DOES THE OCCIPITAL FACE AREA CONTRIBUTE TO HOLISTIC FACE
PROCESSING?

BY

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Abstract

Face perception depends on a network of brain areas that selectively respond to faces over non-face stimuli. These face-selective areas are involved in different aspects of face perception, but what specific process is implemented in a particular region remains little understood. A candidate process is holistic face processing, namely the integration of visual information across the whole of an upright face. In this thesis, I report two experiments that examine whether the occipital face area (OFA), a face-selective region in the inferior occipital gyrus, performs holistic processing for categorising a stimulus as a face. Both experiments were conducted using online, repetitive transcranial magnetic stimulation (TMS) to disrupt activity in the brain while participants performed face perception tasks. Experiment 1 was a localiser in which participants completed two face identification tasks while receiving TMS at OFA or vertex. Participants' accuracy decreased for one of the tasks as a result of OFA but not vertex stimulation. This result confirms that OFA could be localised and its activity disrupted. Experiment 2 was a test of holistic processing in which participants categorised ambiguous two-tone images as faces or non-faces while TMS was delivered to OFA or vertex. Participants' accuracy and response times were unchanged as a result of either stimulation. This result suggests that the OFA is not engaged in holistic processing for categorising a stimulus as a face. Overall, the current results are more consistent with previous studies suggesting that OFA is involved in processing of local face features/details rather than the whole face.

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1. Introduction

Faces are an important social stimulus. We see many of them each day and thousands in our lifetime. However, faces are not just important socially. There is a lot of evidence suggesting that faces are handled differently compared to other objects by the visual system. The neurologist Joachim Bodamer's case studies of three prosopagnosia patients who demonstrated selective deficits in face recognition after head injuries (Bodamer, 1947) were an early investigation into this notion of the specialness of face processing.

Over the last 50 years, cognitive neuroscience research has suggested that face perception depends on processes that are unique to the face perception system. A classic example of the cognitive research is Yin's (1969) demonstration that upside-down, or inverted, faces are difficult to recognise, much more so than inverted objects. A common explanation for this is that face perception employs unique processes called holistic processing, and that holistic processing is lost when faces are inverted. Other cognitive demonstrations of holistic processing are the part-whole effect (Tanaka & Farah, 1993) and the composite face illusion (Young, Hellawell, & Hay, 1987). In the part-whole effect, it is easier to recognise a face part such as eyes or nose when it is presented within the context of an upright face than in isolation. In the composite face illusion, it is harder to recognise the identity of the top half of an upright face where the top and bottom halves are from two different people and aligned, compared to when the two halves are shown misaligned.

The cognitive evidence lead people to believe faces were processed differently, and brain studies have continued to support the notion. In the 1970s and 1980s, neurons that responded only or significantly more to faces compared to non-faces were found in the inferotemporal cortex of non-human primates (Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982; Desimone, Albright, Gross, & Bruce, 1984). In the mid-1990s, electroencephalography (EEG) studies in humans documented the N170, an event-related potential (ERP) component characterised by a more negative deflection when participants see faces compared to non-faces (Bentin, Allison, Puce, & Perez, 1996). In the late 1990s, functional magnetic resonance imaging (fMRI) studies identified the so-called *face-selective areas*, namely regions of cortex that respond much more strongly to faces than to a wide range of other objects. Kanwisher, McDermott, and Chun (1997) were reliably able to localise two such regions, namely the fusiform face area (FFA) in the fusiform gyrus, and the face-selective posterior superior temporal sulcus (pSTS). A third region in the inferior

occipital gyrus called the occipital face area (OFA) was later identified (Gauthier et al., 2000).

Despite the convergence of cognitive and brain findings, little is known about which specific brain region is involved in which cognitive process of face perception. In this thesis I investigate whether the OFA contributes to holistic processing, specifically holistic processing involved in *categorising a stimulus as a face*. To do so I use transcranial magnetic stimulation (TMS), a powerful method for characterising the causal relationship between regions of the brain and the cognitive processes they are responsible for. In recent years TMS has been used to study the role of the OFA in face processing (Pitcher, Walsh, Yovel, & Duchaine, 2007; Pitcher, Garrido, Walsh, & Duchaine, 2008; Pitcher, Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Kadosh, Walsh, & Kadosh, 2011; Dzhelyova, Ellison, & Atkinson, 2011; Pitcher, Goldhaber, Duchaine, Walsh, & Kanwisher, 2012; Solomon-Harris, Mullin, & Steeves, 2013; Pitcher, 2014; Pitcher, Duchaine, & Walsh, 2014; Kietzmann et al., 2015; Bona, Cattaneo, & Silvanto, 2016), and so my thesis aims to extend this growing literature. The remainder of this thesis proceeds as follows. Section 2 provides background on holistic processing. Section 3 provides background on face-selective areas. Section 4 provides an overview on TMS. Section 5 reports Experiment 1, in which I localise OFA as a target region of stimulation. Section 6 reports Experiment 2, in which I test whether OFA makes causal contributions to holistic face processing. Section 7 discusses and concludes.

2. Holistic face processing

A central idea in the last 50 years of face perception literature is *face-specificity* – the notion that face recognition is carried out by specialised processes that play little role in the recognition of other objects (McKone et al., 2007; Kanwisher, 2010; Rossion, 2008). These specialised processes are widely known as holistic face processing, and they are generally thought of as the integration of local/featural elements of an upright face into a singular, whole percept (Tanaka, & Farah, 1993). The exact nature of holistic processing and the extent to which it is face-specific remain debated (Maurer et al., 2002; Rossion, 2008; Robbins, & McKone, 2007; Gauthier, & Bukach, 2007), but researchers agree that holistic processing involves a representation of a whole, upright face that is more than just a serial sum of local face features such as eyes, nose, and mouth. As described by Francis Galton (1883): *"The differences in human features must be reckoned great, inasmuch as they enable us to distinguish a single known face among those of thousands of strangers, though they are*

mostly too minute for measurement. At the same time, they are exceedingly numerous. The general expression of a face is the sum of a multitude of small details, which are viewed in such rapid succession that we seem to perceive them all at a single glance."

Holistic processing is considered important for face perception for a variety of different reasons. Individuals with acquired and developmental prosopagnosia demonstrate a reduction or loss of holistic processing (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010; Palermo et al., 2011) suggesting that holistic processing is required for normal face perception. Faces from people of our own race are perceived more holistically than faces from another race (Michel, Rossion, Han, Chung, & Caldara, 2006), as are faces from people our own age (Susilo, Crookes, McKone, & Turner, 2009), suggesting that holistic processing is related to how we see particular types of faces. Brain studies have also shown cortical responses specific to the perception of whole, upright faces in humans (Kanwisher, McDermott, & Chun, 1997; Liu, Harris, & Kanwisher, 2010), and macaques (Freiwald, Tsao, & Livingstone, 2009).

Holistic processing can be experienced first-hand using simple demonstrations such as in Figure 1. In the *composite face illusion*, it is difficult to identify the top half of a face when it is aligned on top of another face's bottom half, compared to when the halves are misaligned (Figure 1; Young, Hellawell, & Hay, 1987). In black and white images called *Mooney faces*, an array of patches suddenly give rise to a percept of a whole face, without the need for serial, part-by-part inspection of local elements (Figure 2A, Mooney, 1957). These demonstrations provide a way to measure different aspects of holistic processing and to quantify them in experiments.

Figure 1. Example of aligned and misaligned composite faces (image adapted from McKone et al., 2013). In the composite face illusion, the face is composed of halves from two people. When the halves are aligned (left) the halves form a new, single face and it is harder to identify the individual halves. This illusion is broken when the faces are misaligned (right) and the two halves are seen independently and are easily recognised.

2.1. Holistic processing for face categorisation versus face identification

One way to think about face recognition is that it is a process that proceeds along at least two stages (Liu, Harris, & Kanwisher, 2002). First is the categorisation of the stimulus as a face (i.e. *face categorisation*). Second is the recognition of specific individuals from the face (i.e. *face identification*). These stages involve different types of holistic processing.

Holistic face categorisation is thought to be activated by the presence of the normal configuration of a face, that is the T-shape formed by eyes on top of the nose which is in turn above the mouth (Diamond, & Carey, 1986). This type of holistic processing is commonly measured using ambiguous stimuli that first require perceiving the face configuration and registering that the stimulus is a face before individual face parts are discernable. Some examples of these stimuli are Mooney faces, Arcimboldo faces, and the face versus face-parts stimuli (Figure 2).

Figure 2. Examples of stimuli used to test holistic face categorisation. A) Mooney face. B) Arcimboldo face. C) face-versus-face parts.

Mooney faces are black-and-white, two-tone pictures with little detail and relatively ambiguous figure/ground distinctions (Mooney, 1957). Arcimboldo faces are faces comprised of other objects such as fruits and vegetables, originally painted by Giuseppe Arcimboldo in the 16th century. The face versus face-parts stimuli are simplified line drawings of faces surrounded by line drawings that resemble local face parts (Garrido, Duchaine, & Nakayama, 2008).

In contrast, holistic face identification is engaged not to categorise the stimulus as a face, but rather to tell different faces apart. This type of holistic processing is typically measured using the face inversion, the part-whole task, and the composite face task (Figure 3).
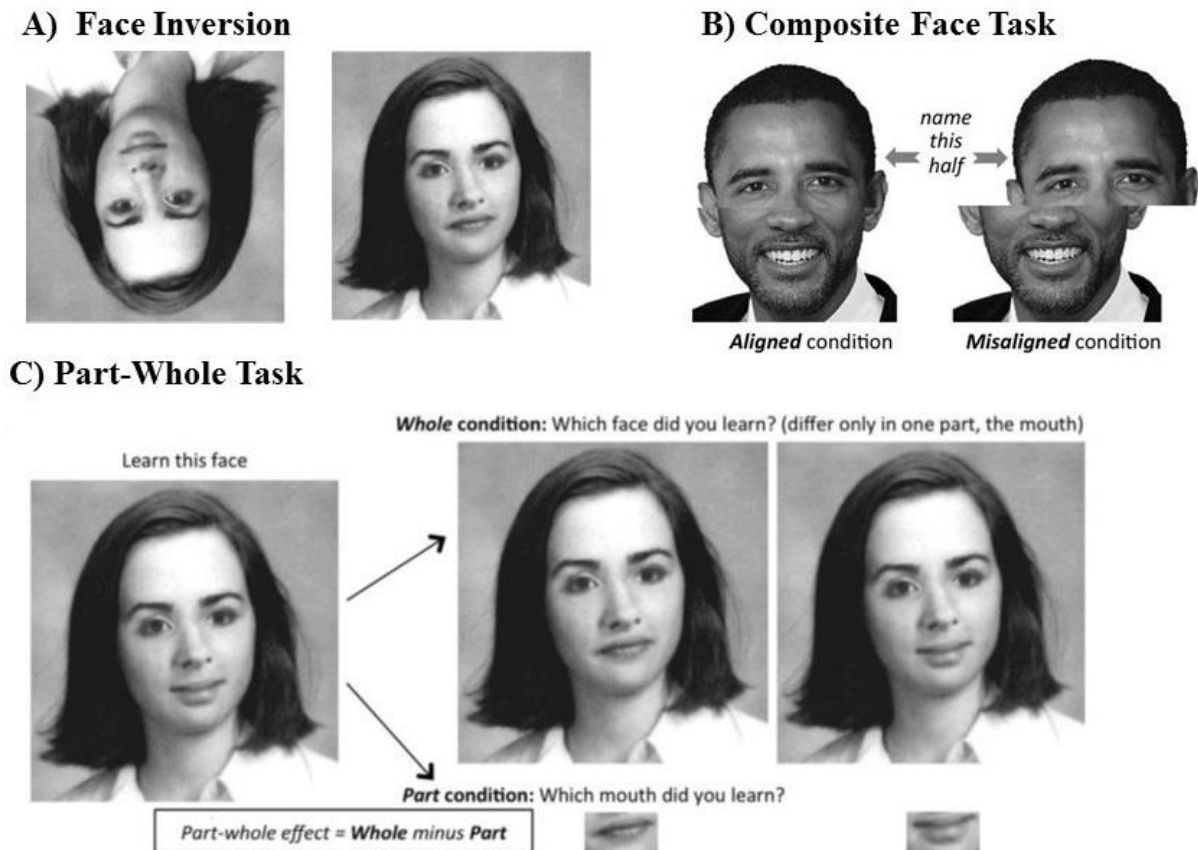
A) Face Inversion

B) Composite Face Task

name this half

Aligned condition   **Misaligned** condition

C) Part-Whole Task

Whole condition: Which face did you learn? (differ only in one part, the mouth)

Learn this face

Part condition: Which mouth did you learn?

