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CHAPTER

Face Processing and TMS

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Abstract

Faces are rich sources of social information that simultaneously convey someone's identity, attentional focus, and emotional state. Humans process this wealth of socially relevant information in a network of face-selective regions distributed across the brain. This chapter reviews studies that have used transcranial magnetic stimulation (TMS) to study the cognitive operations and functional connections of the face network. TMS has been used to disrupt brain areas contributing to the processing of facial identity, facial expression, eye-gaze direction, head direction, trustworthiness, and the auditory-visual integration of speech. TMS has also been combined with neuroimaging to map how transient disruption of a targeted face area impacts connectivity across the face network. I also review chronometric TMS studies that have established when faces are processed across different brain areas down to a millisecond resolution.

Keywords: facial identity, facial expression, eye-gaze direction, head direction, trustworthiness, the auditory-visual integration of speech

Subject: Cognition and Behavioural Neuroscience, Neuroscientific Techniques, Neuroscience

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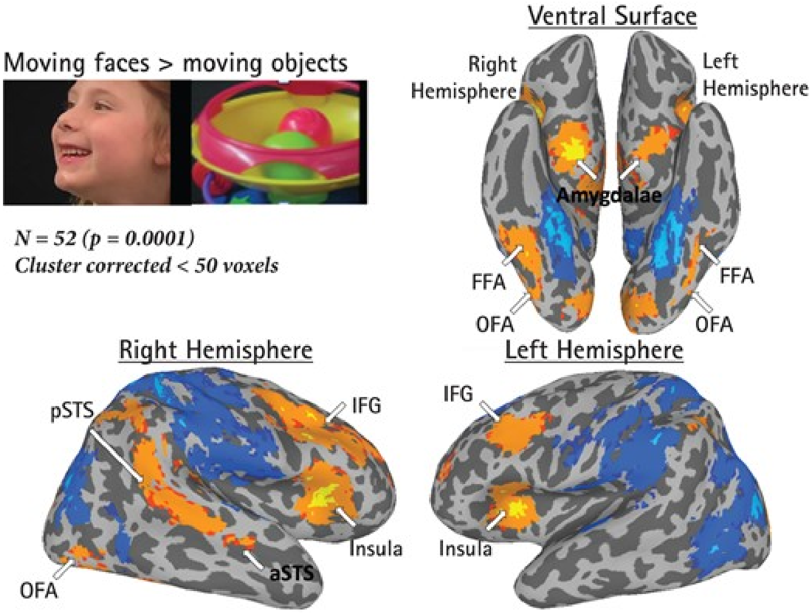
Introduction

Face-selective areas are found across the entire brain (Figure 1). This makes the study of the face network an excellent proxy model for studying the brain as a network. In addition, because the functional roles of these face-selective regions have been extensively studied with neuroimaging, the face network is an excellent model system in which to establish how complex cognitive operations (e.g., facial expression recognition and facial identity recognition) are processed across different brain areas (Allison et al., 2000; Kanwisher and Yovel, 2006; Pitcher et al., 2011c; Todorov, 2012). Neuropsychological studies of patients with face-selective deficits, or prosopagnosia, have provided the strongest evidence that faces are processed in a functionally specific cortical network, but such patients are rare (Sergent and Signoret, 1992; Barton et al., 2002; Rossion et al., 2003; Rezlescu et al., 2014; Susilo et al., 2015). It is also rare to have premorbid data from these patients. So, we cannot know the location of their face-selective areas, or have measures of their behavioral face recognition abilities prior to the incident that caused their prosopagnosia (Farah, 2004). In addition, studies of neuropsychological patients must account for any compensatory neural plasticity that may have occurred after the incident, leading to changes in their behavioral performance (Robertson and Murre, 1999).

Transiently disrupting face-selective regions with transcranial magnetic stimulation (TMS) in neurologically normal experimental participants is not limited by these issues. TMS studies enable researchers to systematically build on more than two hundred years of neuropsychological research. This chapter describes studies that have used TMS to systematically disrupt face-selective regions while participants performed concurrent behavioral tasks which measured different aspects of face processing (e.g., identify or facial expression discrimination). TMS has also been combined with fMRI to measure how transient disruption of a targeted face-selective region impacts other face-selective regions (Pitcher et al., 2014; Pitcher et al., 2017; Handwerker et al., 2020).

