (48.50)	-23.13 (36.71)
Colourscales	.15	.19	1.37	-10.43 (42.82)	-23.00 (40.08)
CV dichotic Listening	-.88	-.75	22.37***	-18.12 (34.17)	21.85 (31.19)
EmoDL short	.54	.42	6.84*	1.31 (36.11)	-19.52 (26.72)
Lateral Naming	-.07	-.21	1.78	0.09 (0.26)	0.16 (0.18)
VHF Face task	.04	.02	0.01	-1.28 (6.27)	-1.48 (6.81)
VHF Word task	.14	-.04	0.06	2.54 (6.13)	2.99 (7.31)

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 4.8 summarises the group membership results of the classification routine. The overall percentage of the level of hemispheric classifications was 82.5%. Of the variables investigated, CV dichotic listening was the most discriminating and VHF face categorisation the least.

Table 4.8

Classification results of the discriminant analysis for body dominance

Group	Number of cases	Correctly classified, n (%)	Misclassified, n (%)
Left hemisphere	40	37 (92.5)	3 (7.5)
Right hemisphere	23	15 (65.2)	8 (34.8)

4.3.4 Emotional Prosody

Out of the 63 individuals who took part in the study, 45 were categorised as right hemisphere dominant for emotional prosody, and 18 as left hemisphere dominant. Table 4.9 describes the average scores for each of the predictors and each group. Histograms for each predictor and hemispheric group can be seen in Appendix E. A discriminant analysis was used to determine the linear combination of predictor variables that best classified the cases into the two groups, however, the discriminant analysis showed that Wilks' lambda, as a test of discriminant function, was not significant, $\lambda = .82$; χ^2 (7) = 11.39, $p = .123$. This means that the predictors used could not significantly discriminate right and left hemisphere dominant individuals.

Table 4.9

Means (SDs) and ANOVA results for right and left hemisphere dominant participants grouped according to dominance for emotional prosody for each of the predictor variables

Predictor variable	F ratio	Left hemisphere mean LI (SD)	Right hemisphere mean LI (SD)
Chimeric Faces 2.0	4.57*	6.25 (45.04)	-19.07 (41.43)
Colourscales	1.39	-28.06 (38.81)	-14.56 (41.93)
CV dichotic Listening	2.88	-5.22 (37.95)	12.25 (36.48)
EmoDL short	2.98	-1.13 (32.35)	-16.23 (30.95)
Lateral Naming	0.27	0.16 (0.20)	0.12 (0.22)
VHF Face task	0.23	-2.04 (6.78)	-1.16 (6.54)
VHF Word task	0.01	2.96 (5.95)	2.78 (7.25)

* $p < .05$

4.3.5 Emotional vocalisations

Out of the 63 individuals who took part in the study, 33 were categorised as right hemisphere dominant for emotional vocalisations, and 30 as left hemisphere dominant. Table 4.10 describes the average scores for each of the predictors and each group. Histograms for each predictor and hemispheric group can be seen in Appendix E. A discriminant analysis was used to determine the linear combination of predictor variables that best classified the cases into the two groups, however, the discriminant analysis showed that Wilks' lambda, as a test of discriminant function, was not significant, $\lambda = .89$; $\chi^2 (7) = 6.85$, $p = .445$. This means that the predictors used could not significantly discriminate right and left hemisphere dominant individuals.

Table 4.10

Means (SDs) and ANOVA results for right and left hemisphere dominant participants grouped according to dominance for emotional vocalisations for each of the predictor variables

Predictor variable	F ratio	Left hemisphere mean LI (SD)	Right hemisphere mean LI (SD)
Chimeric Faces 2.0	1.72	-4.31 (40.82)	-18.69 (45.66)
Colourscales	0.05	-19.67 (44.43)	-17.27 (38.71)
CV dichotic Listening	0.06	6.09 (42.90)	8.32 (32.36)
EmoDL short	4.65*	-3.10 (35.26)	-19.93 (26.44)
Lateral Naming	0.05	0.14 (0.20)	0.13 (0.23)
VHF Face task	1.34	-0.41 (5.46)	-2.32 (7.40)
VHF Word task	1.21	1.83 (5.73)	3.73 (7.72)

* $p < .05$

4.4 Discussion

This is the first study to examine the predictive value of several perceptual behavioural tests in determining hemispheric dominance for different functions. The aim of the current chapter was to identify perceptual predictors of hemispheric dominance in individuals who had been scanned and taken part in the perceptual battery of asymmetry tests. The collective set of factors were able to predict hemispheric membership for three out of the five 'dominances' investigated; language, faces and bodies. The perceptual tests were not able to predict an individual's dominance for emotional prosody or emotional vocalisations.

Language dominance was discriminated best by CV dichotic listening (with left hemisphere dominant participants having a REA, on average, and right hemisphere dominant participants having a LEA, on average), second best by chimeric faces (LFA, on average, for left hemisphere dominant participants and RFAs for right hemisphere dominant participants), followed by lateral naming (left hemisphere dominant more accurate for words in RVF and reduced to no error bias in the right dominant group) and lastly emoDL short (LEA for left dominant group and reduced to no LEA in right dominant group).

In fact, the VHF face task did not help to predict group membership, and neither did the colourscales tasks. As suspected, the perceptual tests used do not always relate as directly to the underlying cerebral asymmetry as may be suspected. This result further confirms the assumption from Chapter 2 that CV dichotic listening seems to be a good language-related measure of hemispheric asymmetry; as seen in Chapter 2, it was the best task for producing rates of REAs and LEAs in right-handed and non-right-handed participants, most comparable to those derived from Wada testing. Interestingly from Chapter 2, the rates of visual field bias in the VHF words task differed between the handedness groups, with an increased proportion of RFA in right-handers, but the handedness groups did not differ in the lateral naming task. Nonetheless, the lateral naming task helped to separate individuals of different dominance when the VHF words task did not. Perhaps the lateral naming task is only predictive in the tails of its distribution. A similar result was reported by Van der Haegen et al. (2011), as it was found that consistent strong visual field advantages predicted hemispheric dominance, but that those individuals with inconsistent or weak advantages could lateralise 'either way'. Van der Haegen et al. (2011) used RT measures for their analysis whilst the current study made use of the error scores derived from the task. Error scores were opted for as RT were not strongly lateralised in either right-handers or non-right-handers in Chapter 2.

Two 'right hemispheric' tasks also helped to predict language dominance. The first of these, and also second-best predictor, was the chimeric face task. This finding is perhaps not surprising given the theory that face processing should anti-localise with language processing,

and the associations between the two fMRI measures seen in the previous chapter, for language typical individuals at least. Indeed, the group of individuals with right hemisphere dominance for language had, on average, a RVF advantage on this task. EmoDL short also contributed to the model, but here, the LEA was only reduced, and not reversed, in the right dominant group.

A combination of the predictors could also help predict hemispheric dominance for face processing. Surprisingly, neither of the two perceptual face tasks contributed to the discrimination in the model. The best discriminant item was CV dichotic listening (with right hemisphere dominant participants having a REA, on average, and left hemisphere dominant participants having a LEA, on average), followed by emoDL short (right dominant group had a LEA, and left dominant group had a REA), and the VHF words task (both groups had a comparable RFA). A previous study found a relationship between FFA asymmetry and chimeric faces (Yovel et al., 2008). The chimeric face task did not contribute to the model, but was useful when the other predictors were not controlled for (indicated by a structure matrix correlation of .48). This finding is also implicated in the univariate analysis, as there was a difference in chimeric face LI scores between the two groups, with right dominant individuals having a LFA and left dominant individuals having a RFA. It may be that chimeric faces on its own, helps to predict face dominance, but when included with other predictors, its effect is captured by some of the other predictors. The opposite can be seen for the VHF words task; it helped predict as part of a model, but was not related to hemispheric dominance on its own, or did not differ in LI between those who were right hemispheric and those who were left hemispheric.

Hemispheric dominance for emotional prosody and emotional vocalisations could not be predicted by the behavioural data. This failure to predict dominance was not because the distributions of the LI values for prosody and vocalisations were much closer to zero as compared with the other measured asymmetries, as this might have meant that it was harder to capture variance in the scores. Surprisingly, emoDL scores did not differ in terms of mean LI for prosody dominance, but mean LIs were different for emotional vocalisations.

Interestingly, body dominance could be successfully predicted, even though no perceptual measure of body asymmetry was included as any of the predictors. Only dichotic listening and emoDL short were contributing factors in this model. Again, chimeric face LI was correlated to the hemispheric dominance on its own, and it may be that variance is captured by other predictors. In fact, CV dichotic listening is not only the best predictor for language dominance, but also for face dominance, and body dominance (and strongly so). As seen in Chapter 3, there were strong anti-localising links between language processing and face

processing in typically lateralised individuals. There were also strong links between language processing and body processing in typically lateralised right-handers.

In summary, some tests seem to work for several functions, whilst some tests, like colourscales and the VHF face task, seem to work for none, even though the tests themselves were highly lateralised in groups of right-handers and non-right-handers. The lack of a difference between non-right-handers and right-handers might be relevant here**.** Perhaps colourscales would work to predict dominance in an attentional task, like the landmark task, but that this function is relatively unrelated to the dominances measured here.

A major curiosity of the present results is the failure to successfully classify atypicality so routinely in the three fMRI-derived asymmetries where significant models were found. For the current set of analyses, participant numbers are not hugely discrepant in each of the typical and atypical dominance groups. Even with the current reasonably balanced sample sizes, is was easier to predict typicality (~90% accuracy for typical dominance and 60% accuracy for atypical dominance for each of the three models). This unexpected difference is not obviously related to group fMRI LI values, and their approximate spread, as these were similar in typical and atypical groups. Individuals that were left hemisphere dominant and right hemisphere dominant were matched, in terms of depth, for each function in this sample. One plausible explanation is that individuals in these groups are more inconsistent in the way they lateralise for different functions, which results in more variable results for the perceptual tests. As seen in the previous chapter, language atypicals alone were more heterogeneous than both typical groups for most functions as measured directly by fMRI. It is crucial to note that the sample size here is small, and any interpretations are limited. Data on all indirect and fMRI measures are skewed towards typical lateralisation. Therefore, conducting these analyses with confidence would require large sample sizes, mainly of course to accumulate a sufficient number of atypical cases. Controlling for handedness effects in such analyses is also desirable but adds considerably to the power issue already present.

In conclusion, results on the perceptual tests were able to predict hemispheric membership for language, faces, and bodies, but not for emotional prosody or emotional vocalisations. The models for language, faces, and bodies were good at classifying typically lateralised individuals, but classified atypically lateralised individuals with much less accuracy These kinds of data, comparing several asymmetries measured with both perceptual tests and fMRI localisers, is the first of its kind in laterality research.

CHAPTER 5

General discussion

Previous research has linked a number of different specialisations with the right cerebral hemisphere. However, the breadth of these asymmetries, and whether or not/how they relate to handedness in a similar fashion as that seen for language is unclear. The main aim of this thesis was to examine several asymmetries linked with the right hemisphere, in both right-handed and non-right-handed participants. The goal was to examine, describe, and quantify these asymmetries in individual people using both behavioural and neuroimaging techniques. An important foundation of this work was that the analytical approach did not restrict itself to the typical inferential statistics that focus on measures of central tendency.

The study in Chapter 2 collected, collated and summarised data from a large-scale behavioural battery of perceptual tests. The focus was on examining breadth and depth of typical and atypical asymmetries in right-handers and non-right-handers for a variety of functions, including language processing, face processing, emotional processing and attentional processing. In Chapter 3, fMRI was used to examine asymmetries in perception of emotional prosody, emotional vocalisations, bodies, and neutral/emotional faces, in individual people using a threshold-independent technique. These data were also grouped according to dominance in a verbal fluency task, in order to examine complementarity of these right hemispheric asymmetries with language. Finally, in Chapter 4, fMRI data and behavioural data were combined to examine if a combination of behavioural predictor could be useful for predicting functional lateralisation.

5.1 Chapter 2 – Perceptual asymmetries in right-handers and non-right-handers

In Chapter 2, the results from the behavioural battery of perceptual tests were summarised, all which have been related to cerebral asymmetries of the left and right hemispheres. In absence of previous strong evidence from non-right-handed participants for many of the included tests, one-tailed predictions were made for all of the tests, using the ‘complementary’ perspective that language and non-language asymmetries should, more often than not, anti-localise for the two hemispheres. In other words, both right-handers and

non-right-handers were expected to have significant biases in the typical direction for all tasks, but with reduced breadth in the non-right-handed group. In fact, this reduced breadth in non-right-handers was only found for five of the ten included tests.