Part-whole effect = **Whole** minus **Part**

Figure 3. Examples of face inversion task, part-whole task, and composite face task (adapted from McKone et al., 2013). A) Participants find it more difficult to determine whether the photos are of the same person when one is turned upside down (this effect is much smaller for non-face objects such as dogs). B) Participants find it easier to recognise which eyes belong to Jim when they are within the context of his face, rather than isolated from it. C) Participants find it easier to recognise the top half of a head when the top and bottom halves are misaligned compare to aligned.

Several lines of evidence support the distinction between the two types of holistic processing (Maurer, LeGrand, & Mondloch, 2002). Firstly, face inversion disrupts people's ability to recognise the identity of an individual face but they are still able to identify what they're seeing as a face (Freire, Lee, & Symons, 2000). This contrasts with Mooney images as when a Mooney face is inverted people find it difficult to tell that there was a face in the image (Kanwisher, Tong, & Nakayama, 1998). This demonstrates that holistic face categorisation and holistic face identification can be selectively disrupted. Secondly, patients with acquired prosopagnosia have been found to have difficulty with holistic processing for face identification but not for face categorisation. Patient PS could categorise faces in Mooney and Arcimboldo images (Rossion, Dricot, Goebel, & Busigny, 2011) but showed abnormal performance on inversion tasks (Busigny & Rossion, 2010). Similarly, patient GG

could also categorise faces in Mooney and Arcimboldo images, but showed abnormal performance on inversion, composite, and part-whole tasks (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010). On the other hand, patient DF failed to show either holistic face categorisation or holistic face identification (Steeves et al., 2006). Thirdly, fMRI studies demonstrate a dissociation between the brain regions involved in holistic face categorisation and those linked to holistic face identification. Kanwisher, Tong, and Nakayama (1998) showed that the difference in FFA response to upright and inverted Mooney faces was larger than difference in response to upright and inverted grey-scale faces, while Rossion, Dricot, Goebel, and Busigny (2011) found that only the FFA responded to when participants saw Mooney images. On the other hand, Schiltz and Rossion (2006) showed that both the FFA and the OFA responded in the same way to the face composite task – both regions were equally sensitive to the perceived change on identical top-halves of faces when they were aligned with different bottom-halves.

3. Face-selective areas

Throughout the history of brain research, many have proposed that the brain contains modular units that are specialised for certain types of cognitive functions (Broca, 1861; Ferrier, 1873; Kanwisher, 2010). In face perception, this claim was initially supported by the discovery of patches of neurons in non-human primates that responded selectively to faces (Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982; Desimone, Albright, Gross, & Bruce, 1984). In one of the earliest studies, macaques were shown images of different object categories with different visual features (e.g., simple visual objects like bars and edges, and complex objects like flowers, faces, hands, and snakes) while the activity of neurons in inferotemporal cortex was recorded (Desimone, Albright, Gross, & Bruce, 1984). Most neurons responded to the basic shape elements of the stimuli shown, but a patch in the superior temporal sulcus was found to contain neurons that respond only to face stimuli.

While evidence from non-human primates is important, they could not necessarily be used to claim that the human brain had similar regions of face-selective cortex. This changed in the 1990s with the development of fMRI. Kanwisher, McDermott, and Chun (1997) used fMRI to investigate responses in the brain when people viewed pictures of different objects. They found a region in the middle fusiform gyrus whose response to faces was significantly higher than its response to any other image category presented. This area became known as the fusiform face area (FFA). In the same study, another patch of cortex was seen to respond

selectively to faces in the posterior superior temporal sulcus (pSTS). Studies had suggested a region of face-selective cortex in the inferior occipital gyrus (Haxby et al., 1994; Clark et al., 1996; Puce, Allison, Agari, Gore, & McCarthy, 1996) that was named the occipital face area (OFA; Gauthier, 2000). The three posterior areas of FFA, pSTS, and OFA are widely considered the core of the face processing network (Figure 4). In recent years, additional face-selective areas have been found in more anterior part of the brain including the anterior temporal lobe (Rajimehr, Young, & Tootell, 2009), the inferior frontal gyrus (Chan, & Downing, 2011), and the anterior superior temporal sulcus (Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011), but these areas are considered beyond the core network.
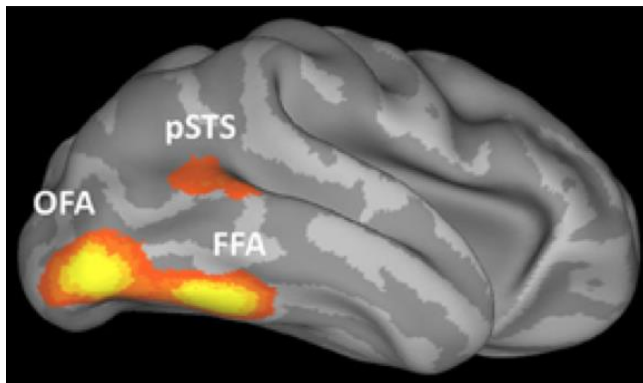

Figure 4. Core face-selective areas shown in the right hemisphere (image taken from Huang et al., 2014).

3.1. Models of face-selective areas

How do the core face-selective areas connect to each other, and what specific processes in face perception are implemented in each region? Three models have been proposed to provide a framework to address these questions.

One model is a hierarchical, feed-forward model, in which low-level input from early visual cortex goes to the OFA as the first node of the face processing network (Haxby et al., 2000; Figure 5). In this model, the OFA is tasked with analysing a stimulus for the presence of face parts or features such as eyes or mouth – regardless of their position or location within the face – and uses them to produce the initial face percept. This percept is then sent to the FFA for analysis of identity or to the pSTS for analysis of expression and lip reading.
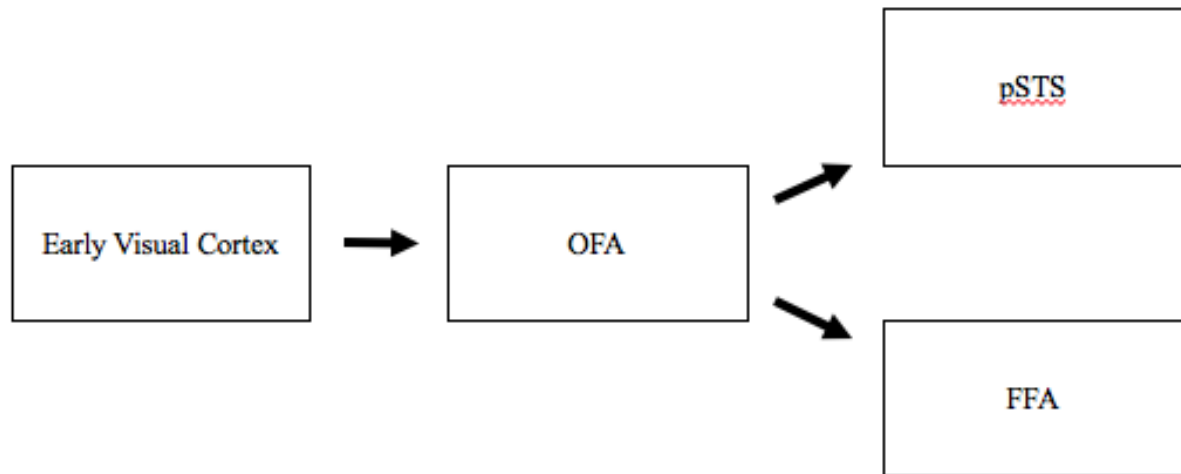
Figure 5. Haxby, Hoffman, and Gobbini's (2000) model of face-selective areas.

A second model modified this strict hierarchical model by placing all face-selective regions in direct contact with early visual cortex, suggesting that the face processing network runs a parallel process rather than a serial one (Duchaine & Yovel, 2015; Figure 6).
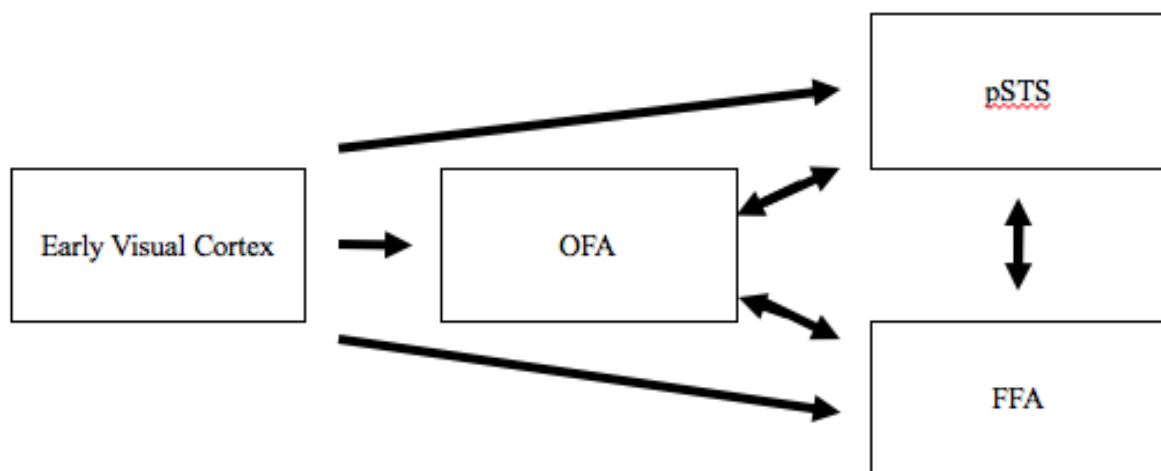
Figure 6. Duchaine, and Yovel's (2015) model of face-selective areas.

The third model flips the original feed-forward model by proposing that the first node in the face processing network is the FFA rather than the OFA (Rossion, 2008; Figure 7). The FFA builds a face percept, which is then sent to OFA for fine-grained analysis and back in what is called re-entrant processing, and this back and forth is what produces the stable face percept.

Figure 7. Rossion's (2008) model of face-selective areas.

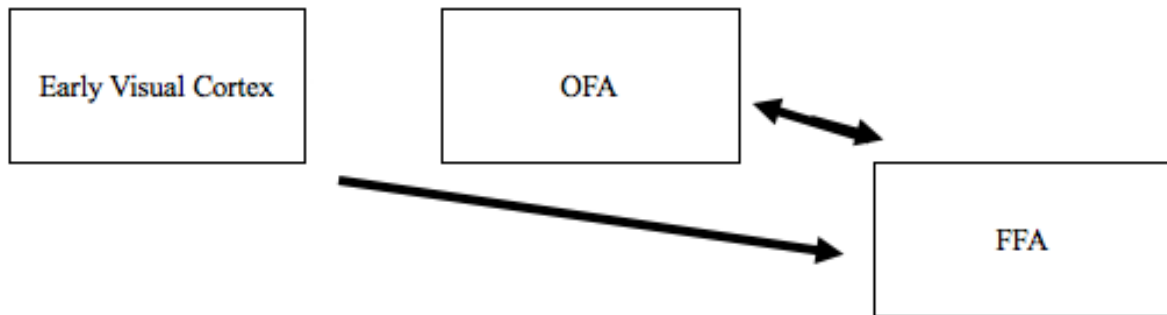The three models make different proposals about how information flows between the core face-selective areas, but for the most part they ascribe the same basic processes to each area, particularly FFA and OFA. All models suggest that FFA runs holistic procedures that operate at the level of a whole face, whereas the OFA runs part-based analyses that work at a finer level of detail or specifically with face parts. For example, while the Haxby et al. (2000) model implies that the OFA is involved in categorising stimuli as faces in the environment, this face categorisation is done via an analysis of face-like parts. The Rossion (2008) model implies that the OFA is involved in the analysis of already-detected faces, but this additional analysis is performed at a fine, local, part-based level. What does the evidence say about the contributions of the OFA? While the OFA's contribution to part-based processing is relatively well-supported, it is still unclear whether or not the OFA participates in holistic processing. The next section will review this research.

3.2. The Occipital Face Area

Several studies in the 1990s found a face-selective area in the occipital cortex (Haxby et al., 1994; Clark et al., 1996; Puce, Allison, Agari, Gore, & McCarthy, 1996), however it was Gauthier et al. (2000) that named that region the occipital face area (OFA). Rossion et al. (2003) comprehensively showed the OFA's face-selectivity and since then the OFA has been more reliably localised in the right hemisphere (Gauthier et al., 2000; Yovel, & Kanwisher, 2005; Rossion et al., 2003). Because of this, in this thesis, OFA will typically refer to the right OFA specifically unless otherwise specified.