Figure 1



Group whole brain analysis (*N* = 52) showing a contrast of moving faces (orange) greater than moving objects (blue) (Pitcher et al., 2011a). Results show face-selective voxels in the core areas of the face network, the occipital face area (OFA), fusiform face area (FFA) and superior temporal sulcus (STS). Face-selective voxels were also seen in the amygdala, insula and inferior frontal gyrus (IFG).

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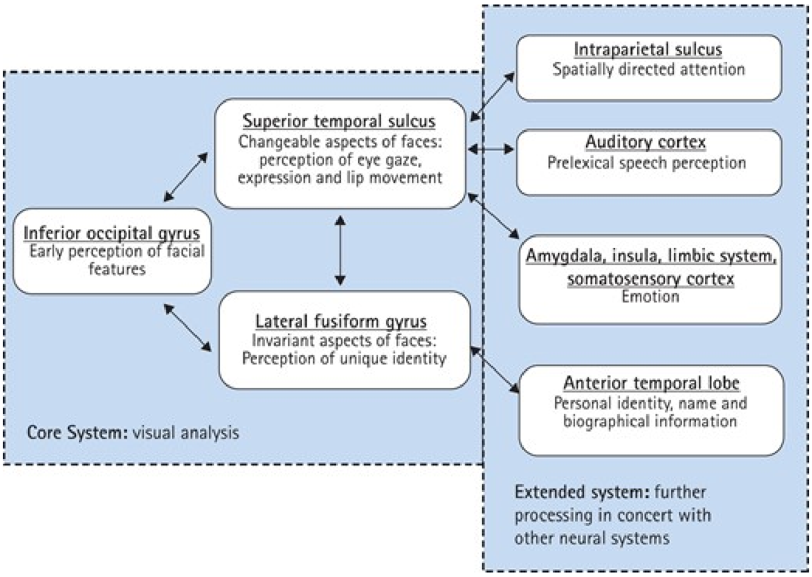
The Face Network

Models of face perception (Figure 2) propose that recognizing someone's identity, as opposed to recognizing their facial expression, are dissociable cognitive processes (Bruce and Young, 1986) that are preferentially processed in different parts of the brain (Haxby et al., 2000; Calder and Young, 2005). These different functions are preferentially processed in two functionally distinct face processing pathways that begin in occipitotemporal cortex. The ventral pathway, that includes the fusiform face area (FFA) (Kanwisher et al., 1997; McCarthy et al., 1997) preferentially processes invariant facial aspects, such as individual identity (Grill-Spector et al., 2004; Rotshtein et al., 2005). The lateral pathway, that includes the face-selective area in the posterior superior temporal sulcus (pSTS) (Puce et al., 1996) preferentially processes changeable facial aspects such as facial expression and eye gaze direction (Hoffman and Haxby, 2000; Winston et al., 2004). Despite these functional differences both pathways are thought to begin in the occipital face area (OFA) (Gauthier et al., 2000), an area that acts as the gateway for the extended face processing network (Figure 2).

The OFA, FFA, and pSTS are often referred to as the core areas of the network because they are involved in the visual analysis of faces. Haxby et al. (2000) proposed that these core areas are functionally connected to other brain areas that preferentially process a range of cognitive functions. These include the intraparietal sulcus (attention), auditory cortex (speech perception), and the anterior temporal lobe (person specific identity information). There are also connections to multiple brain areas that process emotion, these include the amygdala, insula, limbic system and the somatosensory cortex.

Figure 2



The extended face network.

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The spatial resolution of TMS is approximately 1–2 cm from the coil (Kammer, 1999). This limits the number of areas in the face network that can be directly stimulated in TMS studies. To date, areas in the face network that have been directly targeted include the OFA (Pitcher et al., 2007), the pSTS (Pourtois et al., 2004), the parietal cortex (Beck et al., 2006), the somatosensory cortex (Pitcher et al., 2008). Other areas such as the FFA and the amygdala remain outside the effective range of direct stimulation. One way to study the effects of transient disruption in these deeper face areas is to combine TMS with functional magnetic resonance imaging (fMRI). Neural activity can be measured across the face network using fMRI before and after lateral face-selective areas such as the OFA or pSTS are stimulated. The remote effects of this stimulation can then be measured in remote areas such as the FFA (Pitcher, 2014) and the amygdala (Pitcher et al., 2017; Handwerker et al., 2020).