Three of the tests linked with specialisation of the right hemisphere differentiated between right-handers and non-right-handers (chimeric faces 1.0, chimeric faces 2.0, and emoDL short) but three of the tests did not (colourscales, emoDL long, and the VHF faces task). The two chimeric faces tasks suggest that face processing may anti-localise with language, or at the very least differ in its breadth between right-handers and non-right-handers, in a direction consistent with complementarity. Both tasks found a consistent reduced breadth of approximately 14% of the typical right hemisphere bias in the non-right-handed sample. Unfortunately, the VHF face task did not produce any differences between the handedness groups, although the breadth of asymmetry significantly favoured the right hemisphere (.58 in both groups).

A particular challenge for this type of research is to distinguish between two possibilities in these instances of failure to discriminate, in the expected way, between right- and non-right-handers. The first possibility is that the test in question does noes not adequately measure the underlying construct. These types of failure could include a range of possibilities, from an insufficient number of trials to poor mapping to the underlying construct. For example, the 48 unilateral trials in the VHF face and word tasks were somewhat limited. Hunter and Brysbaert (2008) recommend the use of > 150 trials to account for intrasubject variability and practise effects. This claim, however, was not evaluated empirically. It would be worthwhile examining cumulative subsets of the data and testing the resulting LI scores against the large item total (192 trials in their task). In this chapter, all of the tests were specifically designed with the intention of use in a multiple-test single session battery. Therefore, short administration times were prioritised. The underlying assumption of the approach was that many individual units, even with high variability and low test-retest, might be combined statistically to produce more robust predictors of an underlying asymmetry or asymmetries. This idea was examined in Chapter 4.

A second possible reason for failing to discriminate between handedness groups is that a test is in fact equivalently asymmetrical in right-handed and non-right-handed groups. The more direct measure of asymmetry in Chapter 3 seemed to suggest that small differences, at least, should be obtained for face processing between the two handedness groups. A likely possibility in this particular instance is that either the stimuli, the number of trials, or the sex judgement utilised in the VHF task were not appropriate for this sort of purpose. For example, low level visual features (such as eyebrow density) were poorly controlled for in the stimuli.

For whatever reason, experience in the lab suggests that only chimeric face tasks seem to produce reliable LVF biases.

One interesting finding to highlight is that some functions may just not differ between right-handers and non-right-handers, and, by inference, be unrelated to speech and language asymmetries. Evidence in this thesis (perceptual asymmetries; Chapter 2), Whitehouse and Bishop (2009; fTCD) and in the shared data from the Bordeaux and Auckland neuroimaging groups (fMRI; Badzakova-Trajkov et al., 2010; Zago et al., 2016) suggest that this, at least, is the case for one kind of attentional processing. Relatively robust leftward biases were obtained in the colourscales task, but these were present in both handedness groups to the same breadth and depth. Although it is not entirely clear what precise mechanism underlies the asymmetries seen in the colourscales task, patient data support that the leftward bias in greyscales results is due to a right-hemispheric attentional asymmetry (Mattingley et al., 1994; Mattingley et al., 2004). It would have been desirable to confirm these results in a second perceptual measure of attentional asymmetry. However, no alternative which yielded robust leftward asymmetries was found when searching the literature for tasks to include in the perceptual battery. One option would have been to include a line bisection task, often described in neurotypicals as a measure of pseudoneglect. There is some indication that there are handedness effects in line bisection, with a reduced depth of leftward bias in non-right-handed groups (Jewell & McCourt, 2000; Ochando & Zago, 2018). Some sort of landmark task might also be worth considering, but at face value may assess an underlying mechanism quite similar to what drives the colourscales bias (Chen et al., 2019).

The lateralisation of emotional prosody from the two dichotic listening tests was less conclusive. Although both tests suggested leftward biases for both handedness groups, the data from the short version suggests a reduced breadth in the non-right-handed group of .11, with confidence intervals that did not overlap with zero. However, non-right-handed participants actually had increased breadth, as compared to right-handers, on the long version of emoDL. Although the short version was optimised by removing items with strong stimulus dominance items, these four removed pairs were unlikely to have changed a participant's overall ear advantage, unless the participant score was very close to zero (no overall ear advantage). It should also not be linked to the items selected for inclusion in the final version, as there were strong correlations (r = .81) between the LI scores for items that were included and those taken out.

As Grimshaw and others note, matching words produced with emotional prosody is difficult. For example, some of the prosodic cues indicating sadness, compared with fear or happiness, result in longer utterances and means that there will be a slight mismatch between

stimulus length in the two ears. Stimulus *amplitudes* were normalised to the same level, however, changing the duration of the sound file will influence the emotional perception of that sound. The difference in duration was unavoidable, even though care was taken to match words as well as possible. This is not an issue in other language dichotic listening tasks, such as the CV dichotic listening. These syllables are spoken in a neutral tone and with a constant intonation and are easily matched in duration (Rimol et al., 2006). Furthermore, for CV pairs, spectral and temporal overlap of the paired stimuli is carefully matched which means that the syllables are likely to perceptually fuse, which also reduces the cognitive demands of the paradigm (Westerhausen, 2019).

The CV dichotic listening, lateral naming, VHF words, and the octave illusion have all been related to left-hemispheric processes (Deutsch, 1983; Hugdahl & Anderson, 1984; Hugdahl & Franzon, 1985; Hunter & Brysbaert, 2008). For the octave illusion, no differences were found between right-handers and non-right-handers, and neither of the groups had an overall bias for one ear over the other. For the three language tasks, right-handed and non-right-handed participants had significant biases towards the right ear/visual field, on average. A mean difference between the two handedness groups was only found for CV dichotic listening, and differences in breadth of asymmetry were found for CV dichotic listening and the VHF words task, but not for lateral naming. For CV dichotic listening, .85 of right-handers and .78 of non-right-handers had biases for syllables presented to the right ear. For the VHF words task, this was reduced in both groups to .75 for right-handers and .66 for non-right-handers. Both of the proportions seen for these tests is lower than what is seen in the population as measured by more direct techniques (Carey & Johnstone, 2014). Of course, it was not expected for these tests to be perfect predictors of language dominance, achieving as high proportions as suggested by neuroimaging and Wada methods. However, at this stage of this research, CV dichotic listening has the best (albeit modest) relationship to an asymmetric language construct(s), given the right-handed and non-right-handed differences on this test, as well as its relative utility for predicting neuroimaging group membership (Chapter 4).

In summary, evidence provided in this chapter only suggests face processing as a contender function that anti-localises with language processing. The historical absence of perceptual data from non-right-handed participants for non-verbal asymmetries was unfortunate. Here, relatively large numbers of right-handed and non-right-handed participants were tested, meaning that some outstanding questions are starting to be addressed.

5.2 Chapter 3 - Functional asymmetries in right-handers and non-right-handers

The second empirical chapter utilised fMRI to examine breadth of right hemisphere processing of emotional prosody, emotional vocalisations, bodies, and neutral/emotional faces in both right-handed and non-right-handed participants. The main approach here concentrated on the question of anti-localisation with language, by recruiting language typical and language atypically lateralised individuals. Although people are starting to examine several asymmetries within the same individuals (attention and language, and faces and language to some extent) they do not quantify asymmetries in the same way that is carried out here. Instead, the usual focus remains on central tendency (in the case of imaging, group average statistical maps, see for example Biduła et al., 2017). Strengths of the research presented in this chapter was the large (power questions notwithstanding) sample of language atypically lateralised individuals, and the use of a threshold-independent technique to examine LI values in individual people.

The data collected in this chapter suggests that complementarity with language was reasonably high in language typical right-handed individuals for all functions measured. Non-right-handed individuals and language atypicals were much more varied in their lateralisation patterns. This variability was observed even though all three language groups were matched in terms of their magnitude of language lateralisation. Language atypically lateralised individuals did not have group-level breadth of asymmetry patterns for any of the measured specialisations.

The examination of breadth and depth of right hemispheric processing of emotional prosody in individuals with known language dominance was a sub-aim of Chapter 3. Prosody perception, like its counterparts in language, was the subject of considerable interest in neurology long before the rise of neuroimaging. The neuroimaging work itself has largely replicated the neuropsychological evidence for right hemispheric specialisation, depending on task. Hemispheric dominance of prosody compared with syntax/segmental processing in language has been the subject of some speculation, particularly in models which suggest differences in hemispheric processing of auditory temporal frequency information (Friederici, 2017; Zatorre & Gandour, 2007). These arguments suggest the atypical language dominance, if assessed by an appropriate test, should lead to left hemispheric processing of emotional prosody.

This is not what was seen in the results from this study. Although most language typical right-handers were found to process emotional prosody in the ‘non-language’ hemisphere (.87), this was not seen in the language typical non-right-handers (.65) or in language atypicals (.41). Of course, it may be that the lower-level one-back auditory task used here might not be

the most appropriate for measuring lateralisation of prosody. Nevertheless, some of the subvocal labelling demands of previous studies might engage left hemispheric mechanisms in a way that would not have been desirable for the present purposes.

Emotional vocalisations provided a surprisingly different picture, in asymmetry terms, than expected. The planned contrast with neutral vocalisations (such as coughs and throat clearings) produced little in the way of lateralised activity, or, for that matter, activity in regions claimed by the small extant literature. The unplanned contrast, with neutral non-words, produced a much more understandable pattern of laterality results. However, as acknowledged previously, word-like non-word stimuli can drive lateralised temporal lobe circuits normally interested in more linguistic stimuli. An informal analysis comparing emotional vocalisations against rest provides a pattern more like the second unplanned contrast than the first, planned contrast. A second, speculative, possibility is that emotional vocalisations may be a type of auditory primitives (especially for emotion) that requires little participation of cortical circuitry under normal circumstances. Of course, a similar case could be made for some facial expressions, which clearly did not result in the same sort of questions posed by emotional vocalisations. In may sound trite to say so, but further research, in a different laboratory, may be needed.

Unlike the prosody literature, were the link to complementarity is slightly more indirect, faces have been linked to the non-language hemisphere in recent models (Behrmann & Plaut, 2015; Centanni et al., 2018; Dehaene et al., 2010; Plaut & Behrmann, 2011). The depth for both emotional and neutral face processing was considerable in all three groups. Intriguingly (see Figure 3.19), the proportion data tell quite a different story; evidence for complementarity is only obtained for the two typical groups. These latter data by themselves are puzzling, and support the argument made here (several times) that both proportions and means need to be the subject of scrutiny.

The LI values for bodies is particularly noteworthy for at least two reasons. Firstly because of the difference seen in breadth of asymmetry in the three groups even when language dominance is controlled: non-right-handed language typicals were less likely to be right lateralised than their right-handed counterparts. Secondly, even when controlling for hemispheric processing (i.e. dividing participants according to an LI value of ± 0 creating a 'right hemisphere' groups and a 'left hemisphere' group), the LI values for body processing were reduced in the non-right-handed sample of typically lateralised individuals. When categorised in this way, bodies were the only measure that differed between the handedness groups. The breadth of body processing in the right-handed group is also worth commenting on, as, with emotional prosody, it was considerable.

5.3 Chapter 4 - Behavioural predictors of functional cerebral asymmetries

In Chapter 4, it was found that a combination of behavioural predictors could be used to classify typical and atypical hemispheric processing for language, faces, and bodies. Emotional prosody and emotional vocalisations could not be classified from the included tests. It was found that some behavioural tests seemed to help predict hemispheric dominance better than others. For example, CV dichotic listening and emoDL were predictors in all three significant models, whilst colourscales and the VHF face task did not help with prediction in any of them.

Interestingly, the perceptual asymmetry test with the highest loading in the discriminant function was in some instances not necessarily the test related to that process assessed with neuroimaging. For example, CV dichotic listening had a numerically higher weighting than chimeric faces for predicting group membership for neutral faces. Furthermore, the VHF face task did not significantly aid in prediction. This result, in need of extension/replication, supports the idea that, even with perfect complementarity, some perceptual tests will pick up on variance that others do not, which can be related independently to the brain asymmetry measured with fMRI. On one occasion, CV dichotic listening, for example, did receive the highest weighting for predicting fMRI-derived language dominance. Such a result might be surprising to theorists like Hickok and Poeppel (2007), who would place fluency tasks firmly at the articulation end their language model (lateralised), with perception of syllables at the other end (not lateralised). These weightings, in the context of measuring multiple cerebral asymmetries in the same participants, can provide some useful information about the inclusion of such a test in any general asymmetry battery. Theoretically, such investigations can speak to how close or far a test is from measuring one or more core asymmetries, which might be useful in the search for complementarity (or the elimination of complementarity from a model).