Studies of patients with lesioned OFAs demonstrate that the OFA is necessary for normal face perception (Rossion, et al., 2003; Steeves et al., 2006; Dalrymple et al, 2011). Patient PS, who suffered a lesion to her right OFA, has a far reduced capacity to tell apart one face from another, although her ability to tell a face from other objects was preserved (Rossion et al., 2003). Another patient, DF, had neither a right nor left OFA and was

impaired in all aspects of face perception (Steeves et al., 2006). A review of 100 cases of acquired prosopagnosia did not find a single, contiguous area of lesion overlap (which is reasonable due to the distributed nature of face processing areas in the brain), but the lesions most commonly overlapped at the general location of the OFA (Bouvier, & Engel, 2006). These studies demonstrate the importance of the OFA for normal face perception.

The OFA is necessary for face perception, but what it specifically contributes to face perception remains unclear. According to the three models of face-selective areas discussed previously, the OFA is mainly involved in processing local features of a face such as eyes and mouth. Several lines of evidence support this view. Using fMRI, Liu, Harris, and Kanwisher (2010) found that the OFA responds significantly more to face parts than to black ovals replacing face parts whether or not they are in the appropriate configuration of a face. In another fMRI study, Rotshtein and colleagues (2005) found that the OFA is sensitive to changes in face features regardless of whether those changes result in the perception of a different identity. Using multi-voxel pattern analysis, Nichols, Betts, and Wilson (2010) showed that the OFA contains a higher proportion of face-part sensitive voxels than whole-face sensitive voxels (with the reverse pattern in the FFA). These fMRI findings are consistent with TMS studies that showed that stimulating the OFA only disrupted face identification when the faces differed by their parts compared to when they differed by the spacing between the parts (Pitcher, Walsh, Yovel, & Duchaine, 2007; Solomon-Harris, Mullin, & Steeves, 2013).

Recent studies however suggest that the OFA may be involved not only in analysing face features but also in holistic processing, especially for face categorisation. Brain stimulation studies have shown that the OFA contributes to holistic processing through the use of ambiguous, two-toned, black-and-white stimuli known as Mooney images (Mooney, 1957). Due to their ambiguity, Mooney images are thought to require top-down, holistic processing of the image to determine what is being depicted (Verhallen, & Mollon, 2015). Two recent studies directly tackled this issue using tDCS and TMS. Renzi et al. (2015) used transcranial direct current stimulation (tDCS) and found that stimulation of the OFA had an effect on perception of Mooney faces and Mooney guitars. Bona, Cattaneo, & Silvanto (2016) used TMS to disrupt categorisation of faces and objects such as animals, fruits and man-made objects and found a similar result. These studies suggest that the OFA contributes to holistic categorisation of not only faces but also other complex objects. A small number of studies (specifically fMRI studies) have studied holistic identification as well, finding

evidence to support the involvement of the OFA (Yovel, & Kanwisher, 2005; Rossion, & Schiltz, 2006; Harris, & Aguirre, 2008; Rhodes, Michie, Hughes, & Byatt, 2009).

At the outset of this project, there had been few direct tests of whether the OFA participated in holistic face categorisation. Renzi et al. (2015) had found evidence of involvement but the results were unclear due to practice effects and the spatial resolution of tDCS is such that the OFA may not have been the only area affected. Bona, Cattaneo, and Silvanto (2016) found evidence of involvement but they neglected to report accuracy data as is most common in TMS studies of face perception. Another study by Solomon-Harris, Mulllin, and Steeves (2013) showed no effect of TMS stimulation to the OFA when participants categorised images as faces or non-faces, but the non-face stimuli they used contained face parts. Previous work (Liu, Harris, & Kanwisher, 2010) suggested that the OFA is sensitive to parts regardless of configuration, therefore stimulating the OFA would likely disrupt performance with both faces and non-faces in this task. Alongside this, the evidence for the OFA's contribution to holistic processing comes primarily from fMRI. fMRI studies are able to show the areas of the brain that are involved in face perception, but not how they are involved. It could be that they are causally required for a task or that they are not required but are responsive to the task or stimuli. This thesis aims to fill these gaps by using TMS to gather causal evidence concerning the OFA's involvement in holistic face categorisation.

4. Transcranial Magnetic Stimulation

Transcranial magnetic stimulation (TMS) is a non-invasive brain stimulation technique whereby magnetic pulses are applied to the brain through the scalp in order to "reversible functional disruption" of nervous tissue (Walsh, & Cowey, 1998). TMS has thus been described as a "lesion" method whereby it produced disruptions to cognition as if by temporary lesions (Walsh, & Cowey, 1998; Walsh, & Cowey, 2000). TMS depends upon Michael Faraday's discovery of electromagnetic induction where a magnetic field is produced perpendicular to the direction of an electrical current flowing through a wire (Walsh, & Pascual-Leone, 2003). His discovery sparked a long-running interest in the magnetic stimulation of the human body, and specifically the brain. In 1985 transcranial magnetic stimulation of the brain was shown to be capable of producing behavioural effects (Barker, Jalinous, & Fresston, 1985). Since then TMS has been used widely to study brain and cognition.

4.1. TMS basics

TMS uses a coil of wire through which an electric current is passed. This electric current induces a magnetic field which then induces current in the neurons of the nervous tissue below the coil. This induced current acts to depolarise neurons, making them more likely to propagate action potentials. This increased likelihood to propagate constitutes increased noise in the signal-to-noise ratio (Walsh, & Pascual-Leone, 2003). TMS does not distinguish between excitatory or inhibitory neuronal activity, nor does it differentiate between action potentials propagating along the axon away from or towards the soma (Walsh, & Pascual-Leone, 2003). Therefore, TMS is said to disrupt activity, not enhance or decrease it.

There are two main considerations in the design of a TMS study. Firstly, TMS may be given as a single pulse or repetitively. Single pulses and their magnetic fields only last around 1 ms, but the cortical effects of stimulation may last longer (e.g., seconds; Walsh, & Pascual-Leone, 2003). Repetitive TMS (rTMS) is when a series of pulses are given at once (Rossi et al., 2009). This might involve one pulse every 100 ms (frequency of 10 Hz) for a burst lasting 500 ms (high-frequency rTMS) or one pulse every 1000 ms (frequency of 1 Hz) for 10 minutes (this is considered low-frequency rTMS). Single-pulse and repetitive TMS can be used to answer different questions. Single-pulse TMS can be used to characterise when a cognitive process happens in the region of interest. A range of time in which the candidate process may be active can be derived from behavioural or EEG/ERP studies and TMS can be given at different points within this range. Repetitive TMS might be chosen when the question concerns whether a particular area is involved with a cognitive process regardless of timing, as this type of stimulation likely lasts throughout the duration of the task.

A second consideration is whether TMS is given online or offline. Online TMS refers to stimulation that occurs concurrently with the task performance. Offline TMS refers to stimulation that occurs before the task is performed. Commonly, this is between a pre- and post-test. With online TMS it is important that participants do not respond until after stimulation has ceased. This is because stimulation may disrupt normal responding separately from its disruption of any cognitive process. As such, responses would optimally be left until after the task. This artificial latency between cognition and response may render response times less useful as a measure. This can be avoided using offline TMS, however offline protocols often require a lot of time and can cause discomfort as participants undergo 10-20

minutes of non-stop stimulation. Moreover, it is unclear whether the effect of stimulation continues throughout the course of the entire experiment.

The spatial resolution of TMS is such that separate areas as close as 1 to 2 cm apart can be individually stimulated (Pitcher, Walsh, & Duchaine, 2011). This high spatial resolution makes TMS specially suited for the study of specific regions of cortex. As part of the ventral visual pathway, the OFA is closely neighboured by other areas involved in different, specific functions. For example, the object-selective lateral occipital complex (LOC), the extrastriate body area (EBA), and the occipital place area (OPA) all surround the OFA and contribute to the processing of different stimuli. The spatial resolution of TMS allows the selective stimulation of the OFA, achieving greater precision when localising cognitive function in the brain. This is compared to transcranial direct current stimulation (tDCS) which is another non-invasive method of brain stimulation that has a much lower spatial resolution, leaving it less precise when trying to map cognition to cortex.

When using TMS to study a specific brain area, a target site has to be selected that will result in stimulation of the area of interest. This is often done the same way that the face selective areas were discovered in the first place; by comparing fMRI activity in response to different object categories. While fMRI localisers are the gold standard (Sack et al., 2009), lots of different methods can be used to select a site for stimulation. Sandrini, Umiltà, and Rusconi (2011) describe a few different methods. One is called the *hunting method* in which an initial target is selected on the basis of previous research and peripheral targets are marked around it. TMS is used at each of these targets alongside *behavioural assays* (short tasks expected to depend on the area of interest; Walsh, & Pascual-Leone, 2003) until one site is shown to reduce response times in the assay task. Other methods involve the use of anatomical landmarks, stereotaxically-derived coordinates, and the use of the 10-20 EEG scalp coordinates. Of these alternative methods, the hunting method likely has the most power to localize. However, it is time consuming as it must be done for each participant and the final decision over whether a site increases response times is typically made without statistics (Sandrini, Umiltà, & Rusconi, 2011; though signal detection indices like *d'* have been used by Oliver, Bjoertomt, Driver, Greenwood, Rothwell, 2009).

4.2. TMS studies of face perception

TMS has been used to study face perception and face-selective areas, especially the OFA and to some extent the pSTS. Several TMS studies have assessed the extent to which the OFA is face-selective. Some studies show that stimulation of the OFA disrupted

same/different judgments with faces but not houses (Pitcher et al., 2007), bodies, or novel objects (Pitcher et al., 2009), and that this happens very early after stimulus presentation (100-110 ms; Pitcher, Goldhaber, Duchaine, Walsh, & Kanwisher, 2012). Other studies however show that stimulating the OFA affects not only face perception but also symmetry perception (Bona, Cattaneo, & Silvanto, 2015) and perception of shape rotation (Silvanto, Schwarzkopf, Gilaie-Dotan, & Rees, 2010).

Other TMS studies investigate what specific elements of a face the OFA is concerned with; whether it is concerned with face parts, the whole face, and/or dynamic face representations (i.e., whether the face seen is moving and changing or still like an image). Some studies suggest that the OFA is primarily concerned with face parts (Pitcher et al., 2007; Solomon-Harris, Mullin, & Steeves, 2013), while others found evidence for the OFA's involvement in the categorisation of Mooney faces (Bona, Cattaneo, & Silvanto, 2016). Stimulating the OFA was also found to affect the sensitivity (as seen in fMRI) to static faces in the OFA, FFA, and pSTS, while stimulation of the pSTS reduced the sensitivity to dynamic faces in the pSTS itself, suggesting that the OFA is more concerned with static faces and face parts, whereas the pSTS is concerned with elements which are changeable and socially interpreted like mouth movements while talking, eye movements, and emotional expression (Pitcher, Duchaine, & Walsh, 2014.

TMS has also been used to study higher level judgments made about faces, like sex, trustworthiness, emotional expression, and identity. For example, Dzhelyova, Ellison, and Atkinson (2011) demonstrated that stimulation of the OFA disrupted participants' ability to judge the sex of face images but not their trustworthiness, while stimulation of the pSTS resulted in the opposite. Studies have demonstrated that stimulating the OFA disrupts emotional expression recognition (Pitcher, Garrido, Walsh, & Duchaine, 2008; Pitcher 2014; Kadosh, Walsh, & Kadosh, 2011), and suggests that the OFA is involved in emotional expression recognition earlier and for a shorter time than was the face area of the somatosensory cortex (Pitcher et al., 2008) and the pSTS (Pitcher, 2014). In regards to identity processing, the early evidence suggested that the OFA was not involved (Pitcher et al., 2008; Gilaie-Dotan, Silvanto, Schwarzkop, & Rees, 2010), while more recent evidence using different methods suggest that it might be (Kadosh, Walsh, and Kadosh, 2011; Ambrus, Windel, Burton, & Kovács, 2017).

Finally, TMS has been used to investigate whether the OFA is involved in identification or categorisation. There has been quite a lot of support for the OFA's

involvement in face identification as many of the TMS studies of the OFA use an identification/discrimination task (e.g., Pitcher et al., 2007; Pitcher et al., 2008; Pitcher et al., 2009), however there have been fewer TMS studies of the OFA in face categorisation. Solomon-Harris, Mullin, and Steeves (2013) stimulated the OFA while participants categorised faces and scrambled faces and found no disruption, while Bona, Cattaneo, & Silvanto (2016) had participants categorise Mooney faces and found a disruption with OFA stimulation.

As seen, TMS has been used to investigate the causal involvement of the OFA in a variety of face- and non-face-selective processes. However, much of the focus in studies of the OFA using TMS has been on identification or telling the difference between faces. Only two studies have looked at the causal role of the OFA in categorising a stimulus as a face with TMS, and their findings are mixed (Solomon-Harris, Mullin, & Steeves, 2013; Bona, Cattaneo, and Silvanto, 2016). The aim of this thesis is to contribute to this literature and help clarify whether the OFA contributes to the holistic categorisation of faces.