Combining TMS with fMRI to Study Face Network Connectivity

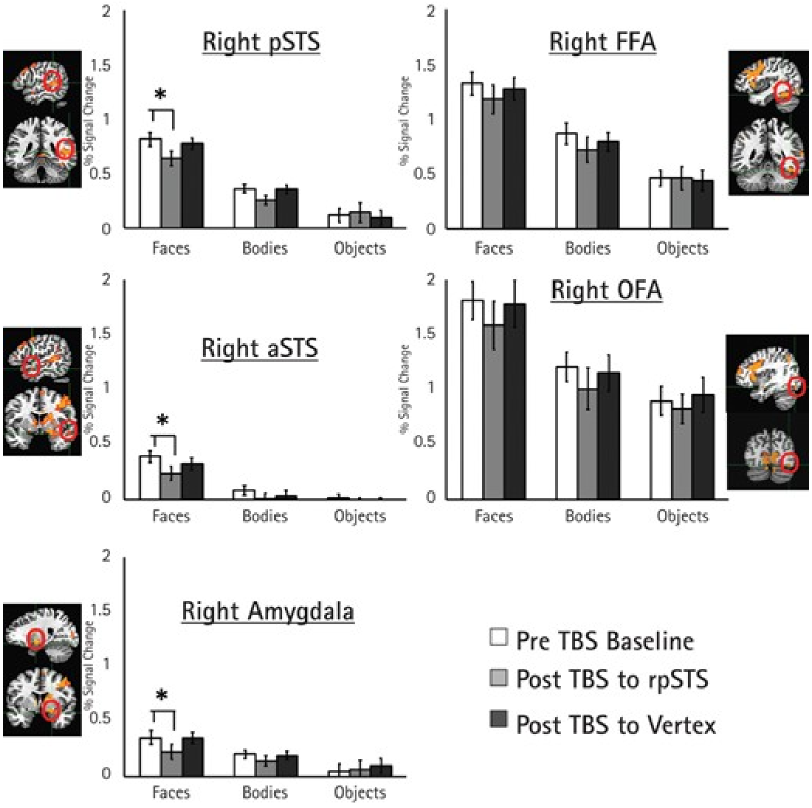
As stated above, existing models propose that the OFA is the sole entry point for the extended face network (Haxby et al., 2000; Calder and Young, 2005). Other models have challenged this hypothesis by proposing that there are multiple face pathways with independent cortical inputs from early visual cortex. Neuroimaging studies of healthy participants demonstrate that the pSTS exhibits a greater response to moving faces, more than static faces, while the OFA and FFA show little or no preference for moving faces (LaBar et al., 2003; Fox et al., 2009; Schultz and Pilz, 2009; Pitcher et al., 2019). This preferential response to motion suggests that the pSTS is receiving functional input from the motion-selective brain area hMT+ (O'Toole et al., 2002). Anatomical studies in humans and macaques also report cortical connections between motion-selective areas and the STS (Boussaoud et al., 1990; Gschwind et al., 2012). This cortical pathway projects down the superior temporal sulcus and along the lateral brain surface. Finally, neuropsychological patients with lesions to brain areas where the OFA is typically located can still exhibit face-selective activity in the FFA and pSTS (Rossion et al., 2003; Steeves et al., 2006; Rezlescu et al., 2012) challenging the hypothesis that the OFA is sole entry point for the wider face network.

Pitcher et al. (2014) tested the hypothesis that there are two cortical pathways that project from early visual cortex into the face network in a combined TBS/fMRI study. TBS was delivered over the OFA, or the pSTS, while participants were scanned with fMRI while watching short videos of moving faces or static images taken from these videos. Results demonstrated that TBS delivered over the OFA and pSTS produced a dissociation in the impairment to moving and static faces in the pSTS. TBS delivered over the rpSTS only reduced the neural response to moving faces in the rpSTS, while TBS delivered over the OFA only reduced the neural response to static faces in the rpSTS. By contrast TBS delivered over the OFA only reduced the response to static faces in the FFA. This pattern of results is consistent with the hypothesis that changeable face information can reach the pSTS via cortico-cortical connections from early visual cortex that are independent of the OFA (O'Toole et al., 2002). This conclusion is consistent with a neuropsychological study of a prosopagnosic patient with a right ventral occipitotemporal lesion (Sliwinska et al., 2020a). The neural response in the patients right pSTS was comparable with control participants while the responses in his right OFA and FFA were impaired.