A second important conclusion to draw from the results of Chapter 4 is the remarkably poor prediction of atypicality for any of the functions, ranging from a 57% hit rate for face dominance, to a 65% hit rate for body dominance. This poor prediction is probably not completely accounted for by skew in the dataset, as a reasonably large number of atypicals were included for each of the five cerebral asymmetries measured in fMRI. Obviously, more atypicals need to be identified and scanned to clarify this poor predictability. Increased variance in the atypicals of any of these groups is often observed for both the perceptual tests and neuroimaging-derived asymmetries. One possible source of this variance comes from fluctuating asymmetries in individuals with (a) particular underlying genotype(s). More on this topic below.

It would be tempting to add a few additional tests to the perceptual battery to capture additional variance that is currently unaccounted for. In fact, even the shortest review of the huge perceptual asymmetry literature suggests too many possible tests to count (Bryden, 1982; Ocklenburg & Gunturkun, 2017). One imaging task that did not have a direct comparable behavioural measure as such (in the same domain at least) was body processing. Even so, body dominance could be significantly predicted based on the included perceptual tests. It would be desirable to create a perceptual task related to body processing, like a chimeric body silhouette test of some sorts, but that would not load too heavily on other potential visuospatial mechanisms that are also right hemispheric, such as mental rotation and/or left/right discrimination (Corballis, 1997; Ratcliff, 1979). It would also be desirable to have a neuroimaging attentional measure in the same participants, to compare against the obtained colourscales scores and note the potential predictive power of tests like CV dichotic listening. Especially if this attentional measure really is unrelated to language, as suggested by at least three large datasets available from other labs, using both fMRI and fTCD (e.g. Badzakova-Trajkov et al., 2010; Whitehouse & Bishop, 2009; Zago et al., 2016).

5.4 Remaining themes and questions

One of the most interesting findings in this thesis is that it provides support for complementarity of functions in language typically lateralised right-handers. Most right-handed participants processed each of the 'right hemisphere' functions in the opposite hemisphere to language. Although complementarity was high, it was around 80-90% in all of the measured asymmetries (emotional vocalisations > neutral vocalisations aside). What constitutes as sufficient complementarity, or in other words, how many exceptions to the rule of complementarity would be accepted before it is instead seen as evidence for a statistical theory, is also a question for debate. Statistically, it was examined if the proportion was higher than 50%, but could of course also be tested to see if it is lower than 100%.

In contrast to the right-handers, non-right-handers were more varied in their lateralisation patterns. This was especially seen in language atypical individuals (a group that mainly consisted of non-right-handed participants), but also in language typicals to some extent. This finding suggests that cerebral asymmetries differ in handedness groups. One possibility to why these differences are seen relates to genetic models of handedness and cerebral asymmetries (e.g. McManus, 1999; Annett, 2002), that propose that certain recessive genes will result in chance determination of handedness and/or cerebral asymmetries. Thus, any individuals with both recessives would be 50:50 for *any* asymmetry. The consequence of such models is that some unknown proportion of a group of, say right-handers, are from a distribution of

handedness that is half right, half left. Similarly, within that special subgroup of right handers, half will be left-lateralised for language. Similarly, in that sub- subgroup, half will be right-hemispheric for faces and half left. Of course, this consequence means that any models of complementarity of hemispheric specialisations, such as those related to reading and face processing will be violated to *some extent*. By collecting frequency data on multiple asymmetries in the same people, inferences could be made about how frequently these 'rules' are violated, and, interestingly, how frequent the chance determination recessive type occurs in any given sample.

It may instead be that complete complementarity can be obtained with other, better measures of the same underlying asymmetries. Of course, what type of language task, or, for that matter, what type of face processing task would be most appropriate for any attempt to estimate breadth of complementarity is anyone's guess. For example, neuroscientists interested in language and speech asymmetry have used a number of different tasks, including verbal fluency, sentence comprehension, and verb generation amongst others (Bradshaw et al., 2017). In the fMRI face processing literature, no one has discussed the optimal type of face stimulus and/or task for quantifying direction and magnitude of the hypothesised right hemisphere specialisation. Most localisers have used simple one-back block-design tasks with neutral faces. Nevertheless, task selection and design issues seem unlikely as full explanations of differences in breadth of LI values between the three groups for some of the tasks: 'sub-optimality' should affect all the groups equivalently. Of course, confidence in these possible differences could be improved. A key outstanding question, given the temporal and financial costs of such endeavours, and open science initiatives (which encourage detailed pre-planning), is that of how much more data really is necessary for more definitive answers.

One of the most pressing issues within this thesis relates to power and precision. This concern is obviously not as much of an issue for the perceptual battery as it is for the fMRI data. Sample sizes in fMRI are pragmatically constrained, and a neuroimaging study with 68 participants is not of modest size. However, when divided into sub-groups and proportions are of interest, power becomes more of a concern. This problem is especially true when examining lack of differences in functions. Traditional power analysis tools in fMRI are overwhelmingly designed for factorial designs (e.g. Joyce & Hayasaka, 2012; Mumford & Nichols, 2008). Even though recent moves towards pre-registration have put more emphasis of ways of dealing with power in a variety of designs, there is no straight forward way to derive sample size numbers for these kinds of extensive analyses. One alternative would be to use a precision approach, which emphasise effect sizes and confidence intervals (Cumming, 2014). Even so, there were

limitations, without previous data or pilot data, to plan the sample sizes for Chapters 3 and 4 in particular. Now that this thesis has provided an initial estimate, the proportions reported here can be used to decide how large of 95% confidence intervals are acceptable, depending on the particular research question of interest.

In fact, the kind of large numbers required for these proportional analyses lend themselves rather nicely to a multi-lab approach which for example, has been used recently to great effect in examining VHF studies of lexical decision (Hausmann et al., 2019). Fortunately, the general movement towards a more open and reproducible science means that larger collaborations are being formed and encouraged. This multi-lab approach is more challenging in regards to fMRI data, as large concerns about combining data from different scanners have been expressed (Conner, Ellmore, Pieters, DiSano, & Tandon, 2011). However, this challenge *should* be less of a concern if the goal is to combine LI values for identical or near-identical tasks, carried out at different research centres, and derived from the same threshold-independent method using the same brain regions. An alternative, if central tendency and proportion data are not well matched between different centres, would be to approach these questions meta-analytically, where each centre provides a separate effect size estimate. This latter possibility seems perhaps overly conservative, given the lack of detailed, large distribution data, for example, of datasets which are known to be relatively skewed.

These kinds of data, if sufficient numbers are obtained, can be used to start modelling frequency distributions of (LI values) asymmetries for different functions. This was recently carried out by Mazoyer et al. (2014) for a word generation task. They took their dataset containing LI values for a word generation task from a large number of right-handers (144) and non-right-handers (153) and tried to determine distributions seen in the data (see Figure 5.1). As with the data presented in this thesis, it is clear that most individuals are strongly lateralised in this language task, including those that are atypically lateralised, and that it is not just a normal distribution shifted to the left hemisphere. Of course, the data presented in Chapter 3 is not unselected, as language atypical participants were of particular interest. Nevertheless, many unselected individuals have been scanned, and surprisingly few of them, even non-right-handers, have LIs near 0 for the core asymmetries presented here.

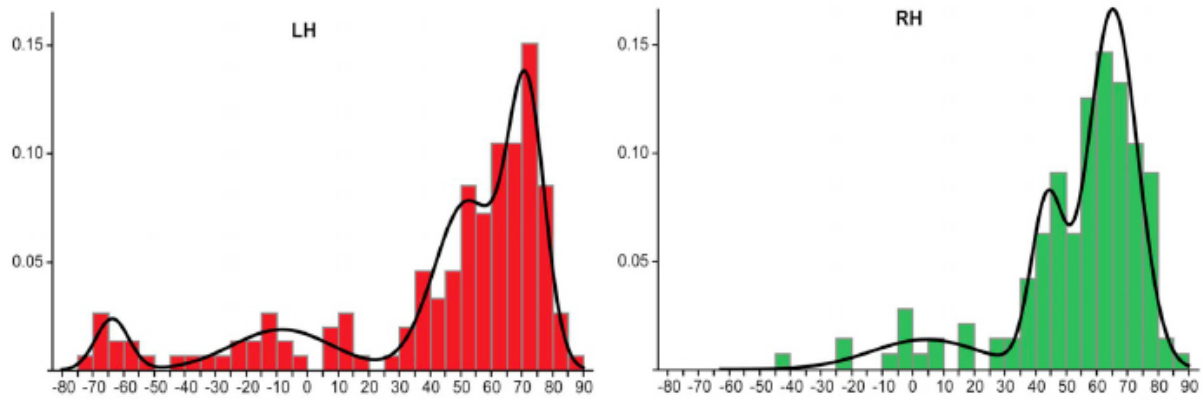


Figure 5.1. Histogram distribution of LI values from the sentence generation task in Mazoyer et al. (2014). The non-right-handers (LH) are presented in the left panel in red, and right-handers (RH) in the right-side panel in green. Solid lines represent fits of these distributions by Gaussian mixture modelling. The majority of individuals in both groups are strongly left lateralised.

Another future endeavour, and exciting possibility, was identified when a local colleague suggested that some functional brain networks can be identified, even at the level of a single participant, from resting state scans alone. A resting state scan measures spontaneous fluctuation in BOLD and how they covary in different regions over time (Bijsterbosch, Smith, & Beckmann 2017). This technology, if it lives up to such promise, could circumvent many of the challenges of long-term recruitment and screening of right- and non-right-handers. Of course, the interesting localisation information about where relevant clusters are during different tasks would not be available. That limitation might be well compensated for by the ability to extract additional data from resting state scans that have already been collected. For example, the default mode network, the core face network, the two attentional networks, etc. If many of these networks, some yet to be described, are asymmetrical, they can be compared with techniques such as the LI toolbox. This 'cumulative collection' seems a very promising approach for generating the statistical power needed to find network asymmetries that are related to one another, and ones that are not.

In order for this field of research to evolve, identifying atypically lateralised individuals are of particular importance. In the first instance, the lab has preliminary data suggesting the left footedness, left sighting dominance, a LEA on CV dichotic listening, coupled with left-handedness, is roughly 80% successful in predicting atypical language dominance. This kind of profile will be replicated and formalised statistically once sample sizes improve. The field is wide open for identifying other atypical asymmetries. Understanding the anatomical localisation of core and extended face networks in face typicals and atypicals could provide

important information for necessary and sufficient conditions for intact face processing. Prediction of atypicality, for the present battery at least is limited. Increased numbers of atypical seems the obvious first step.

Finding right-handers with right hemisphere language dominance is one of the more exciting challenges inspired by this thesis. In absolute terms, if the 5% estimate of speech and language-related atypicality in right-handers is accurate, then these individuals are more frequent in the general population than non-right-handed language atypicals. Of course, in the absence of any additional information, the 'hit rate' for finding atypicals in three times higher in non-right-handers. As noted above, left-footedness, sighting dominance, and a LEA on CV dichotic listening improves this hit rate considerably, but has only been observed within non-right-handers. Two right-handed language atypicals have been identified, and apart from the obvious observation of hand preference, neither of them are left-footed or left-eyed. One of them is quite knowledgeable about asymmetry tests, so her visual test biases, in particular, may be suspect. Nevertheless, both of these individuals had a LEA in CV dichotic listening and tended to show rightward biases on the visual perceptual tasks. An additional group for the comparisons used in this thesis would be extremely interesting. For example, there were strong suggestions of handedness effects when right-handed language typicals were compared with non-right-handed language typicals for some of the right hemisphere asymmetries. A right-handed language atypical group could complete the picture, and differences or similarities to the relative contrast group (e.g. handedness or language dominance) would be extremely interesting for questions relating to handedness and constraints of brain organisation in the field.

Having a reliable way of identifying atypically lateralised individuals is also important for many other research questions beyond complementarity of functions. They can be used to evaluate the limited number of contemporary neuroanatomical models of language which predict how language is asymmetrically represented in the brain (Hickok & Poeppel, 2007; Peelle, 2012; Poeppel, 2014; Price, 2012). For example, according to Hickok and Poeppel (2007), the cortical organisation of speech processing is characterised by a left-hemisphere dominant dorsal stream that is responsible for language production versus a ventral stream that is bilaterally organised and is responsible for comprehension (see Figure 5.2). Typically and atypically lateralised individuals can be used to evaluate these models all the way from input to output, including speech production.