5. Experiment 1: Localising OFA

Experiment 1 is a "localiser". The purpose of this experiment is to confirm that the OFA can be localised with TMS. Most studies use fMRI to localise the OFA by scanning participants as they view images of face and non-face stimuli. By comparing the fMRI response to faces and non-faces, the OFA can be identified as a cluster of voxels in the inferior occipital gyrus that are more responsive to faces than to non-faces. Typically, the coordinates of the voxels with the highest response in each individual are selected as the TMS stimulation site for that person.

To localize the OFA, I took OFA coordinates from a previous fMRI localisation study (Rossion et al., 2003). My approach is similar to that of the first TMS study of the OFA (Pitcher et al., 2007). The same coordinates were used to guide stimulation in all participants. This group level approach did not include any other peripheral targets like in the hunting method – the coordinates were expected to localise the OFA on average as they were averaged coordinates from multiple people. The current localiser adopted this approach and used the face identification task used by Pitcher et al. (2007). In this task, participants will indicate if two faces presented sequentially are the same or different while receiving TMS at the coordinates of the OFA and a control site. If the targeted coordinates match the location

of the OFA in participants and the OFA can be affected by stimulation, then stimulation at these coordinates will reduce participants' accuracy in the face identification task.

5.1. Participants

Twenty-three individuals (16 female) with a mean age of 25 years ($SD = 4.6$ years) participated in Experiment 1. All participants were registered in the Victoria University of Wellington TMS participant database and all had undergone an MRI scan. All participants were screened for contraindications (e.g., past head injuries, current psychotropic medicine use) based on the criteria developed by Rossi et al. (2009) and they gave written consent to participate. This study was approved by the School of Psychology Human Ethics Committee under delegated authority of Victoria University of Wellington's Human Ethics Committee (application ID 22575).

5.2. TMS Stereotaxy

Prior to the experiments reported here, all participants underwent an MRI scan in Wellington Hospital's 1T scanner (Philips, Medical Systems, Bothell, USA; three participants were scanned in a 3T scanner at the same location). The resulting T_1-weighted, high-resolution magnetic resonance images were normalized and used to target the area of interest through Brainsight 2 (Rogue Research, Canada). Brainsight is a frameless, stereotaxic, neuronavigation system. With Brainsight, each participant's MR images were uploaded and from them a three-dimensional model was constructed. For each participant, a marker was placed at the Talairach (Talairach, & Tournoux, 1988) coordinates 38, -80, -7, as seen in Figure 8. These coordinates were used in a previous TMS study of the OFA (Pitcher, Walsh, Yovel, & Duchaine, 2007) and were initially derived from the average of the coordinates for the peak activation in an area identified as the OFA in a previous functional imaging study of face processing (Rossion et al., 2003). Another marker was also placed at the vertex. In these studies, an anatomically defined vertex site was chosen. Rather than taking the vertex as the midpoint between the inion and nasion, and the left and right tragal notches, the vertex target was placed based on the point on the medial longitudinal fissure where the central sulci of each hemisphere meet (or a point between them on the medial longitudinal fissure if they do not meet directly).
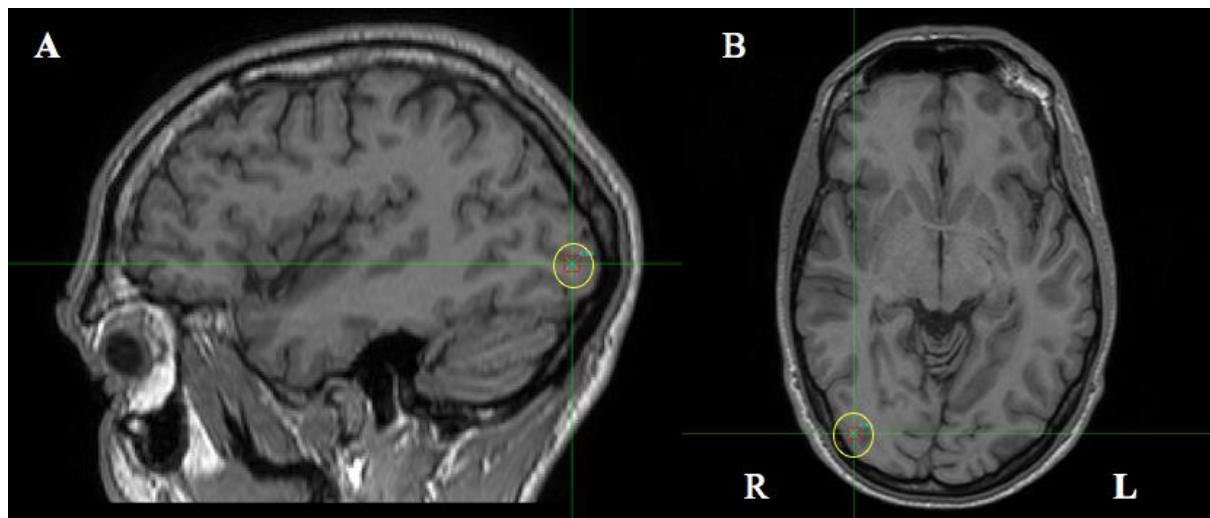
Figure 8. Example of the OFA target (Talairach coordinates 38, -80, -7) on a single participant's brain. A) Longitudinal view of the medial portion of the right hemisphere. B) Coronal view with right and left inverted.

Participants' heads were registered with Brainsight so that they could be tracked in space by the Polaris optical tracking camera (Polaris, Canada). This was achieved by having the participant wear a head-band with reflective components that can be detected by the Polaris camera and provide an indication of the head's three-dimensional position, orientation, and movement. Four points on the participants' heads were used to register the head's position in space; the nasion, the tip of the nose, and the left and right ears (above the tragal notches). These sites were registered with a pointer which also had reflective components to be tracked by the Polaris camera.

5.3. TMS protocol

Cortical magnetic stimulation was delivered via a 70 mm, figure-eight, fan-cooled coil from a Magstim Rapid[2] (Magstim; Whitland, Wales) biphasic stimulator. The coil was mounted on a stand with a movable arm. An online, high-frequency stimulation protocol was used such that stimulation was delivered at a rate of 10 Hz for 500 ms with the onset of stimulation concurrent with the onset of the second stimulus in each pair of sequentially-presented faces within each trial (1 pulse every 100ms, totaling 5 pulses per trial). Stimulation was delivered at 60% of maximum stimulator output. A single intensity was used for all participants following previous TMS studies of OFA (Pitcher et al., 2007; Pitcher et al., 2009).

The coil was positioned based on the tracking information provided by Brainsight. The Polaris camera tracked the coil in space and its relation to the participants' heads. A

measure of the distance (in millimetres) and the angle of eccentricity (in degrees) from the optimal position for stimulating the cortical target is shown onscreen in order to aid in positioning the coil. I corrected the coil position online to minimise the shift of the coil from the original coordinates when participants moved in the chin-rest.

5.4. Stimuli and apparatuses

I used two different versions of a same/different discrimination task in which participants indicated whether two sequentially presented faces were the same or different. Both versions have been used in previous TMS research of OFA and other studies of face-selective regions (Pitcher et al., 2007; Pitcher et al., 2008; Pitcher et al., 2009; Kadosh, Walsh, & Kadosh, 2011; Pitcher, Duchaine, Walsh, Yovel, & Kanwisher, 2011; Pitcher, Goldhaber, Duchaine, Walsh, & Kanwisher, 2012; Solomon-Harris, Mullin, & Steeves, 2013; Pitcher, 2014). The two versions differ in terms of stimuli and presentation time.

The first task (*the photo task*) and stimuli (Figure 9A) were used by Pitcher et al. (2007). The stimulus set was made from two, grey-scale images of different male faces, from which a further 16 images were produced (eight from each male face). Those eight images comprised two different subsets based on how they differed from the initial face. One subset differed by the facial features of the face (i.e., a new image was produced by replacing the eyes and mouth with those from other faces but retaining the head shape). The other subset differed by the spacing between facial parts on the face (i.e., a new image was produced by changing the spacing between the eyes, and between the mouth and nose but retaining the head shape). Thus, there were feature and spacing subsets for each of the two initial faces, giving a total of 18 images. One subset was sized 300 x 300 pixels and subtended approximately 7.4 x 7.4 degrees of visual angle while the other subset was sized 163 x 268 pixels and subtended approximately 4.0 x 6.6 degrees of visual angle.
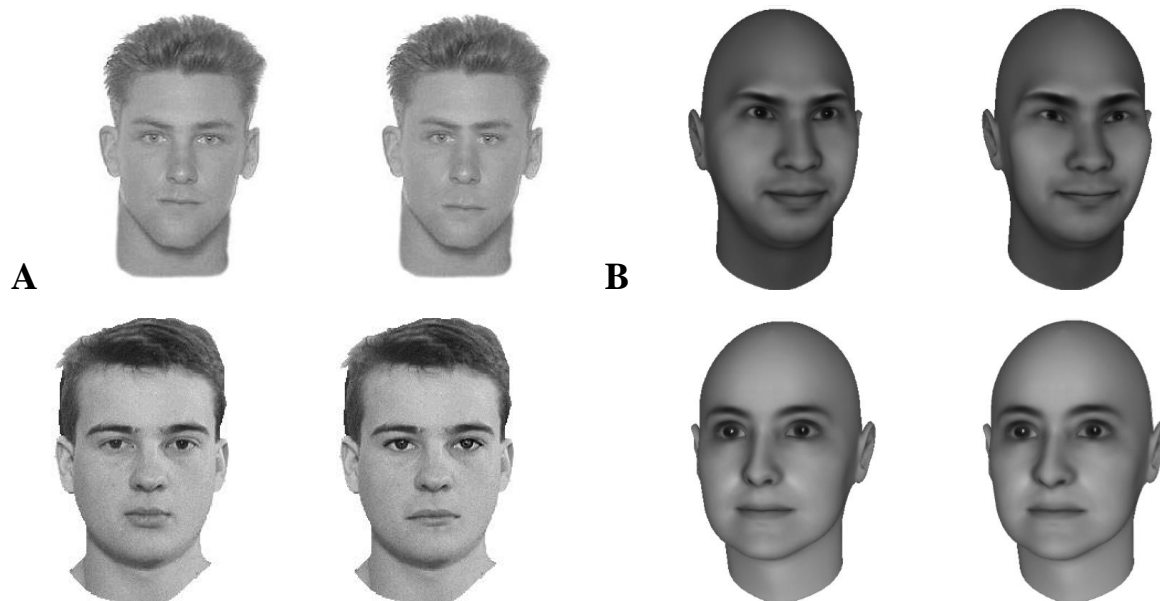
Figure 9. Examples of the images used experiment one (localiser). A) The stimuli used in the photo task from Pitcher et al. (2007) task. The top pair demonstrate difference by spacing. The bottom pair demonstrate difference by parts. B) The stimuli used in the morph task from Pitcher et al. (2009) task. The top pair demonstrate morph difference of 100%. The bottom pair demonstrate morph difference by 50%.

The second task (*the morph task*) and stimuli (Figure 9B) was used by Pitcher et al., (2009). Ten different, grey-scaled, faces that varied in terms of gender and viewing angle were generated using FaceGen (Singular Inversions; Toronto, ON, Canada). The features of these faces were altered in order to create a second face out of each original. A morph series (11 images total, the two initial faces and the nine image morphs between them) was then created using FantaMorph (Abrosoft; http://www.abrosoft.com/). A subset of these images was chosen based on the criteria described by Pitcher et al. (2009). Forty image pairs were made of images that were the same. Another 40 were selected such that 10 pairs differed by 50% on their morph spectra, 20 pairs differed by 80%, and 10 pairs differed by 100%. The images were sized 400 x 400 pixels and subtended approximately 9.8 x 9.8 degrees of visual angle.

The stimuli were presented on a Dell desktop computer, running a 64-bit Windows 7 operating system. The monitor was a 51cm x 29cm Samsung monitor with a 120Hz refresh rate. Participant's head movements were minimized with the use of a combined chin- and forehead rest positioned 57cm from the monitor. The experimental stimuli were presented and data recorded with PsychoPy version 1.82.01 (Peirce, 2007).

5.5. Procedure

The experiment was conducted in four blocks; two blocks each for the photo and the morph tasks, one with stimulation of the vertex and one with stimulation of the OFA. The blocks were completed such that both OFA blocks were performed back-to-back and the same for the vertex blocks while the different versions of the task were counterbalanced. In all blocks there were 80 trials; 40 trials where the faces presented were the same and 40 where they were different. The order of presentation was randomized. For each pair of images, the participant had to indicate whether the images were the same face or different faces by pressing one button on the keyboard for same and one button for different.