Subsequent studies that have combined TBS with fMRI to study face processing have continued to focus on the functional connections of the pSTS. Nonhuman primate neuroanatomical studies report a cortical pathway projecting along the STS into the dorsal banks of the amygdala (Aggleton et al., 1980; Stefanacci and Amaral, 2000). Pitcher et al. (2017) combined TBS with fMRI to test whether they could identify causal evidence for this cortical pathway in the human brain. Results showed that TBS delivered over the right posterior superior temporal sulcus (rpSTS) reduced the neural response to moving faces not only in the rpSTS itself, but also in face-selective voxels in the right anterior superior temporal sulcus (raSTS) and in the right amygdala (Figure 3).

More recently a similar approach was used to study what effect TBS delivered over the rpSTS would have the functional connectivity of the extended face processing network (Handwerker et al., 2020). Participants were scanned using resting-state fMRI (rsfMRI) before, and after, TBS was delivered over the rpSTS or the right motor cortex. TBS delivered over the rpSTS caused a network-wide reduction in resting-state connectivity across the extended face-processing network. This connectivity reduction was observed not only between the rpSTS and other face-selective areas, but also between non-stimulated face-selective areas on the ventral and medial brain surfaces (e.g., between right fusiform face area and the bilateral amygdalae). This demonstrates that TBS delivered over a single node in a brain network reduces the functional connectivity between the distributed nodes of that extended network. Crucially, this disruption was observed between remote nodes that had not been stimulated.

Figure 3



The results of Pitcher et al. (2017). Percent signal change data for the dynamic face, body and object stimuli before and after TBS in the five core regions-of-interest (ROIs): The rpSTS, raSTS, right amygdala, rFFA, and rOFA (Error bars denote Standard Errors). Brain slices show examples of the face-selective (dynamic faces > dynamic objects) ROIs in a typical participant. TBS delivered over the rpSTS selectively and significantly reduced the BOLD response to dynamic faces only in the rpSTS, raSTS, and right amygdala (* denotes significant effects).

TMS Studies of Facial Identity

Neuroimaging studies have identified different brain areas that contribute to facial identity recognition; these include the FFA (Grill-Spector et al., 2004), the anterior temporal lobe (Ramon et al., 2015), and the hippocampus (O'Neil et al., 2013). All are outside the effective range of TMS precluding the direct stimulation of these areas while participants perform facial identity discrimination tasks. Because of this limitation the studies that have used TMS to study facial identity recognition have largely focused on the OFA (Gauthier et al., 2000).

As stated earlier, the OFA is the earliest face-selective area in the visual hierarchy and is thought to preferentially process the component parts of the face (Haxby et al., 2000). This has been causally demonstrated in studies showing that TMS delivered over the right OFA impairs the discrimination of face parts, such as the eyes and the mouth (Pitcher et al., 2007; Kadosh et al., 2011). Interestingly the perception of face parts has also been disrupted by TMS delivered over the left middle frontal gyrus (BA8) suggesting that higher cortical areas may be interacting with visual areas in the perception of facial features (Renzi et al., 2013). This study also demonstrated that TMS delivered over the right inferior frontal gyrus (BA44) disrupted a task in which participants had to judge the spacing between face parts (also configural processing). Disruption of configural face processing has also been demonstrated by TMS delivered over the posterior parietal cortex (Zachariou et al., 2017).