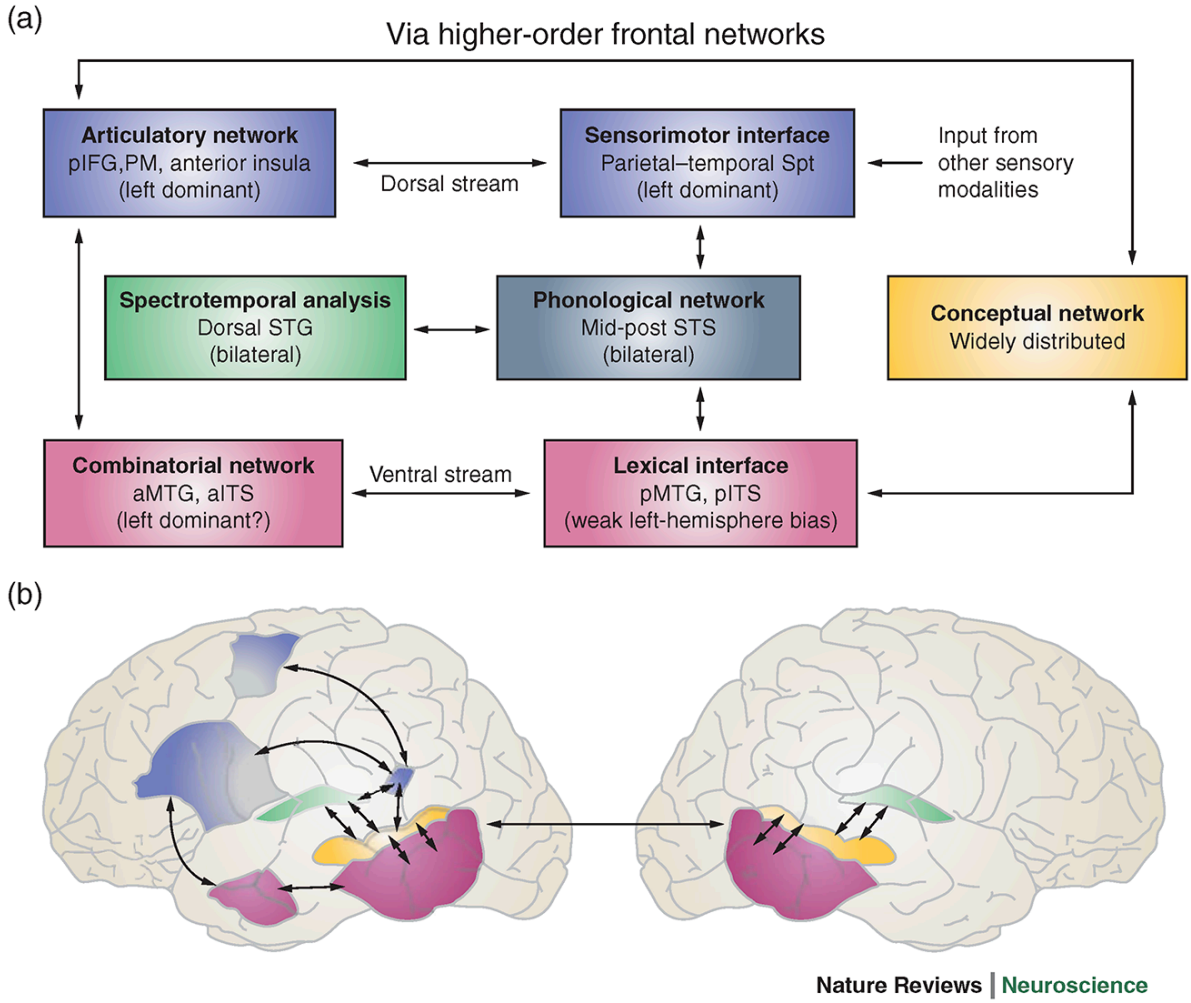


Figure 5.2. Hickok and Poeppel's model of the functional anatomy of language. This is one of the very few models that differentiates between processes that are larger bilateral versus those that are the most left hemispheric in typically lateralised right-handers. Reprinted from Hickok and Poeppel (2007).

These models are, not surprisingly, mostly based on threshold dependent average data from right-handed participants, and needs to be validated on an individual level in order for these different 'sub-components' to be characterised (and the variability seen in laterality of these). Fortunately, researchers are now becoming increasingly interested in examining several of these functions in the same individual people (e.g. Woodhead, Bradshaw, Wilson, Thompson, & Bishop, 2019), although these studies are still mostly limited to right-handed samples. The same is true for any frequency models proposing differences in much earlier, auditory processes (e.g. Friederici, 2017; Zatorre & Gandour, 2007; Schirmer & Kotz, 2006). Atypicals, for any function, are a nice set of participants for testing the limits of models of how functions are instantiated in the brain.

5.5 Concluding remarks

The results in the preceding empirical chapters suggest that there is considerable potential in using neuroimaging and behavioural measures in individual people to help with understanding the complex relationships between different cerebral asymmetries, and how they interact with handedness. The asymmetrical functions examined here, such as language, emotional prosody perception, face perception, and body perception, are essential to the human experience. Why a minority of individuals have these represented in the 'wrong' hemisphere (present author included), and what consequences this has on brain organisation in general is virtually unknown. It is clear that measuring multiple cerebral asymmetries within individual people is an important endeavour for a full appreciation of cerebral dominance and of human handedness. This body of work will hopefully serve as a foundation to inspire further large-scale investigations in this exciting and wide-open field.

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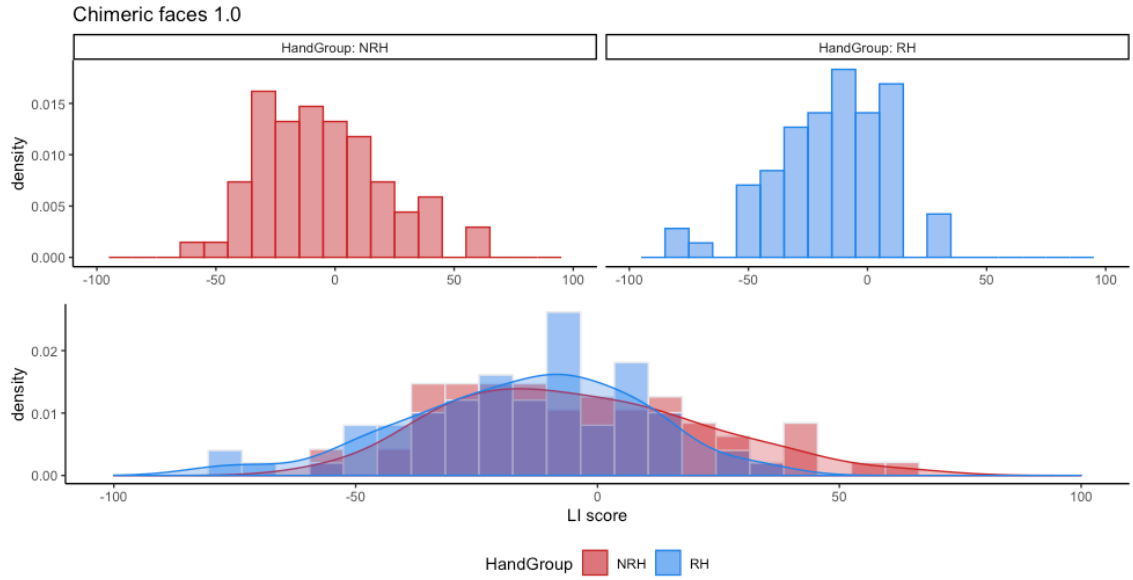
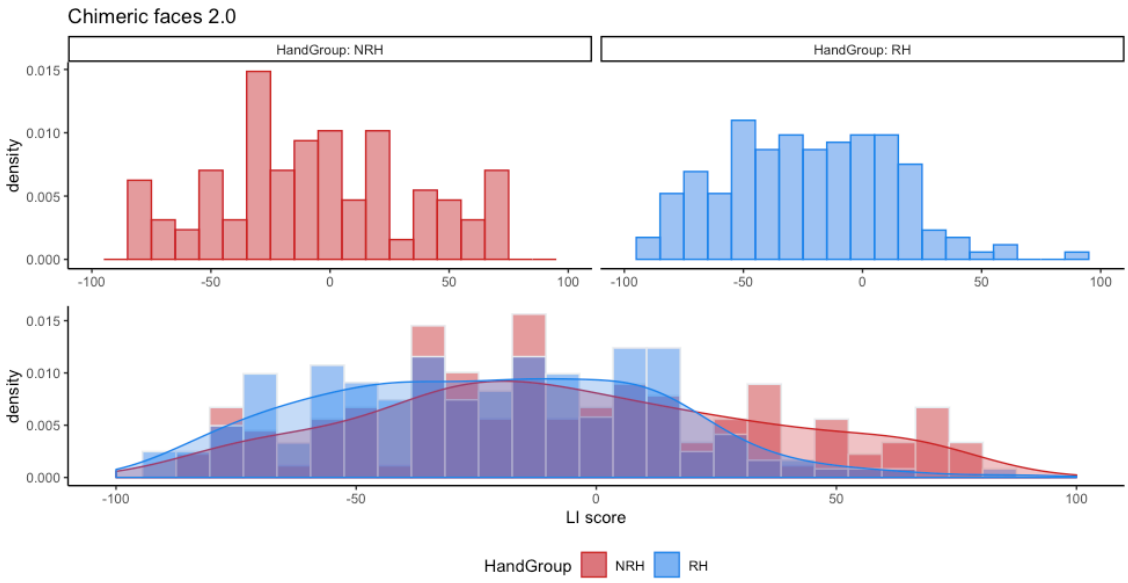
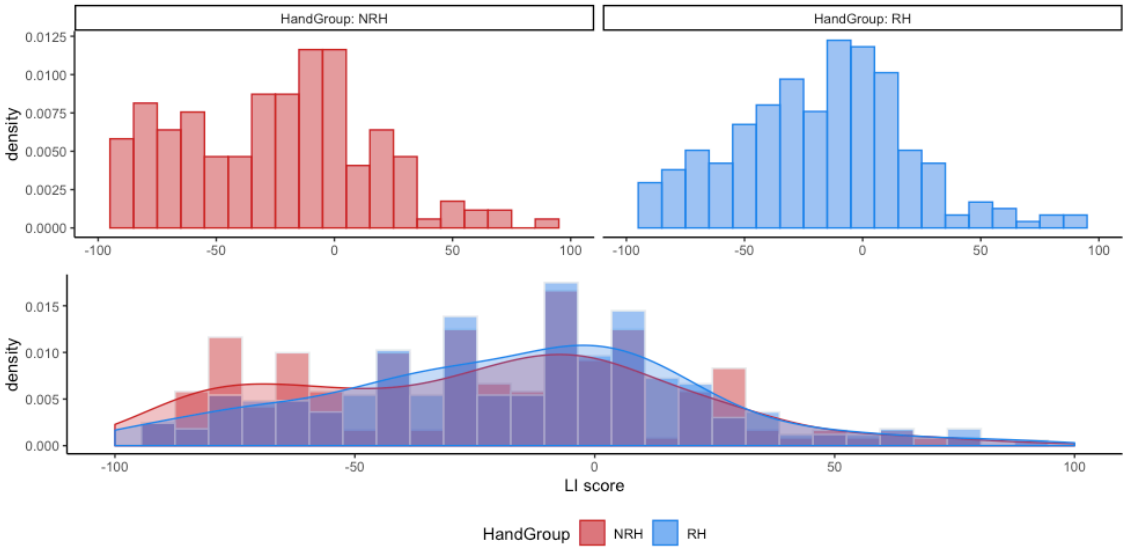
Appendix A

Density histograms showing distributions of scores for non-right-handers (red) and right-handers (blue) separately (top panel), and with the two distributions overlapping (bottom panel) with smooth density estimates represented by red (non-right-handers) and blue (right-handers) lines. Overlapping areas of the distributions are represented in purple. Each of the perceptual measures are plotted in separate graphs.