Figure 10 shows the trial design for the photo task based on Pitcher et al. (2007). A 500 ms fixation cross began each trial, followed by the first image presented for 250 ms. A 500 ms blank screen separated the two face images before the second face was presented for 250 ms. Finally, a blank screen for 1000 ms. TMS stimulation coincided with the onset of the second image and lasted for 500 ms, meaning that stimulation continued for 250 ms into the final blank screen.
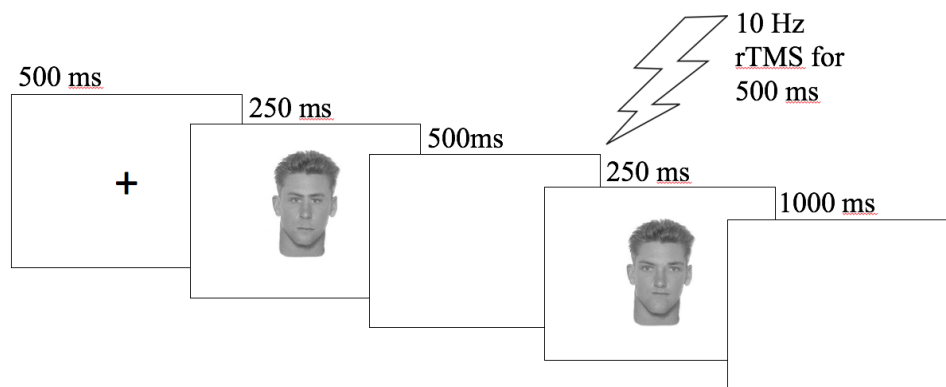
Figure 10. Trial design for the photo task based on Pitcher et al. (2007).

Figure 11 shows the trial design for the morph task based on Pitcher et al. (2009). It is very similar to the first with the primary difference being the inclusion of a mask between the first and second images. The trial begins with fixation for 500 ms before the presentation of the first image for 500 ms. The mask is displayed for 500 ms before the second image for another 500 ms and then a blank screen for 1500 ms. TMS stimulation still coincided with the onset of the second image but this time stimulation ended with the offset of the image. The

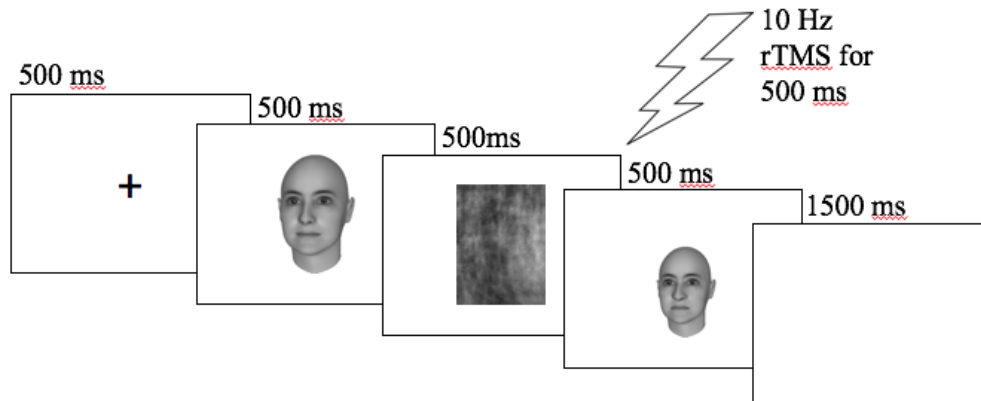task in these blocks was the same as that previously described.

Figure 11. Trial design for the morph task based on Pitcher et al. (2009).

After a brief re-introduction to the TMS lab and the equipment to be used in the experiment (all TMS participants have been introduced to this equipment before in the process of signing up to participate), and completion of the required documentation (participants completed the TMS precautions questionnaire again in case any of the circumstances had changed since their initial display of interest in participation), participants sat at the experiment presentation computer and fitted the tracking head-band to their head. The Polaris camera was positioned such the head-band was in its view. Registration of the participant's head proceeded as described above. Once the participant's head was registered they were instructed to proceed through the first, introductory section of the experiment presented on the computer. This comprised of instructions for completing the task, some demonstrations on what constituted same or different faces, and eight practice trials (this introductory section was performed before each block). Once they completed the practice trials, the coil was positioned. This was done at this point in order to avoid coil position changes during the practice and instruction sections. The coil was held in place by the stand and the participant was told that the experimenter would monitor the movement of the coil though the course of each block. The experimenter stood behind them in case the coil needed to be corrected. This correction would be attempted if the coil moved more than 3mm from the target. The TMS machine was then armed and the participant was instructed to begin. After both blocks at a single site were completed the participant was instructed to take a break after which they completed the next set of introductory practice trials and the coil was repositioned for the second site.

5.6. Results

All analyses were performed using JASP version 0.8.0.0 (JASP Team, 2016). For RT, only correct responses were analysed. One participant was removed from the analysis of the morph task due to their vertex performance being substantially below chance (as such the morph task's $n = 22$). Table 1 shows the mean performance accuracy in percentages and the mean response times in milliseconds for both the photo task and the morph task.

Table 1. Mean accuracy (%) and RT (ms) by block and site in Experiment 1.

	Photo		Morph	
	Vertex	OFA	Vertex	OFA
Mean Accuracy (SD)	79.7% (8.8)	76.9% (9.8)	74.4% (7.4)	72.7% (6.7)
Mean RT (SD)	761 ms (108)	755 ms (128)	822 ms (155)	842 ms (164)

Figure 12 shows the distribution of accuracy results and individual participants' averaged performance in the photo and morph tasks at vertex and OFA. A 2 x 2 analysis of variance (ANOVA) was performed with stimulation site (vertex, OFA) and task version (photo, morph) as repeated measures factors. Main effects of stimulation site ($F(21) = 6.151$, $p = 0.022$, $\eta_p^2 = 0.227$) and task version ($F(21) = 6.916$, $p = 0.016$, $\eta_p^2 = 0.248$) were found, showing that TMS of the OFA resulted in decreased accuracy over both the photo and morph tasks. No interaction was found ($F(21) = 0.527$, $p = 0.476$, $\eta_p^2 = 0.024$). Paired-samples t-tests were further performed to examine the effect of stimulation separately for each task version. For the photo task, a mean difference in accuracy of 2.8% was found ($t(22) = 2.212$, $p = .038$, $d = 0.461$, 95% CI [0.2, 5.5]) suggesting that stimulation of the OFA coordinate site produced lower accuracy ($M = 76.8\%$, $SD = 9.8$) than vertex stimulation ($M = 79.7\%$, $SD = 8.8\%$). For the morph task version, no difference in accuracy was found between stimulation sites ($t(21) = 0.109$, $p = .280$, $d = 0.236$, 95% CI [-1.5, 4.9].

Figure 12. Boxplots of accuracy in Experiment 1. Diamonds represent mean of each condition. Dots represent individual results.

Figure 13 shows the distribution of RT results and individual participants' averaged RT in the photo and morph tasks at vertex and OFA. A 2 x 2 analysis of variance (ANOVA) was performed with stimulation site (vertex, OFA) and task version (photo, morph) as within-subject factors. A significant main effect of task version ($F(21) = 18.467$, $p < .001$, $\eta_p^2 = 0.468$) was found, suggesting that the morph task was more difficult than the photo task. The main effect of stimulation site ($F(21) = 0.596$, $p = .449$, $\eta_p^2 = 0.028$) and the interaction were not significant ($F(21) = 0.292$, $p = 0.595$, $\eta_p^2 = 0.014$).

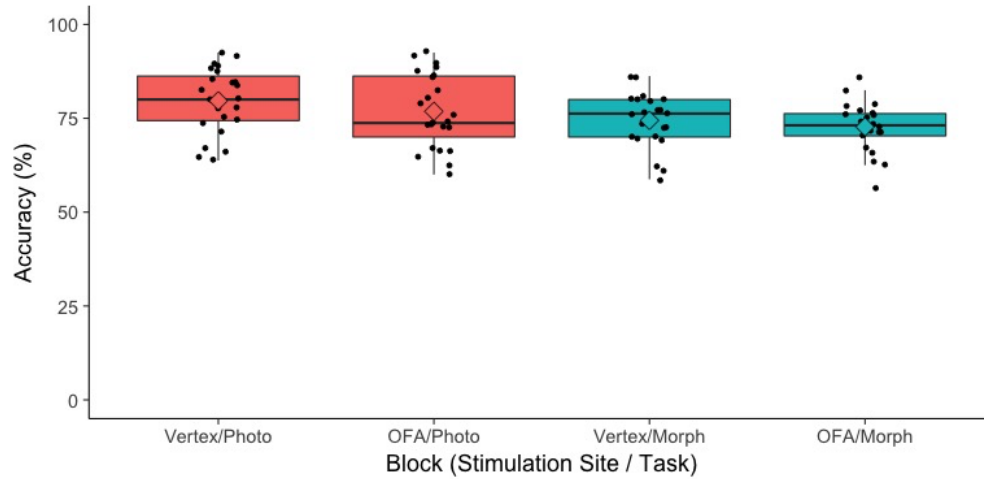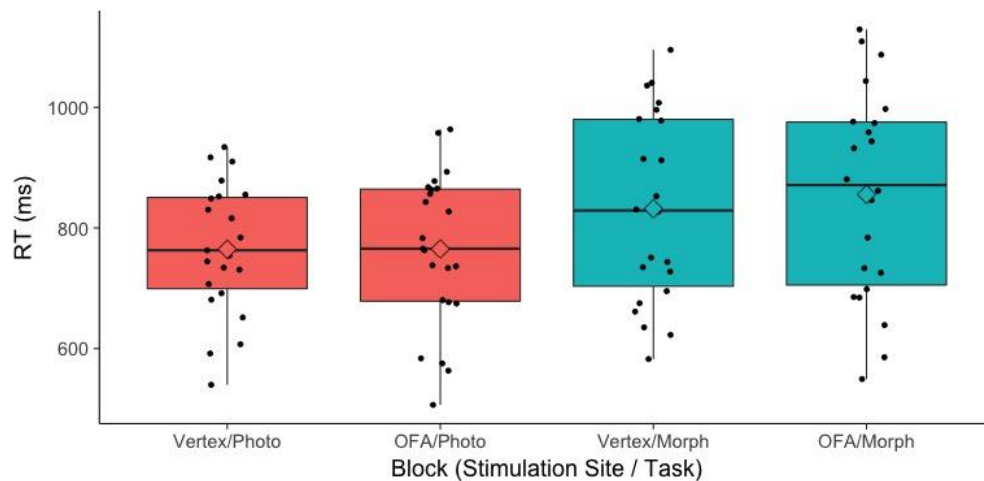*Figure 13*. Boxplots of RTs in Experiment 1. Diamonds represent mean of each condition. Dots represent individual results.

5.7. Discussion

This experiment was run to determine whether the OFA could be reliably localised using TMS. I targeted OFA based on coordinates derived from the average coordinates of peak face-selective activation in the inferior occipital gyrus found by Rossion et al. (2003). Vertex was used as a control site.

My findings show that the task based on Pitcher et al. (2007) showed a decrease in accuracy as a result of stimulating the OFA coordinates but not vertex. This finding replicates the study by Pitcher et al (2007). However, I did not see any effect with the task based on Pitcher et al. (2009), thus I did not replicate Pitcher et al. (2009). I discuss why this might be the case in General Discussion. For now, I take the effect found with the 2007 task as evidence that my TMS protocol can localise OFA and disrupt face processing. This finding sets the stage for my investigation of OFA and holistic face processing in Experiment 2.

6. Experiment 2: OFA and holistic face processing

Experiment 2 is the main experiment of interest. This experiment was designed to investigate whether OFA contributes to holistic processing in the categorisation of faces. Previous fMRI results indicate that OFA is implicated in holistic processing (Yovel, & Kanwisher, 2005; Schiltz, & Rossion, 2006; Harris, & Aguirre, 2008, Renzi et al., 2015), but influential neural models of face processing suggest that OFA's main contribution to face perception is primarily part-based (Haxby, Hoffman, Gobbini, 2000; Rossion, 2008; Duchaine, & Yovel, 2015).

Two previous TMS studies are particularly relevant to this experiment. Solomon-Harris, Mullin, and Steeves (2013) conducted two experiments to look at the OFA's involvement in face identification and categorisation. To assess face identification, they used a same/different discrimination task like Pitcher et al. (2007). To assess face categorisation, they had images of faces with the normal part configuration and faces with the parts scrambled around and asked participants to indicate when the image on screen was a face. They found that TMS disrupted the identification task but not the categorisation task, suggesting the OFA is not involved in face categorisation. This study has been criticised (Renzi et al., 2015) for using non-face stimuli that contain face parts as other work (Liu, Harris, & Kanwisher, 2010) has shown that the OFA is sensitive to face parts regardless of configuration. This would mean that stimulating the OFA would disrupt ability to categorise both faces and non-faces in this task. As well as that, because the task contained face parts, it

means the task could have been tapping a part-based categorisation mechanism and leaves the issue of holistic face categorisation open.