Face parts have also been manipulated in TMS studies that have used morphing software to create a gradual range between two different facial identities (Pitcher et al., 2009; Dilks et al., 2013). These studies demonstrated that TMS delivered over the right OFA disrupted the accurate discrimination of faces but had no effect on tasks using matched control stimuli (e.g., objects, bodies and scenes). Other studies have shown that TMS delivered over the right OFA disrupted the participants ability to match faces of two different identities using face stimuli that had been balanced for contrast, spectral power and brightness (Bona et al., 2018) or had been cropped to remove all external features (e.g., face shape and hair) (Solomon-Harris et al., 2013). These results again demonstrate that the stimuli in identity discrimination tasks of the OFA typically use faces that have subtle physical differences. This is consistent with the functional profile of the OFA which generates an early physical representation of a face. While it is clear that accurate perception of the component parts of a face contributes to identity recognition it is more likely that the holistic integration of an entire face is being processed when recognizing a face. The fact that a TMS OFA study that used color photographs of celebrities failed to find any effect of facial identity processing is also consistent with this conclusion (Gilaie-Dotan et al., 2010).

The most compelling TMS evidence that the OFA is causally involved in processing facial identity comes from three recent studies from Ambrus and colleagues (Ambrus et al., 2017a; Ambrus et al., 2017b; Ambrus et al., 2019). These studies elegantly investigated the feedforward and feedback connections thought to exist between the OFA and the higher face processing areas process the invariant physical representations of unique facial identities (e.g., the FFA and anterior temporal lobe). In their first study participants learnt the faces of two previously unknown individuals using a sorting task that required identifying 60 unique photographs of two different people (Ambrus et al., 2017b). Results showed that TMS delivered over the right OFA impaired the participants ability to accurately the learn facial identities compared to TMS delivered the vertex control site.

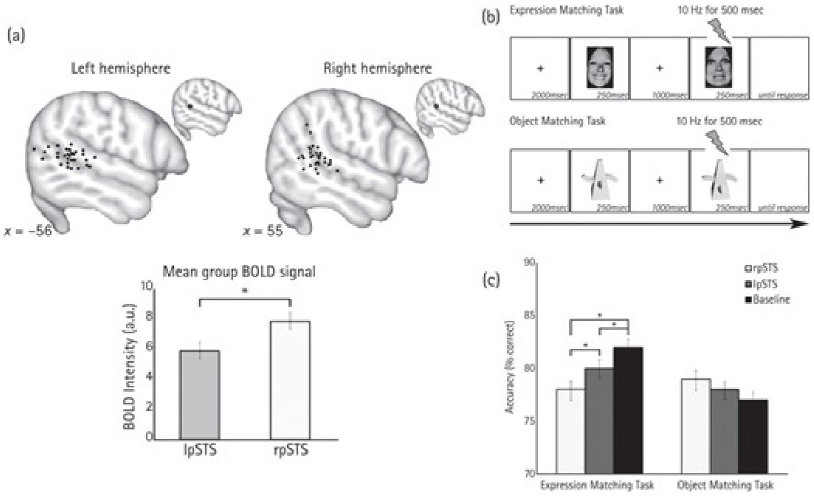
Subsequent studies demonstrated that TMS delivered over the OFA impaired the priming of famous faces (Ambrus et al., 2017a) and the priming of names with famous faces (Ambrus et al., 2019). Taken together these studies demonstrate that the low-level face processing that occurs in the OFA causally contributes to more complex face computations in higher face-selective areas. A causal connection between the OFA and FFA has been demonstrated in neurologically normal participants in combined TMS/fMRI studies. These studies demonstrated that offline TMS delivered over the right OFA reduced the blood oxygen level-dependent (BOLD) response to faces in the right FFA only (Pitcher et al., 2014) and the bilatateral FFA (Solomon-Harris et al., 2016). Future combined TMS/fMRI studies will hopefully further investigate the remote effects of targeted focal disruption in the OFA across the extended face network.

TMS Studies of Facial Expression

TMS has also proven to be an effective experimental tool to study facial expression processing. This is, at least partly, because many of the brain areas involved in processing expressions are located on the lateral brain surface and can be directly stimulated with TMS. TMS studies of expression processing have targeted the OFA (Pitcher et al., 2008), the posterior STS (Pourtois et al., 2004; Sliwinska and Pitcher, 2018; Sliwinska et al., 2020b), premotor cortex (Balconi et al., 2014), the face area in the somatosensory cortex (Pitcher et al., 2008), medial prefrontal cortex (Mattavelli et al., 2013), dorsolateral prefrontal cortex (Zwanzger et al., 2014), and the cerebellum (Ferrari et al., 2018). The fact that expressions are processed across so many areas distributed across the brain demonstrates the saliency of the face when conveying emotion.