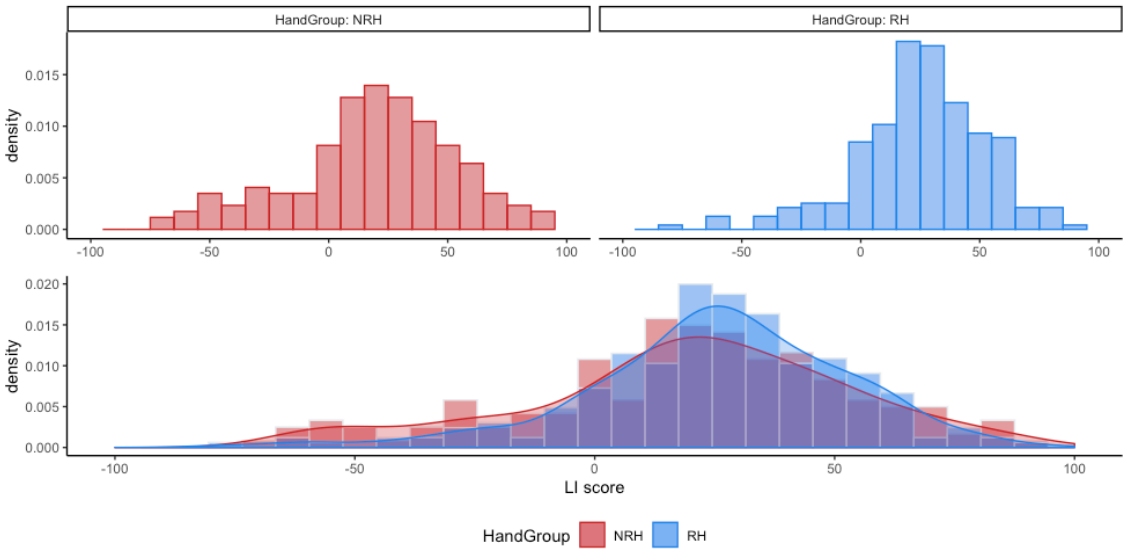




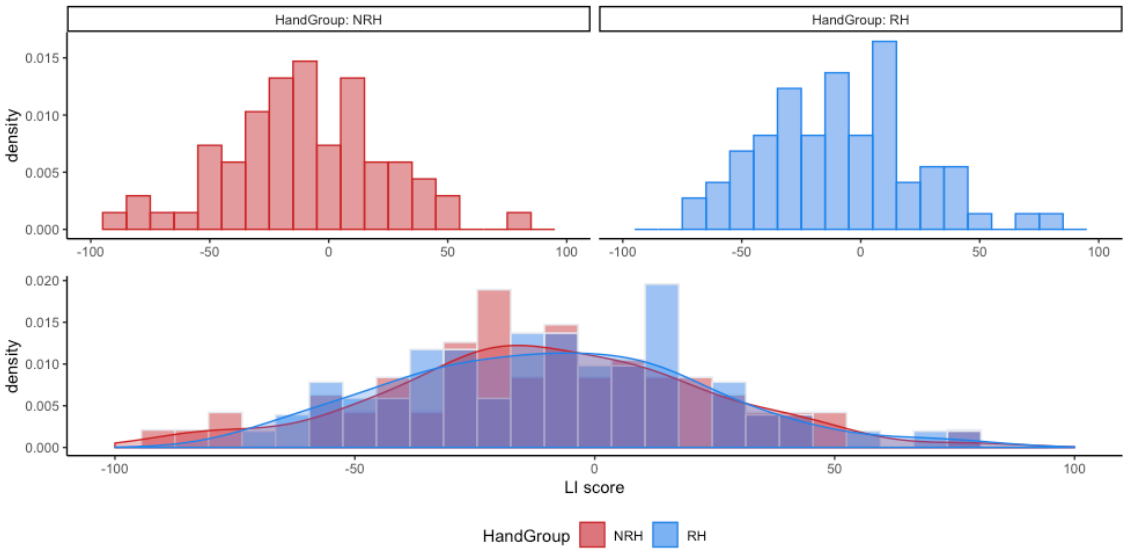
Colourscales



CV dichotic listening



EmoDL long version



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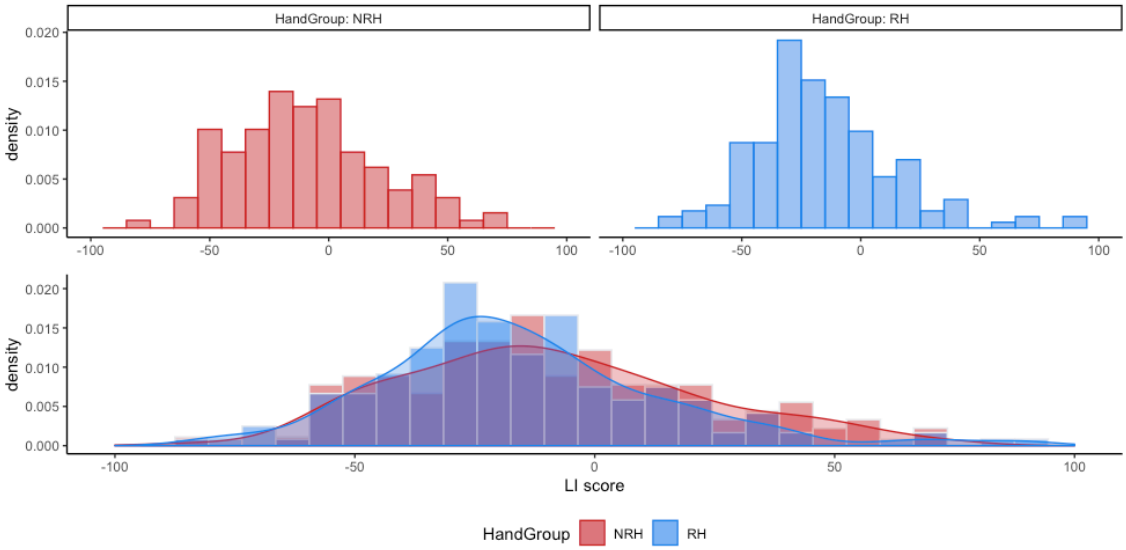
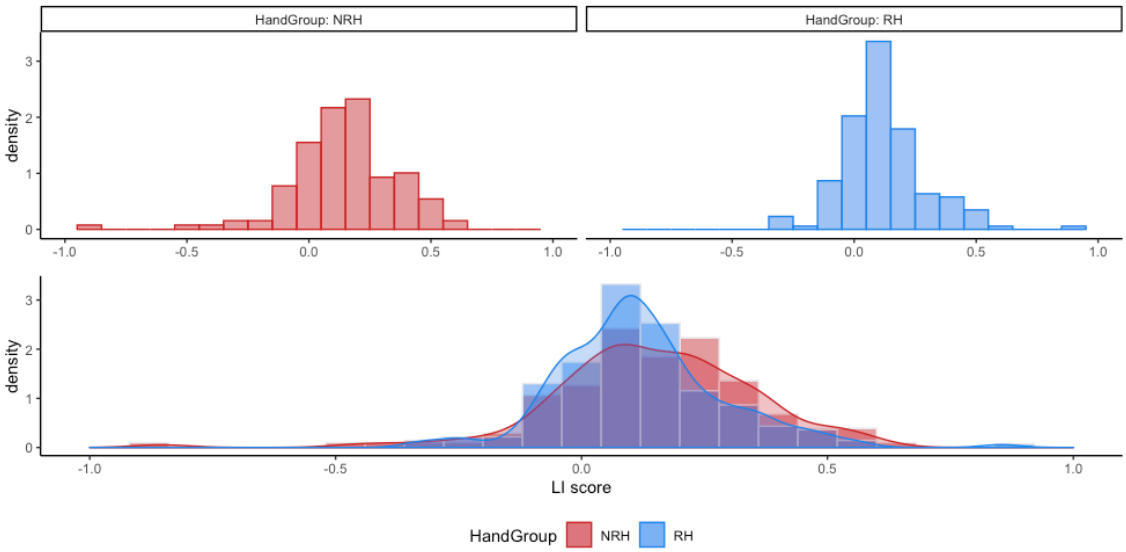
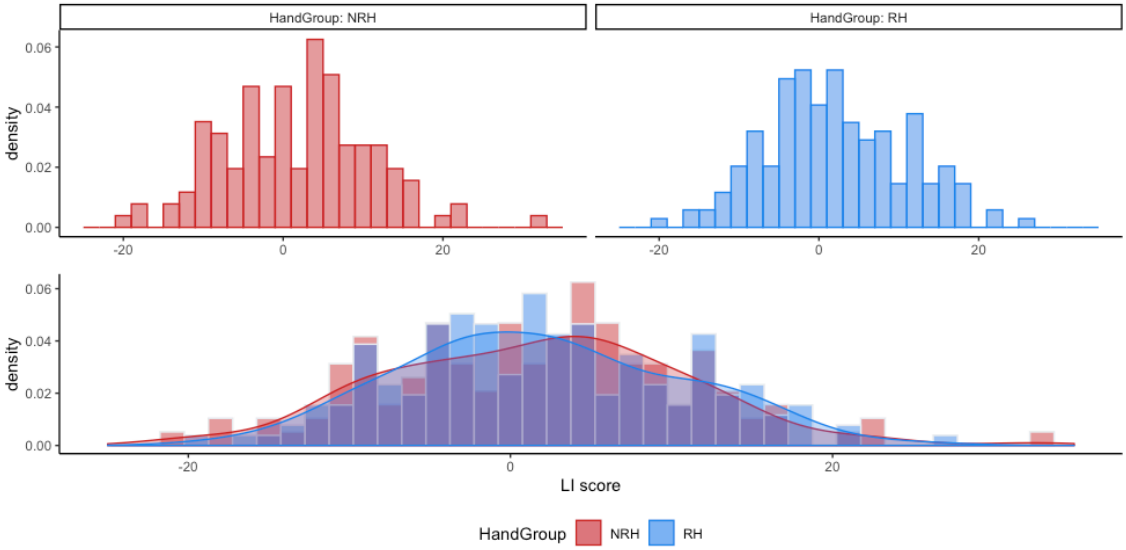