This issue is addressed in a recent study by Bona, Cattaneo, and Silvanto (2016). In this study they used Mooney images to assess categorisation of faces and non-faces. Mooney stimuli are thought to be processed in a top-down, holistic manner because Mooney faces only contain face configuration information that requires analysis of the whole image. Local, or part-based, analysis is not possible as there are no particular elements of the image that look face-like or resemble face parts (Rossion, Dricot, Goebel, & Busigny, 2011, Latinus, & Taylor, 2005). When seen as a whole, the typical face configuration can be seen and local face elements can be identified (Latinus, & Taylor, 2005). Figure 14 demonstrates splitting a Mooney face image into quarters, none of the quarters alone contain enough local face information to be recognisable as part of a face. Bona, Cattaneo, & Silvanto's (2016) participants were to categorise Mooney images seen as either faces or non-faces (scrambled two-toned Mooney images) while they received TMS to the OFA. They found that stimulation slowed down their response time when categorising faces, suggesting that the OFA was involved in the holistic categorisation of faces. However, they also found that stimulation of the OFA impaired performance with non-face, complex objects, leaving open the possibility that the OFA is involved in holistic categorisation of not only faces but complex objects more generally.

Figure 14. A Mooney face split equally into quarters. No individual quarter contains face part/feature information that is recognisable. One needs to recognise the whole face before one can see where the local face parts are.

In Experiment 2, I take a similar approach as Bona, Cattaneo, and Silvanto (2016). Participants will complete a task that requires them to indicate whether or not the Mooney image presented contains a face or a non-face distractor (or, a car or non-car distractor in the control condition). My predictions are as follows. If OFA contributes to holistic processing, stimulation of the OFA but not vertex will result in a decrease in accuracy and/or increase in RT when categorising images as faces or non-faces. If OFA's contribution to holistic processing is face-specific, then TMS effect will be found only for faces, not for cars. But if OFA's contribution to holistic processing is not face-specific, then TMS effect will be found for both faces and cars.

6.1. Participants

Fifteen individuals (9 female) with a mean age of 25.1 years ($SD = 4.7$ years) participated in Experiment 2. All had participated in Experiment 1. This study was approved by the School of Psychology Human Ethics Committee under delegated authority of Victoria University of Wellington's Human Ethics Committee (application ID 22575).

6.2. TMS stereotaxy

This was the same as in Experiment 1.

6.3. TMS protocol

This was the same as in Experiment 1.

6.4. Stimuli and apparatuses

All image manipulation was performed using the GNU Image Manipulation Program version 2.8.14 (GIMP; www.gimp.org). Mooney stimuli were created from images selected from the Faces in the Wild image set (Huang, Ramesh, Berg, & Learned-Miller, 2008). Images were originally selected from this set based on a judgement concerning their suitability for being turned into a black-and-white Mooney image. To convert them into Mooney stimuli a Gaussian blur with radius of 0.5% of the width of the image was applied. The threshold function was applied with a value of 127. This resulted in target face images. To produce distractor images, I followed the procedures of Verhallen and Mollon (2015) and created six different distractors for each target image. The specific procedures for creating the six distractors are included in Appendix A. From these different distractor sets, one distractor was chosen for each target image. This same procedure was followed for the car stimuli, which were initially selected from the Fine-Grained Categorization Car Dataset (Krause, Stark, Deng & Fei-Fei, 2013). Figure 15 shows example stimuli.

Figure 15. Examples of Mooney face and distractor (left, mid-left) and Mooney car and distractor (mid-right, right).

The original set of stimuli consisted of 157 face-distractor image pairs and 160 car-distractor image pairs. The faces and cars were selected based a visual inspection and judgment of their similarity with the original Mooney (1957) images. They were piloted with volunteers from the SampleSize subreddit (https://www.reddit.com/r/SampleSize/) using the online testing platform Testable (www.Testable.org). A target image was presented for 75 ms followed by a mask which remained for 300 ms. Participants were required to press a button indicating whether the target image was a face or a non-face distractor (or a car or non-car distractor). Subsets of images were then selected from this first set based on three hierarchical criteria. Participants had to have accurately categorised the face and its corresponding non-face distractor with no more than a 40% difference in accuracy between them. Secondly, pairs where the distractor accuracy averaged below 60% were rejected. Thirdly, pairs where the target accuracy averaged above 60% were retained. This resulted in a shortlist of 105 face-distractor pairs and 92 car-distractor pairs. These pairs were then piloted on Amazon Mechanical Turk (www.mturk.com) using the same experimental design. The results from the Mechanical Turk pilot were used to further shortlist the remaining images using the same hierarchical criteria described above. Two sets of target-distractor pairs with equal difficulty in this task were then created from these final subsets. The difficulty of the face sets was tuned to an average overall test accuracy of 86%, and for cars difficulty was tuned to an average overall test accuracy of 81%. The images used as masks were selected from the distractors of pairs that did not meet the selection criteria. All images were sized 250 x 250 pixels and subtended approximately 6.5 x 6.5 degrees of visual angle. Three participants were piloted in the lab using the final image sets and showed ceiling performance, so the task was made harder by changing the image presentation times from 75 ms and 300 ms for the target and mask to 50 ms and 450 ms, respectively, as described in the procedure below. This change was piloted by four participants whose average performance was 83% ($SD = 9\%$).

6.5. Procedure

Trials were blocked by image category (faces, cars) and stimulation site (vertex, OFA) such that both blocks of vertex stimulation were performed together and both blocks of OFA stimulation were performed together. Stimulation site was counterbalanced and within stimulation sites the order of face and car blocks was counterbalanced. Additional to this, each order of blocks alternated in their use of the alternate forms of the test such that one order would use the first form then the second and vice versa. Each block consisted of 80 trials and these trials' presentation order was randomized for each participant.

The trial design is depicted in Figure 16. A 500 ms fixation cross started the trial followed by the target image presented for 50 ms. Immediately after the target image a mask image was displayed for 450 ms, after which a question mark appeared to prompt participants to respond. TMS protocol and the online monitoring of the TMS coil were performed as in Experiment 1.
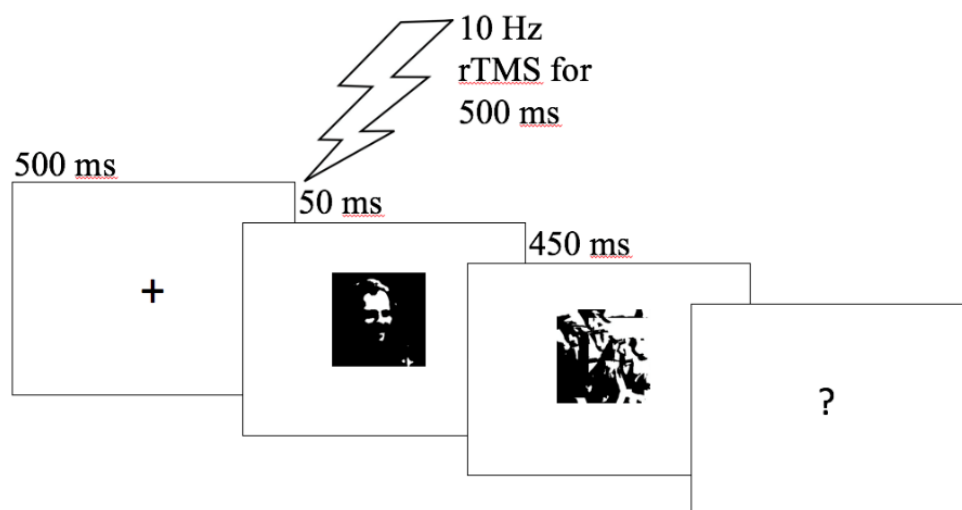

Figure 16. Trial design for Experiment 2.

6.6. Results

All analyses were performed using JASP version 0.8.0.0 (JASP Team, 2016). For RT, only correct responses were analysed. Table 2 shows the mean performance accuracy in percentages and the mean response times in milliseconds for both the face and the car blocks.

Table 2. Mean accuracy (%) and RT (ms) for block and site in Experiment 2.

Measure	Faces		Cars	
	Vertex	OFA	Vertex	OFA
Mean Accuracy (SD)	87.2% (7.7)	88.9% (4.8)	90.9% (5.9)	90.3% (6.1)
Mean Response Time (SD)	292 ms (112)	285 ms (86)	295 ms (116)	263 ms (69)

Figure 17 shows the distribution of accuracy results and individual participants' averaged performance in the face and car task blocks at vertex and OFA. Accuracy results (% correct responses) were analysed using a 2 x 2 ANOVA with stimulation site (vertex, OFA) and image type (face, car) as within-subjects factors. No main effect of stimulation site ($F(1, 14) = 0.152$, $p = .702$, $\eta_p^2 = 0.011$) or image type ($F(1, 14) = 3.539$, $p = .081$, $\eta_p^2 = 0.202$) was found. Neither was there any interaction ($F(1,14) = 1.519$, $p = .238$, $\eta_p^2 = 0.098$).

Figure 17. Boxplots of accuracy results in Experiment 2. Diamonds represent mean of each condition. Dots represent individual results.

Figure 18 shows the distribution of RT results and individual participants' averaged RT in the face and car tasks at vertex and OFA. A 2 x 2 analysis of variance (ANOVA) was performed with stimulation site (vertex, OFA) and image type (face, car) as within-subject factors. No main effect of of stimulation site ($F(1,14 = 0.913$, $p = .355$, $\eta_p^2 = 0.061$) or image

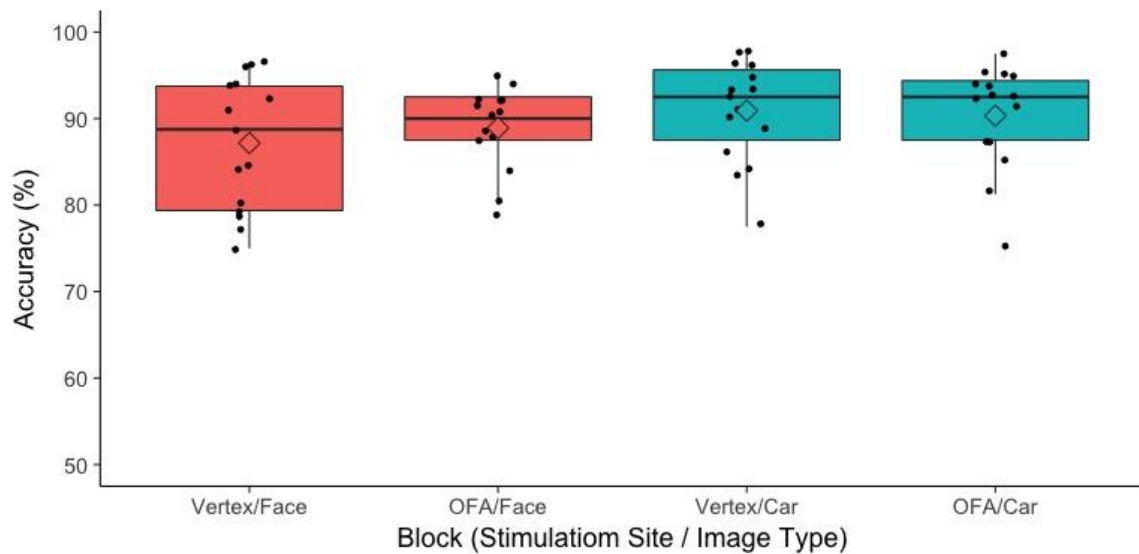type ($F(1,14) = 0.521$, $p = .482$, $\eta_p^2 = 0.036$) was found. Neither was there any interaction ($F(1,14 = 0.770$, $p = .395$, $\eta_p^2 = 0.052$).
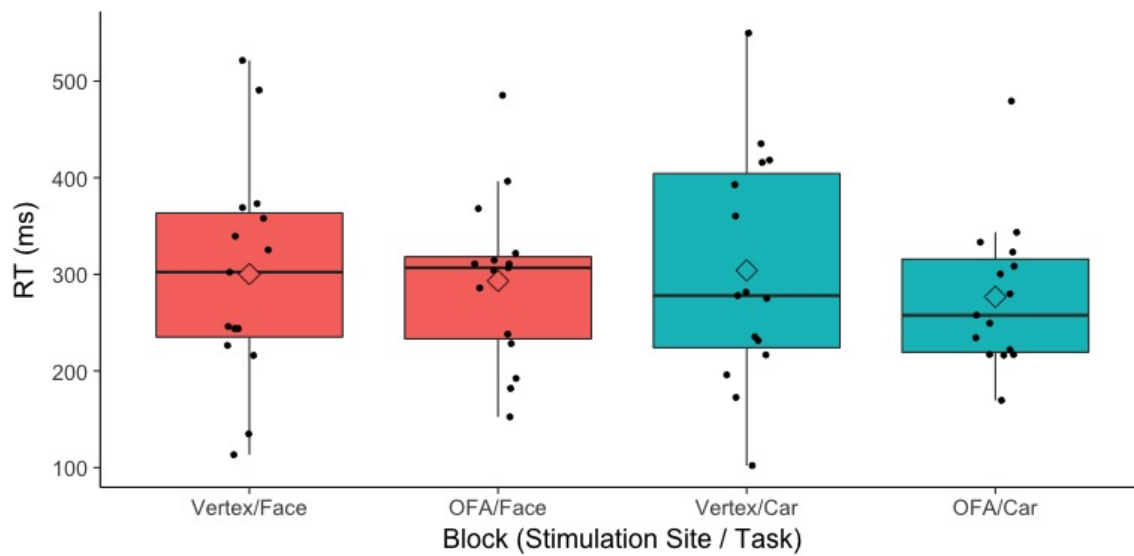

Figure 18. Boxplots of RTs in Experiment 2. Diamonds represent mean of each condition. Dots represent individual results.