Neuroimaging studies have consistently identified the posterior STS as a locus of facial expression processing (Allison et al., 2000). Despite this extensive fMRI evidence, the first TMS study to target the area reported TMS delivered over the right pSTS impaired an eye-gaze task, but had no effect on a facial expression task (Pourtois et al., 2004). However, this study used only two facial expressions (happy and fearful). This lack of variety in facial expressions may account for the lack of TMS induced impairment. Subsequent studies by Pitcher and colleagues using a wider range of expressions (happy, fearful, sad, angry, surprise, and disgust) have reported impairments when targeting the right pSTS (Pitcher, 2014; Pitcher et al., 2020; Sliwinska and Pitcher, 2018).

Figure 4



Sliwinska and Pitcher (2018) demonstrated that TMS delivered over the rpSTS and lpSTS impaired facial expression recognition. A. fMRI analysis showed that the right pSTS had a higher neural response to moving faces than the left pSTS. B. Participants then performed recognition tasks on facial expressions and objects while TMS was delivered over the right and left pSTS. C. TMS results were consistent with the fMRI results. TMS delivered over the right pSTS Produced a greater impairment than TMS delivered over the left pSTS. This suggests that cognitive functions that are seemingly lateralized still rely on processing across both hemispheres for optimum task performance.

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TMS can also be used to systematically investigate the laterality of facial expression processing in the pSTS. Sliwinska and Pitcher (2018) demonstrated this by stimulating the right and the left pSTS in a group of thirty participants while they performed a delayed match to sample expression recognition task (Figure 4). Results showed that TMS delivered over the right pSTS impaired task performance to a greater extent than TMS delivered over the left pSTS. But crucially, TMS delivered over the left pSTS still impaired task performance more than TMS to vertex control site. This result suggests that cognitive functions that are seemingly lateralized still rely on processing across both hemispheres for optimum task performance.

TMS has also been used to test embodied cognition models of facial expression recognition. Theories of embodied cognition propose that recognizing facial expressions is not only visual process. It also depends on somatosensory and motor areas that internally simulate the observed emotion, and that this process aids expression recognition (Niedenthal, 2007). This has been causally demonstrated in TMS studies that delivered TMS over the left premotor cortex (Enticott et al., 2008; Balconi et al., 2014). Rochas et al. (2013) also reported that TMS delivered over the left pre-supplementary motor area (pre-SMA) selectively impaired the recognition of happy faces but not fearful or angry faces. Finally, both Pourtois et al. (2004) and Pitcher et al. (2008) have demonstrated that TMS delivered over the right somatosensory cortex also disrupts the recognition of facial expressions.

Frontal areas have also been targeted with TMS to disrupt facial expression recognition. Mattavelli et al. (2011) demonstrated that TMS delivered over the medial prefrontal cortex (mPFC) significantly increased response latencies on congruent trials in a priming study that matched words (happy or angry) and facial expressions. The same authors extended this result in a later study by again targeting the mPFC in a combined TMS with electroencephalography (EEG) design (Mattavelli et al., 2016). Results showed that TMS delivered over the mPFC reduced two separate face-selective EEG responses recorded from occipital areas peaking at 100 and 170 ms after stimulus onset. The mPFC was also targeted in an exciting study that went beyond basic facial expressions to demonstrate the area was causally involved in judgments of facial trustworthiness (Ferrari et al., 2016). Dzhelyova et al. (2011) also demonstrated that TMS delivered over the right pSTS disrupted judgments of trustworthiness based on facial features.

Zwanzger et al. (2014) investigated the causal role of the right dorsolateral prefrontal cortex (DLPFC) in a combined TMS/MEG study. TMS delivered over the right DLPFC increased the MEG response to fearful faces in a time-interval that occurred 110 to 170 ms after stimulus onset. These demonstrations that TMS delivered over frontal areas can modulate responses recorded from posterior brain areas demonstrate the functional connections between face-selective areas in the occipitotemporal cortex. This is consistent with TMS studies demonstrating that TMS delivered over the OFA impairs expression recognition (Pitcher et al., 2008; Yaple and Vakhrushev, 2016).