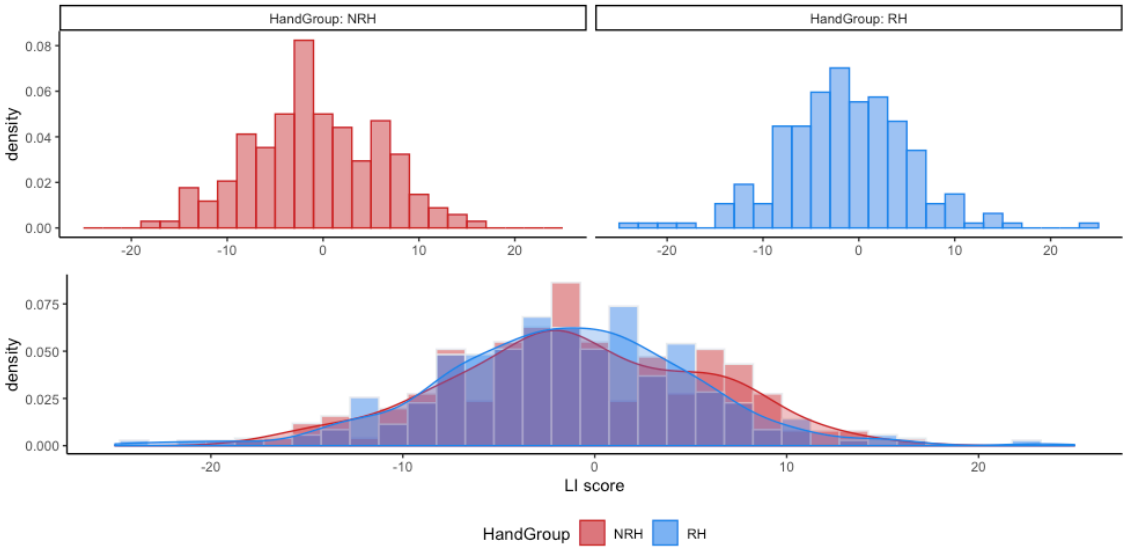
Lateral naming error



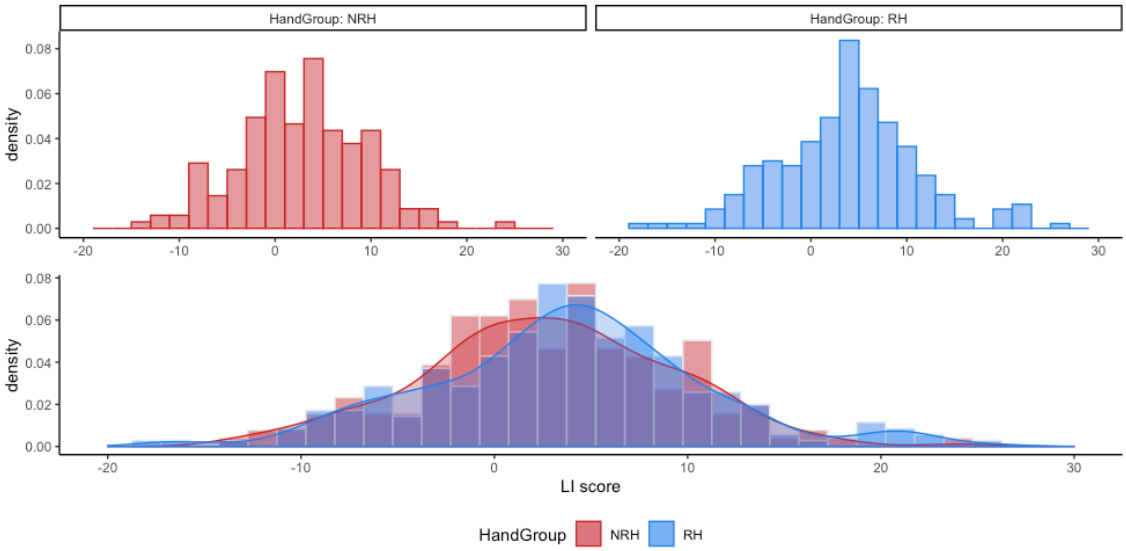
Lateral naming RT



VHF faces task

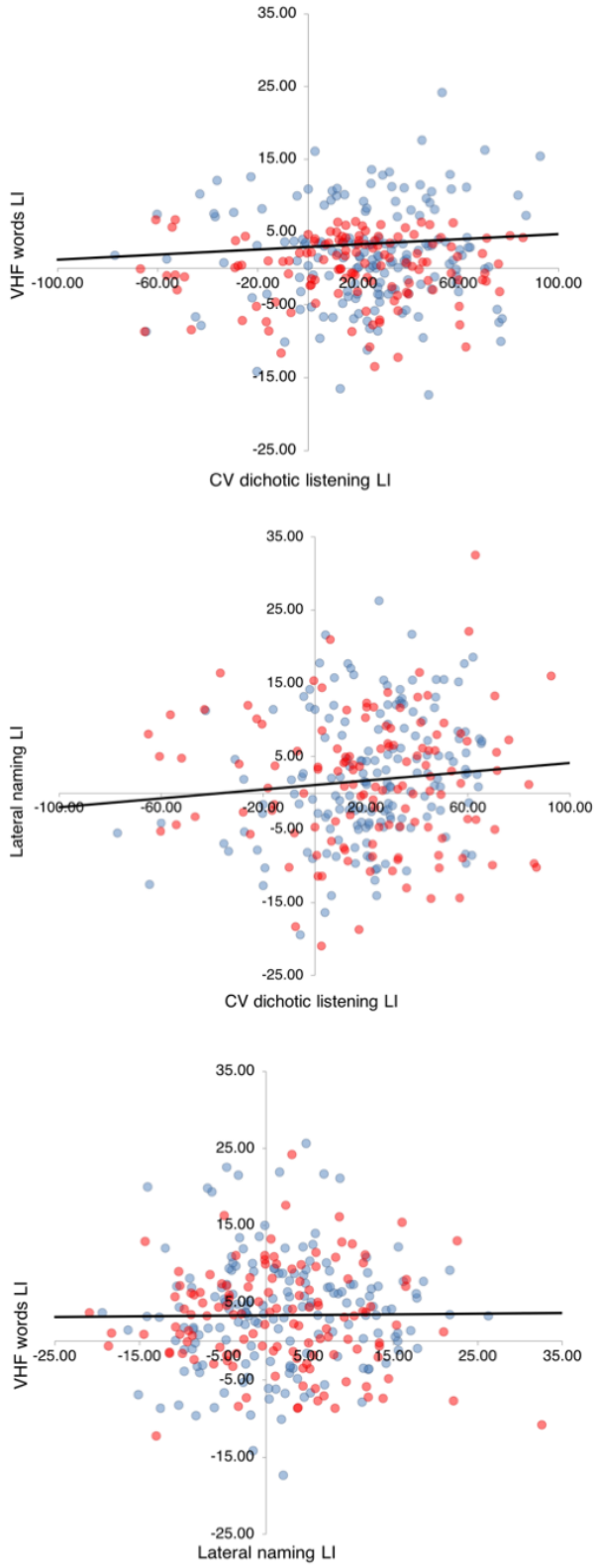


VHF words task



Appendix B

Figure 1. Correlations between lateralisation indices of right-handed (blue) and non-right-handed (red) participants for the three perceptual language tasks in Chapter 2.



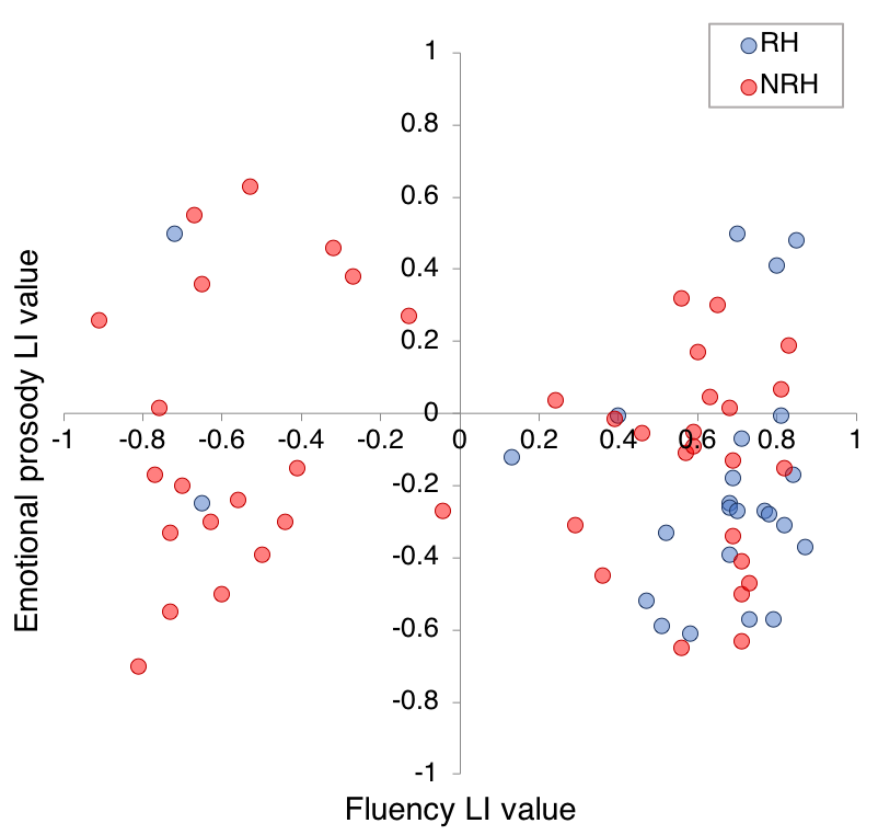
Appendix C

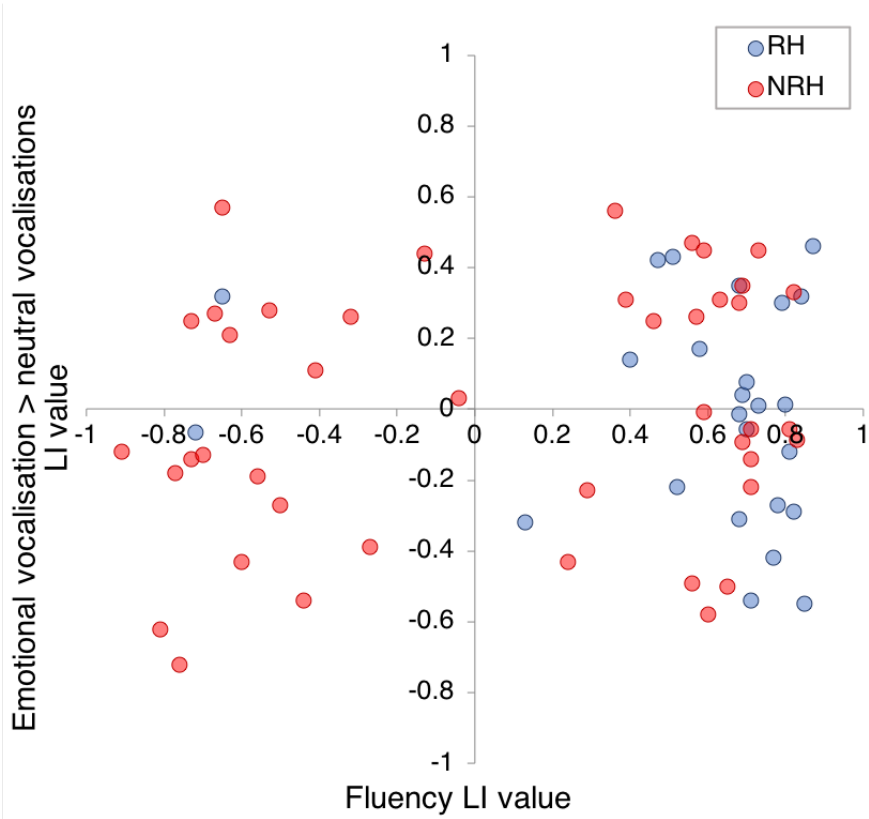
Acoustic measures for each sound category used in the auditory emotions localiser. Mean (SD in brackets) stimulus duration, mean f_0, f_1, f_2, f_3, f_4, f_0 dispersion (f_0SD), harmonics-to-noise ratio (HNR), jitter, and shimmer measured over the whole utterance. Jitter is measured as the average absolute difference between consecutive periods (the amplitudes of consecutive periods), divided by the average period (amplitude), as defined in Praat software.

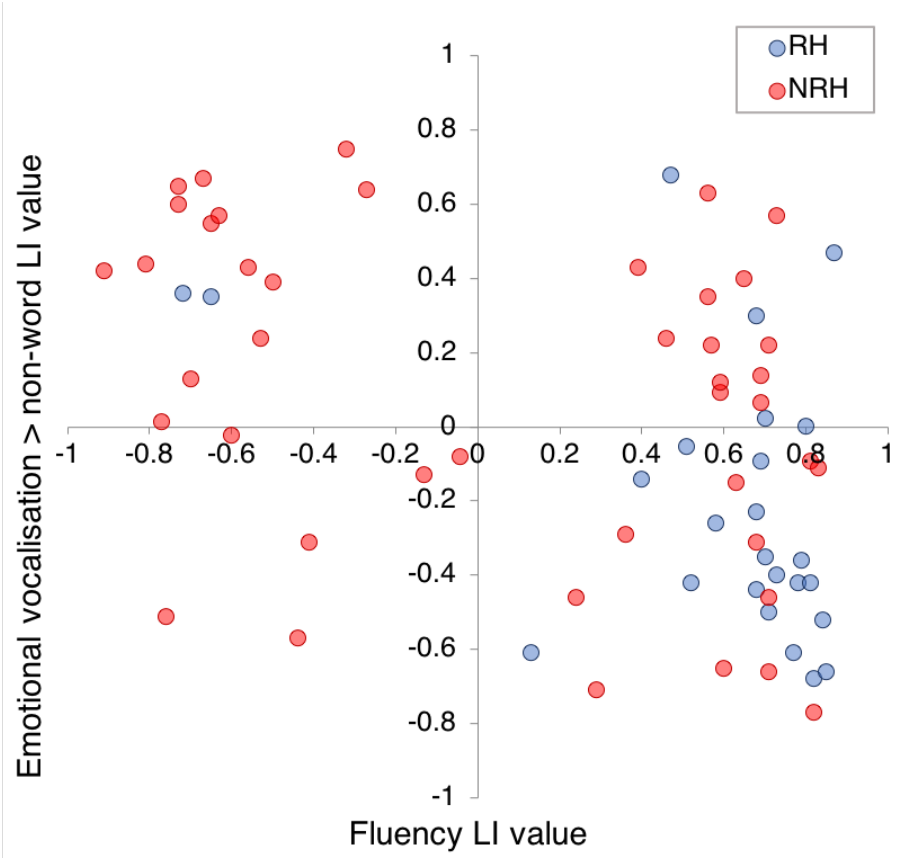
Sound category	Duration (sec)	f_0 (Hz)	f_1 (Hz)	f_2 (Hz)	f_3 (Hz)	f_4 (Hz)	f_0SD (Hz)	HNR (dB)	Jitter (%)	Shimmer (dB)
Emotional Prosody	0.61 (0.12)	333.07 (89.14)	650.14 (93.92)	1158.98 (195.83)	3107.07 (219.93)	3847.39 (215.79)	88.56 (44.65)	14.89 (5.17)	1.30 (0.56)	0.52 (0.12)
Emotional Vocalisations	1.16 (0.65)	389.41 (61.56)	994.10 (89.64)	1650.59 (179.32)	2707.94 (162.46)	3660.36 (373.15)	75.12 (27.50)	14.91 (8.25)	1.97 (0.34)	0.71 (0.45)
Neutral prosody	0.50 (0.04)	209.13 (38.90)	492.23 (61.00)	936.28 (75.81)	3061.74 (208.72)	3964.47 (76.54)	38.14 (32.31)	16.08 (6.25)	1.73 (1.13)	0.49 (0.11)
Neutral vocalisation	0.73 (0.48)	301.38 (83.27)	677.82 (136.32)	1733.63 (198.33)	2786.24 (159.66)	3740.84 (274.00)	69.41 (41.08)	6.63 (4.36)	3.38 (0.82)	1.22 (0.33)
Nonwords	0.60 (0.10)	207.69 (32.19)	742.85 (100.00)	2233.71 (72.88)	3037.84 (121.65)	3953.27 (193.08)	39.76 (52.91)	11.71 (4.55)	1.77 (1.11)	0.66 (0.31)