6.7. Discussion

Experiment 2 was run to examine whether the OFA is causally involved in holistic categorisation of faces. I stimulated participants' OFA and vertex while they completed a task categorizing ambiguous Mooney images as faces or non-faces and as cars or non-cars.

My findings show that stimulation of the OFA produced no difference in face or car categorisation on either accuracy or RT. This finding is inconsistent with the result of Bona, Cattaneo, and Silvanto (2016), who found difference in RT as a result of stimulating OFA in a similar task. I discuss the differences between that study and my study current one in General Discussion.

7.   General Discussion

The current study's purpose was two-fold; firstly, to demonstrate that the OFA could be localised using TMS in situations where fMRI localisation is unavailable; and secondly to address whether or not the OFA contributes to holistic processing, specifically in the categorisation of faces. In order to do that, two experiments were run. The first acted as a localiser. With the localiser I demonstrated that the OFA could be stimulated with TMS using a set of coordinates derived from a previous fMRI localisation of the OFA. The second experiment addressed the holistic processing. Stimulation of the OFA whilst categorising

Mooney faces and non-faces did not result in any decrease in reaction speed or accuracy, suggesting that the OFA is not required for accurate holistic face categorisation. The following general discussion will go through the methodological and theoretical implications of both the localiser and the main experiment before noting some limitations of this current study.

7.1. Localising the OFA

When studying areas of the brain that are functionally defined, a localiser is used. This confirms that the region of the brain being examined is the functional region of interest. This is commonly done with fMRI. While this method of localising functionally selective brain areas is the most common and requires fewer participants, it is not the only way. In fact, depending on the areas being studied, there is a spectrum of methods that range from the least to most precise. fMRI has a major limitation of requiring expensive and complicated technologies that many institutions do not have access to. Other methods depend less on expensive technologies (e.g., localising based on 10-20 scalp locations or other measurements on the scalp, or the hunting method), but they also have their own limitations; for example, low sensitivity to inter-individual variability, and time required. In order to assess the power associated with different localiser methods, Sack et al. (2009) measured the number of participants required to acquire a significant effect of stimulating a region of parietal cortex implicated in automatic magnitude processing. They found a hierarchy of power. fMRI had the highest power requiring the fewest participants ($n = 5$), descending through using structural MRI and anatomical landmarks (9 participants) and grouped Talairach coordinates (13 participants), to using 10-20 EEG sites as the lowest, requiring the most participants (47 participants).

As our lab does not have access to functional imaging technologies, the current localiser reached a middle ground by selecting the target for stimulation based on averaged Talairach coordinates derived from an fMRI localiser performed in a previous study (Rossion et al., 2003). This method utilises functional information but not necessarily structural or individual information. It is, therefore, better suited to group-level localisation (Sandrini, Umiltà, & Rusconi, 2011).

While this method has limitations that could have been addressed by using the complete hunting method it was chosen because it had been used before. Because Pitcher et al. (2007) and Kadosh, Walsh, and Kadosh (2011) both used this set of Talairach coordinates it was confidently expected that the OFA would be localised in a reasonable portion of the

sample. Across the different experiments in Pitcher et al. (2007) and Kadosh et al. (2011) the number of participants ranged from eight to thirteen and in all experiments they found significant effects of stimulating the OFA. This is consistent with Sack et al. (2009).

In the localiser experiment I found a significant reduction in accuracy as a result of OFA stimulation. However, the results were not as robust as those found by Pitcher et al. (2007) even when using the same task. One explanation for this is difference between samples in terms of either the susceptibility to TMS or accuracy of the coordinates in targeting individual OFAs. There is reason to expect that a large portion of participants may not respond to TMS as expected due to differences in anatomy/physiology (for example, skull thickness or cortical excitability). van Koningsbruggen, Peelen, and Downing (2013) found that only 14 out of 26 participants who had had their EBA localised by fMRI actually showed a decrease in performance in a body part identification task. This suggests that localisation is not the only factor and that even an appropriate localiser may still result in participants being unaffected by stimulation. The way that van Koningsbruggen et al. (2013) dealt with this issue was by only proceeding with participants whose EBA was localised and affected by stimulation in the TMS localiser.

Experiment 2's results can be analysed a similar way, by only including the eleven participants who individually showed a decrease in accuracy in the photo task of the Experiment 1 when their OFA was stimulated (Figure 19). When these participants were reanalysed in a 2 x 2 ANOVA (as above) there are still no significant main effects of stimulation site ($F(1,10) = 0.381$, $p = .551$, $\eta_p^2 = 0.037$) or of image type ($F(1,10) = 3.488$, $p = .091$, $\eta_p^2 = 0.259$) and no significant interaction ($F(1,10) = 3.676$, $p = .084$, $\eta_p^2 = 0.269$). This interaction shows a lower p-value and higher effect size than the test run with the full 15 participants, however analysing the data this way has reduced the power. Testing more participants would indicate how likely this interaction is to be real.
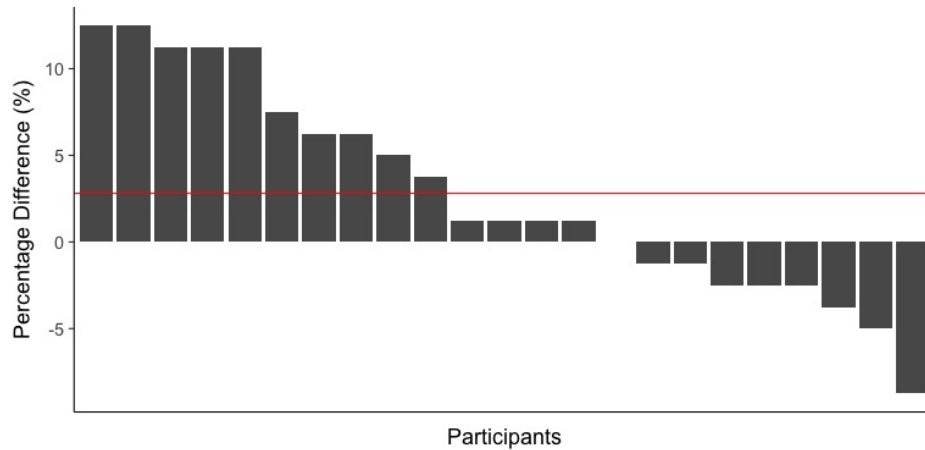
Figure 19. TMS effect (% accuracy Vertex – % accuracy OFA) for each participant in the photo task of Experiment 1. Red line shows mean effect of 2.8%.

Another potential explanation concerns how I measured the effect of TMS. While I used the same stimuli and task as Pitcher et al. (2007), I was not completely replicating that study. Pitcher et al. (2007) analysed the effect of TMS on the parts and spacing conditions separately and found that TMS disrupted perception of faces that differed from each other by parts but not those differing by spacing between parts. The current experiment looked only at the total decrease in accuracy without separating out the conditions. If the effect of TMS is more strongly associated with part-based changes then the null effect of TMS on spacing changes would pull the average effect down. While this could explain why the current experiment's effect is smaller, I did not find this to be the case. In a 2 x 2 ANOVA with site (vertex, OFA) and difference type (spacing, parts), significant main effects of site ($F(1,22) = 4.895$, $p = .038$, $\eta_p^2 = 0.182$) and difference type ($F(1,22) = 10.868$, $p = 0.003$, $\eta_p^2 = 0.331$) were found, but no significant interaction.

While the results of the photo task indicate the participants' OFAs were being stimulated, the results of the morph task show no difference in vertex and OFA stimulation. There are a couple of explanations for this discrepancy. The first explanation is that the exact image pairs used in the morph task were likely to differ from those Pitcher et al. (2009) used. This is due to the way they reported which images pairs they used. Specific image pairs were not reported but the criteria for selecting image pairs was. For example, they report that ten of the trials which had different faces were made of faces which differed by 50% on their morph continuum. Because these could have been any ten images (as long as they differed by 50% on their morph continuum), it is likely that the ten I selected were not the same. This could be a problem if the stimuli differ in their effectiveness. For example, Pitcher et al. (2009) could

have chosen images/image pairs whose differences made them easier to begin with. This could have made them particularly disruptable by TMS (Sandrini, Umiltà, & Rusconi, 2011), whereas the images/image pairs I selected may have been harder in a way that meant that perception of them could have survived the disruption.

Another explanation comes from the fact that Pitcher et al. (2009) localized the individual OFAs of their participants and they did so with the same stimuli and task as they used in the TMS experimental conditions. It is possible that the fMRI localization provided a stimulation target in each participant that was selective for the specific face stimuli used in that study. The stimuli used by Rossion et al. (2003) were cropped, gray-scale photographs of faces, as were the stimuli used by Pitcher et al. (2007), compared to the full, head-and-neck, computer-generated faces used by Pitcher et al., (2009). The average MNI coordinates reported for the OFA by Pitcher et al. (2009) were converted into Talairach coordinates via the MNI to Talairach Coordinate Converter applet (MNI2TAL; www.bioimagesuite.com; Lacadie, Fulbright, Rajeevan, Constable, Papademetris, 2008) and compared to the Talairach coordinates used by Pitcher et al. (2007). While the Y and Z values are very similar, the X values differ by eight units (for scale, the points of peak activation of the OFA and the FFA were found to be separated by 9 X units; Rossion, Hanseeuw, & Dricot, 2012). No indications of variance were given by Pitcher et al. (2009) but this difference shifts the target from a relatively medial position in the cortex for the Pitcher et al. (2007) coordinates to a much more lateral position for the Pitcher et al. (2009) coordinates. Considering the small size of the OFA (ranging from at least 169 mm^3 to at least 571 mm^3; Rossion, Hanseeuw, & Dricot, 2012) it is possible that the difference between them marks the targeting of stimulus set-specific areas of the OFA.

The above explanation suggests a consideration to be made regarding the tasks chosen in TMS localisers. In the current study, the OFA was localised via an identification task *behavioural assay*. I found a decrease in identification accuracy when stimulating at the chosen coordinates and claimed that the localiser had identified the OFA. It is possible, however that the area defined by those coordinates was an area that selectively participated in face identification and had no part in categorisation at all, let alone holistically, and as such TMS at that location would not alter performance in a holistic categorisation task. There is some reason to believe that the OFA is not a singular region but rather an area comprised of different subareas. For example, Henriksson, Mur, and Kriegeskorte (2015) found that the response patterns of the OFA can dissociate different face parts such that different subareas

of OFA were more responsive to certain parts. These face-part selective patches were found to be laid out such that their spacing matched the spacing of face parts on the face, suggesting that the OFA comprises a faciotopic map. This evidence seems to directly support the part-based processing role of the OFA but more generally it demonstrates how the OFA is not a cohesive whole and does contain subareas that respond to different face stimuli differently. It is fair to claim that I localised the OFA, however, it may not have been the relevant part of the OFA. This is an issue of TMS localisers specifically. When localisation is performed with fMRI, face-selective regions will become visible regardless of the task, as long as those areas do anything with face information. TMS, however, disrupts not just stimulus-related activity but task-related activity; whatever is being performed at the site of stimulation. The recommendation from this is that the behavioural assays used in TMS localisers should be selected based on similarity of stimulus and task with the planned experimental conditions.

7.2. The OFA and Holistic Face Processing

Experiment 2 addressed the issue of the OFA's participation in holistic processing. Participants indicated whether Mooney images seen were faces or non-faces (and cars or non-cars) while their OFA and vertex were stimulated. No differences in accuracy or response time were found when participants were stimulated at the vertex compared with the OFA. This suggests that the OFA is not involved in the holistic categorisation of faces. Cars were similarly unaffected and as such will not be further discussed.