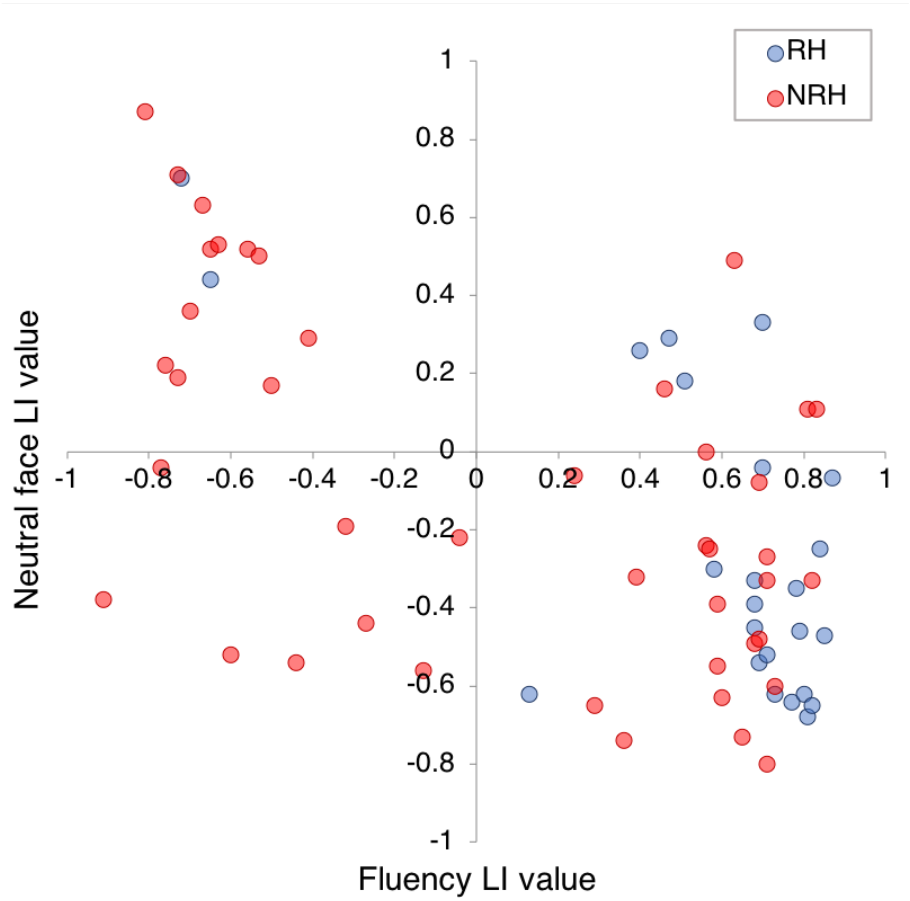
Appendix D

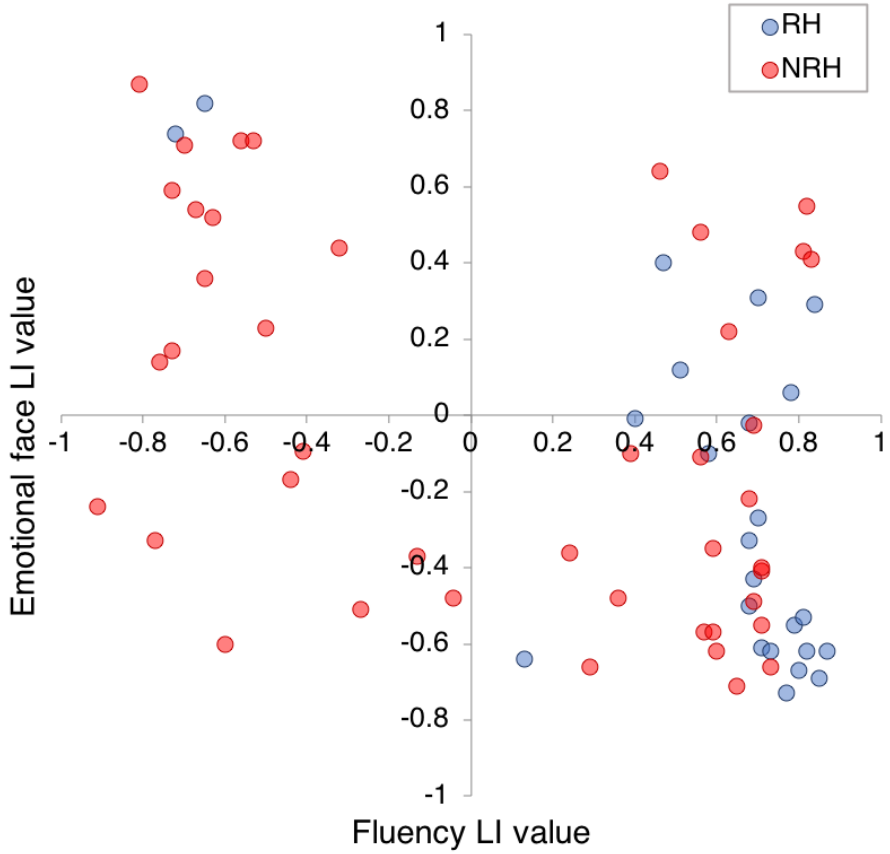
Scatterplots of LI values from the neuroimaging data in Chapter 3. Fluency LI values are plotted on the X-axis and each 'right hemisphere' asymmetry on the Y-axis on each graph. Data are grouped by handedness; blue points represent right-handed participants and red points non-right-handed participants.

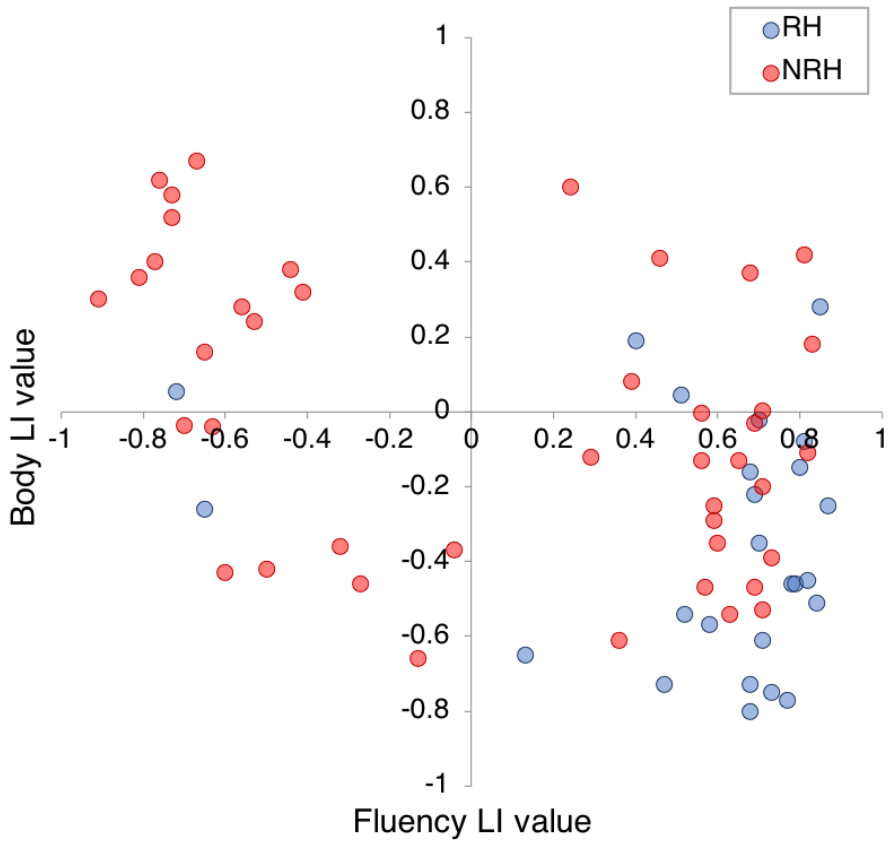





RH
NRH
Emotional vocalisation > non-word LI value
Fluency LI value
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1


RH
NRH
Neutral face LI value
Fluency LI value
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1

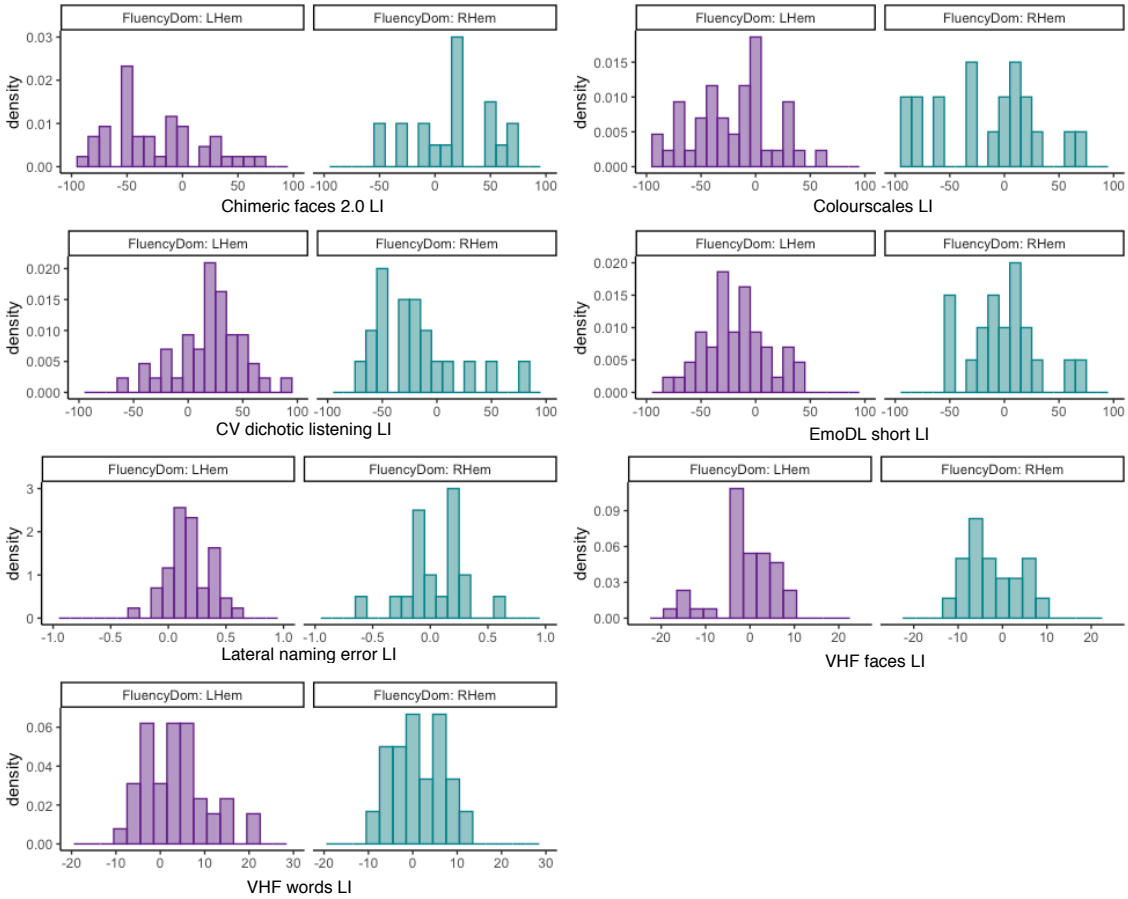

RH
NRH
Emotional face LI value
Fluency LI value
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1


RH
NRH
Body LI value
Fluency LI value
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1