It cannot be claimed from the current study that the OFA specifically participates only in part-based processing, only that it does not appear to participate in holistic processing (or, at least not the holistic processing required by Mooney images). The current study's results are therefore inconsistent with the results of Bona, Cattaneo, and Silvanto (2016) and Renzi et al. (2015), both of which found OFA's involvement in categorising Mooney stimuli. The current study differs from these in a few ways that may impede comparisons between them.

Firstly, Bona, Cattaneo, and Silvanto (2016) do not report their accuracy results by site, only by image type. TMS studies of face perception using an online, repetitive protocol typically find effects in accuracy rather than RT (e.g., Pitcher et al., 2007; Pitcher et al., 2009; Solomon-Harris et al., 2013; Pitcher, 2014). They do report the significant results of their response times. The current study's design emphasizes accuracy by asking participants to hold off their response until after stimulation to respond. As such their response times were all very similar. This makes it hard to compare the results of these two studies.

Renzi et al. (2015) report accuracy data (in which is seen the effect of tDCS on Mooney categorisation) and response times (in which there is no difference). Renzi et al. (2015) had participants categorise Mooney faces and non-face objects in two testing sessions; pre- and post- real or sham stimulation. They found that tDCS diminished the learning effect between pre- and post-tests and concluded the OFA is involved in holistic face categorisation. This study is hard to compare with the current study for two reasons. Firstly, the results are difficult to interpret. For example, a diminished learning effect between pre- and post-tests would suggest that it was a disruption to face memory (i.e., stimulation disrupted the encoding of the previously tested Mooney images so they could not be more easily categorised as faces via recognition), rather than categorisation. Secondly, tDCS is known to affect large portions of the brain due to massive diffusion of the electrical field/current densities produced from the electrodes (Datta et al., 2009). It is possible that their stimulation altered activity in areas other than the OFA, making it difficult to identify which area was responsible for the holistic categorisation of faces.

Secondly, the Mooney stimuli are different. Bona, Cattaneo, and Silvanto (2016; and Renzi et al., 2015) used the original Mooney images (Mooney, 1957). The current study used images generated from a set of photos of famous people. It is possible that current Mooney images were not similar enough to the original Mooney images, particularly in terms of figure/ground ambiguity. The source material for the Mooney images I generated had already been manipulated (by the publishers of the photos) to centre the subject's head and were very often front-on views. As such, the faces may stand out from the backgrounds more. Figure 20 compares the original and the current study's Mooney images both upright and inverted. A way to test the similarity of the images would be to have participants categorise both sets of images, both upright and inverted. If the images created for the current study are equal in their holistic processing requirements, the inversion effects for both sets would be the same.
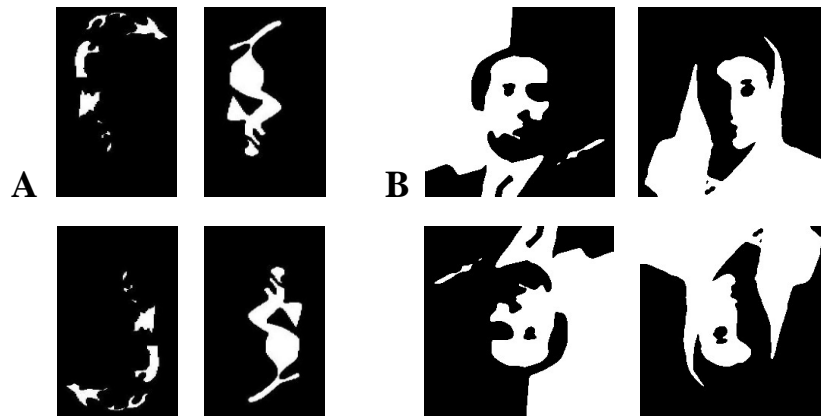
Figure 20. Comparison of the Mooney images. A) The original Mooney faces used by Bona, Cattaneo, and Silvanto (2016) upright (top) and inverted (bottom). B) The Mooney images used in the current study upright (top) and inverted (bottom).

Thirdly, the difficulty of the tasks is different. Even with a much faster display time (50 ms), and the use of a mask, the mean accuracy for faces across sites in the current study was 88.1% (*SD* = 6.25). This is compared to the mean accuracy for faces across sites of 86% (*SD* = 1.01) in Bona, Cattaneo, and Silvanto (2016) which would be expected to be an easier task based on their longer display times and lack of masking image. The current study's task seems to be slightly easier on average and the participants more variable in their ability. This is important because it is possible that an easier task may be less affected by stimulation than a harder task because the cognitive processes behind a harder task may be more spread-out in time and be missed by stimulation (Sandrini, Umiltà, & Rusconi, 2011). This difference in difficulty could be a result of the differences in the stimuli. Participants may have been able to tell when an image was not a face by its lack of figure/ground contrast, or tell when an image was a face by comparatively higher "pop-out" of the face from the ground. These three differences (i.e., emphasizing accuracy over RT, using new stimuli, and having a much less difficult task) make comparison between these two studies difficult, and this is especially important in this case as the previous studies provide evidence for conflicting conclusions (Bona, Cattaneo, & Silvanto, 2016; Renzi et al., 2015; Solomon-Harris, Mullin, & Steeves, 2013).

It is possible that the OFA does, or can, participate in the holistic categorization of faces, but it is not necessary for accurate holistic perception. This could explain the current results as disrupting the OFA would have no effect on the holistic categorization of faces because the cognitive "slack" could be picked up by other regions, such as the FFA. Disrupting the FFA alone and the FFA and OFA together would allow us to see what

incremental contribution (if any) is made to holistic categorization of faces by the OFA. Disruption of the FFA would be expected to result in a decrease in accuracy in Mooney categorization. If the OFA can contribute to, but is not necessary for, holistic categorization of faces we would expect that accuracy in the Mooney categorization task would decrease even further when both the OFA and FFA are disrupted, compared to when just the FFA is disrupted. If there is no such incremental decrease it could be concluded that the OFA does not contribute at all. This procedure was not used in this study because, due to its location, the FFA cannot be stimulated by TMS. A similar procedure could, however, be implemented in patients with electrodes placed on the surface of the brain for the purposes of treating epilepsy, like, for example in Parvizi et al. (2012) where a subset of electrodes in an epilepsy patient's brain lay over the FFA and could be stimulated, causing disruption to normal face perception.

7.3. Future directions

While this study suggests that the OFA is not causally involved in holistic categorisation of faces, there is still the question of whether the OFA has any holistic capacity at all. fMRI studies show that the OFA is responsive to certain holistic tasks and stimuli but it cannot tell us what that response indicates. fMRI responses could be indexing the OFA's response to a task/stimulus without indexing its causal involvement. For example, the OFA might contain information regarding holistic face percepts but that information could be epiphenomenal (i.e., not causally related to the task currently being performed). This would be consistent with Haxby et al. (2001) who found, using multi-voxel pattern analysis, that voxels outside the typically-defined face-selective areas contain information about faces and that that information could be used by a computer algorithm to predict when a participant was viewing a face. Because these voxels fell outside face-selective regions they are thought not to be involved in face perception regardless of the information they carry. Furthermore, Williams, Dang, and Kanwisher (2007) showed how the spatial distribution of fMRI response can distinguish task-related responses from irrelevant responses in category-selective cortex by analyzing the spatial pattern of responses in trials where participants correctly identified the shape presented. An example of this epiphenomenal response can be found in the case of the LOC and its response magnitude to faces. While the LOC does respond to faces (Yovel, & Kanwisher, 2005), stimulation of the LOC does not affect upright face identification (Pitcher et al., 2007; Pitcher et al., 2009). It is possible the results of the current study are showing the same thing; the OFA may respond to holistic face elements but does not use

those elements in the completion of cognitive tasks. A future study using the fMRI method described by William, Dang, and Kanwisher (2007) would shed light on this issue by analyzing the pattern of fMRI responses in the OFA when participants viewed Mooney faces and correlating those response patterns with accurate face categorization performance.

The results of this study agree with the notion that the OFA is primarily, if not only, concerned with the processing of local face details and parts. For example, the current results agree with studies that demonstrate evidence of the OFA's preference for parts over holistic elements like spacing (Pitcher et al., 2007) and configuration (Liu, Harris, & Kanwisher, 2010; Solomon-Harris, Mullin, & Steeves, 2013). They also agree with studies that show evidence of the OFA's preference for identification/discrimination over categorisation (Rossion et al., 2003; Rossion, Dricot, Goebel, & Busigny, 2011; Solomon-Harris, Mullin, & Steeves, 2013). All of these results suggest that the OFA may not be involved in holistic processing of faces but does suggest a preference for identification and discrimination over categorisation. The notion of the OFA's involvement in holistic identification is supported by studies that use other holistic manipulations like face inversion, composite faces, and stereoscopic depth manipulation (Yovel, & Kanwisher, 2005; Schiltz, & Rossion, 2006; Harris, & Aguirre, 2008). TMS could be used to extend these fMRI findings into causal associations with the OFA. This has already been done in the case of face inversion. Pitcher, Duchaine, Walsh, Yovel, and Kanwisher (2011) stimulated the OFAs and LOCs of participants while they made same/different identification judgments of faces both when they were upright and inverted. They found that upright face identification was disrupted when stimulating the OFA only, but inverted face identification was disrupted by stimulation to both the OFA and the LOC. Whatever processes the OFA applies to faces, it does them regardless of orientation. Because it is thought that holistic processing is engaged selectively for upright faces, this suggests that the OFA is applying a face-selective, part-based process to upright and inverted faces. Using TMS with other holistic identification tasks would further elucidate what process/-es the OFA is engaging in and whether it has any causal capacity for holistic processing.

8. Conclusion

The aim of this thesis was to use transcranial magnetic stimulation to investigate the involvement of the occipital face area in the holistic categorisation of faces. In order to do this two experiments were conducted. The first acted as a localiser, confirming that

participants' OFA could be stimulated. Participants determined whether faces presented sequentially on a computer screen were they same or different while receiving stimulation to their OFA (as determined from Talairach coordinates from a previous fMRI study). It was hypothesised that if the OFA was being stimulated then accuracy in the face identification task should decrease. In one of the tasks participants' accuracy was reduced as a result of stimulation and the ability to stimulate the OFA was confirmed. The second experiment was conducted to assess the OFA's role in holistic face processing. Participants determined whether the Mooney images seen on a screen contained a face (or car) or not while receiving stimulation to the OFA. It was hypothesised that if the OFA was involved in the holistic categorisation of faces then participants' categorisation accuracy should drop, or their response speed should decrease, as a result of stimulation. Neither participants' accuracy or response speed were reduced as a result of stimulation, suggesting that the OFA was not participating in the holistic categorisation of Mooney faces.

By using TMS to study the OFA and holistic processing, this thesis expands upon the growing literature that uses TMS to investigate the roles of different face-selective regions in face perception. Further, it builds on the literature concerning the role of the OFA, more specifically that detailing its involvement in categorisation of faces. While there is some evidence in the literature that suggests the OFA participates in the holistic processing of faces, the current study is more consistent with the notion that the OFA is primarily concerned with the perception of face parts. While it now seems unlikely that the OFA is involved in the holistic categorisation of faces, there is still the evidence suggesting it is involved in the holistic identification of faces (Schiltz, & Rossion, 2006; Harris, & Aguirre, 2008). As such it is suggested that further research be done, using TMS, to determine the causal role of the OFA in face perception.

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Appendix A

Procedures for Creating Mooney Distractor Images for Experiment 2 using GNU Image Manipulation Program version 2.8.14 (GIMP; www.gimp.org)

1. Overlay a copy of the original image in 'darken' mode that is translated 56 pixels right and 37 upwards; overlay another copy of the original image in 'lighten' mode, translated 85 pixels right and 22 downwards; overlay another copy in 'darken' mode, translated 100 pixels left and 14 upwards; overlay a final copy in 'darken' mode, translated 16 pixels left and 77 downwards.

2. Flip the original image horizontally; overlay a copy of this image in 'subtraction' mode, translated 134 pixels right and 36 upwards; overlay another copy of the image in 'subtraction' mode and flip it horizontally (back to the original orientation), translated 56 pixels left and 28 upwards.

3. Overlay a copy of the original image and rotate it 11° clockwise; duplicate the original image in 'darken' mode and rotate it 2° clockwise; overlay another duplicate of the original image in 'darken' mode, flip it vertically and translate 108 pixels right and 225 upwards.

4. Overlay a copy of the original image in 'lighten' mode, translated 210 pixels left and 138 downwards; overlay another copy in 'lighten' mode, flipped vertically and translated 208 pixels right and 121 downwards.

5. Invert the polarity of the original image and flip it vertically.

6. Invert the polarity of the original image; overlay a duplicate of the inverted original in 'darken' mode, flipped horizontally and then vertically, and finally rotated 29° anti-clockwise.