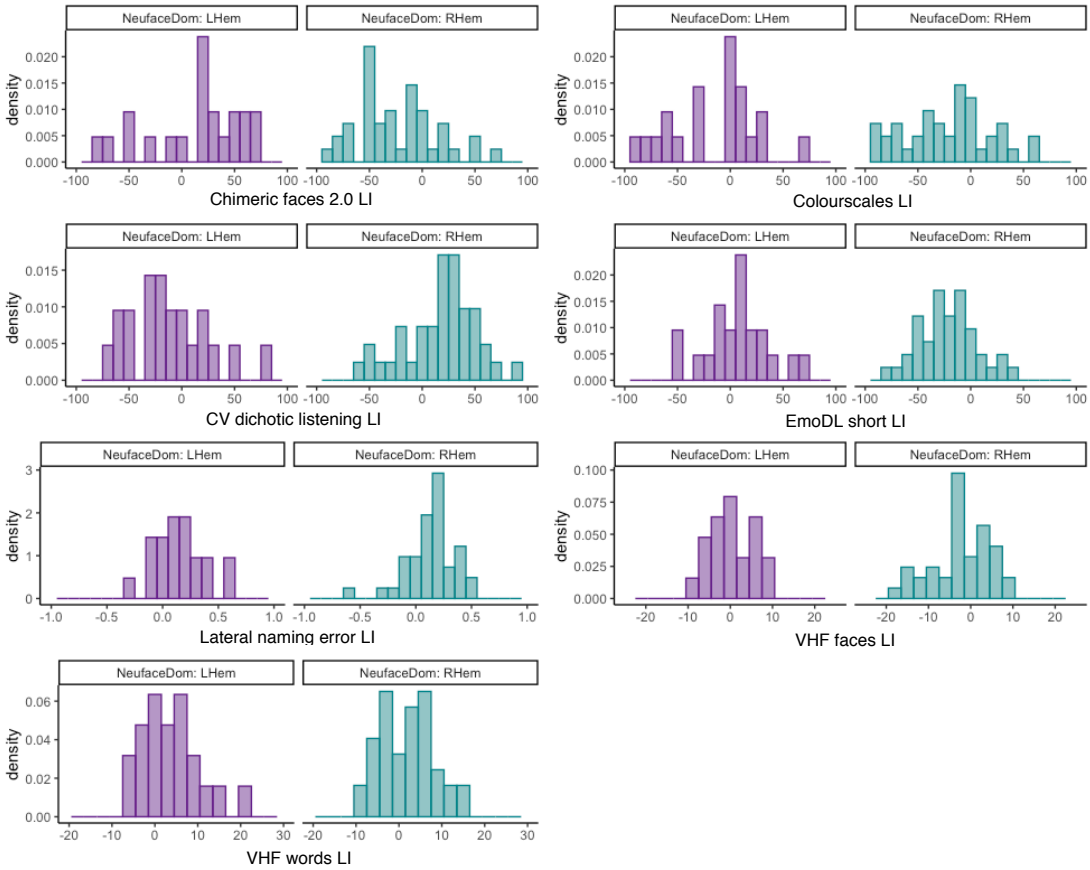
Appendix E

Density histograms showing the distribution of scores for each of the predictor variables included in Chapter 4, grouped by hemispheric dominance, for each fMRI contrast. Left-hemisphere dominant individuals are plotted in purple and right-hemisphere dominant individuals in green.

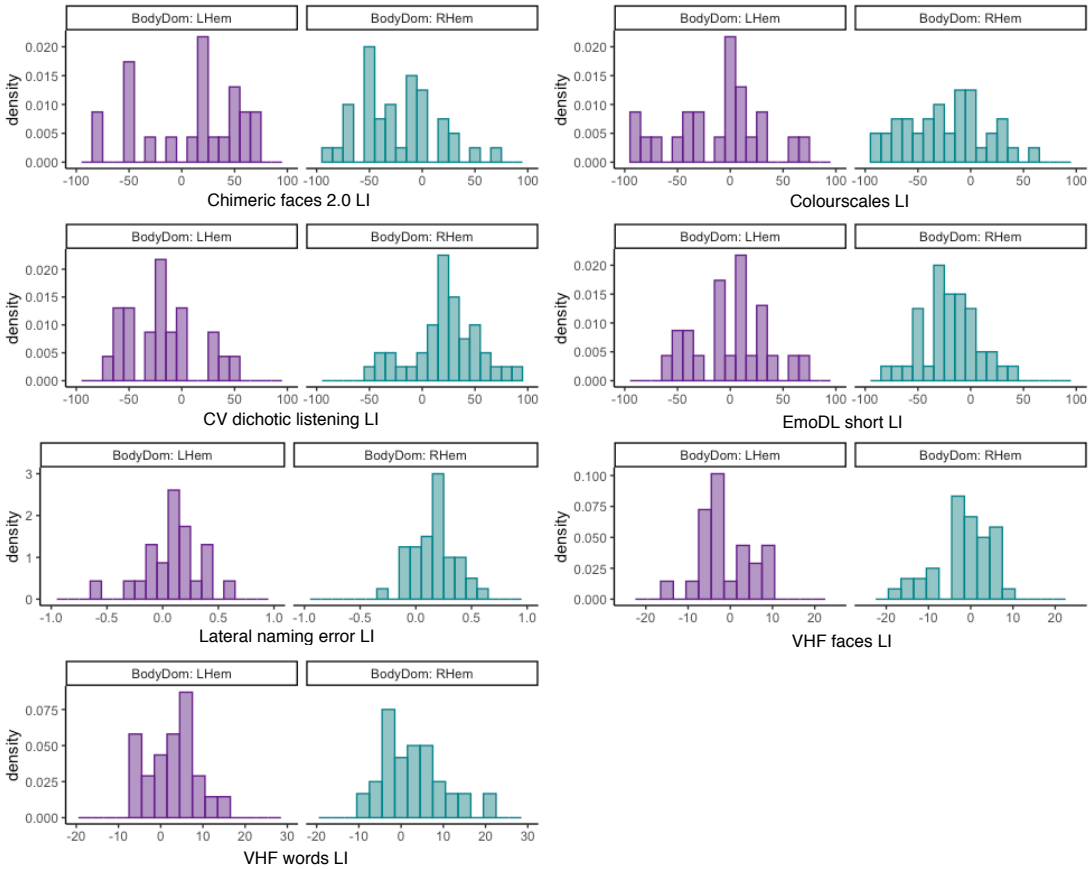
Language:



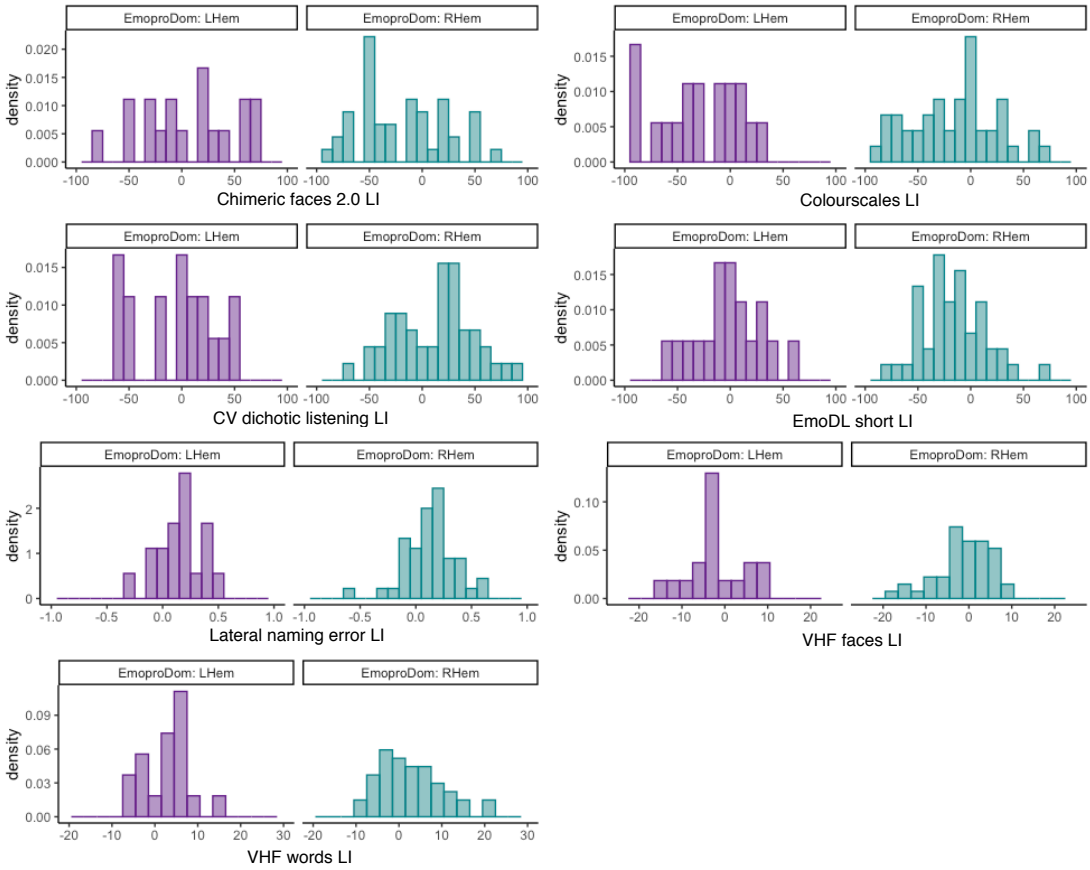
Faces:



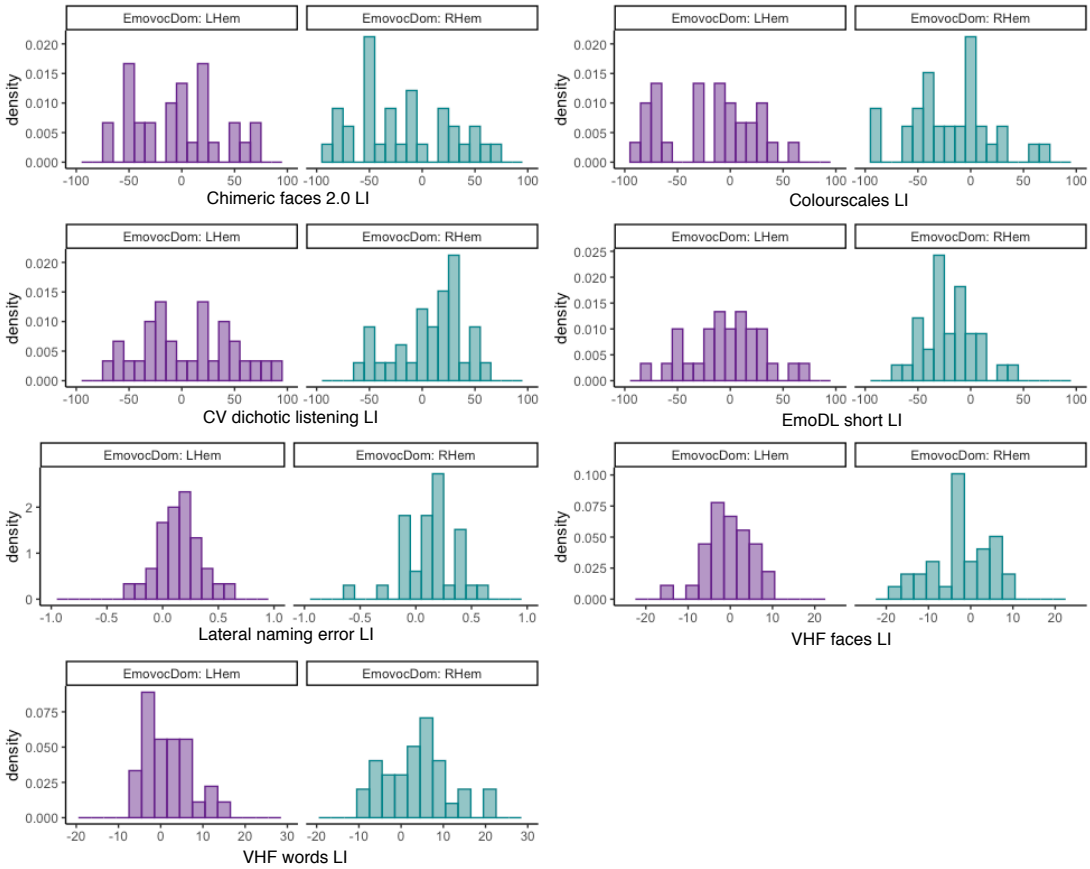
Bodies:



Emotional prosody:



Emotional vocalisations:



Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

Eu. Karboon 07/11/2019