Chronometric TMS Studies of Face Processing

Chronometric TMS can be used to investigate when a targeted brain area is causally engaged in processing the concurrently performed behavioral task. Single pulses of TMS are typically delivered over the target region at different time points after stimulus onset or after the commencement of behavioral monitoring (Amassian et al., 1993). Plotting the temporal pattern of the induced behavioral impairments reveals when the stimulated area is causally engaged in task performance. Single pulse TMS delivered systematically at different time intervals (e.g., 10 ms apart) can give a very precise representation of the temporal activation pattern but it does require a large number of temporal conditions when covering longer time periods (e.g., a time window ranging from 0–200 ms with pulses delivered every 10 ms would require twenty-one different conditions). One way to reduce the number of conditions and expand the duration of the induced disruption is to use two pulses. This is well established in the physiological domain and has been adapted for behavioral experiments. Double pulse TMS separated by 40ms has proven to be a reliable protocol for demonstrating when a variety of functionally distinct cortical areas exhibit peak processing (O’Shea et al., 2004).

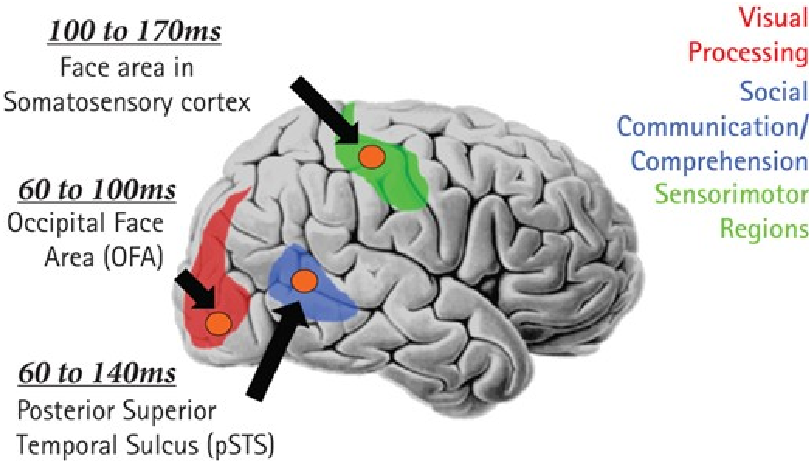
The first chronometric TMS study of face recognition (Pitcher et al., 2007) directly tested the hypothesis that the OFA is preferentially engaged in the processing of face part at an early stage of the face recognition process. TMS was delivered over the right and left OFA while participants performed a delayed match to sample discrimination task with face and house stimuli. These stimuli systematically manipulated either the parts of the faces (the eyes and mouth) and the houses (the windows and door) or the spacing between these parts. Results showed that TMS disrupted the discrimination of the face part task only when delivered over the right OFA (there was a nonsignificant trend at the left OFA). TMS had no effect on the face spacing task or either of the house tasks. While this result demonstrates that the OFA was selectively impaired only for face part discrimination, it does not address when the OFA was causally processing these face parts. This was addressed in a follow-up experiment in which double pulse TMS (pulses separated by 40 ms) was delivered over the OFA at different latencies after stimulus onset ranging from 20–250 ms. Intriguingly, TMS only impaired task accuracy when it was delivered 60 and 100 ms after stimulus onset. Taken together the results of this study demonstrate not only that the OFA is causally engaged in face part processing but also that it does so at a very early latency after stimulus onset.

This approach of conducting an initial TMS study to show an area is causally engaged in a task, and then following this with a chronometric TMS study to reveal when that area is causally active offers a powerful way to study the brain. Beauchamp et al. (2010) used just such an approach in an elegant TMS study of the McGurk effect. In an initial experiment TMS delivered over the right pSTS impaired participants ability to perceive McGurk stimuli, but not the non-McGurk control stimuli. Then in a follow-up experiment the authors delivered single pulse TMS (pulses separated by 100 ms) over the right pSTS at different latencies ranging from minus 300 ms to post 300 ms after stimulus onset. Intriguingly TMS only disrupted task performance in a temporal window ranging from minus 100 ms to post 100 ms demonstrating when the integration of visual and auditory information was being computed in the targeted brain area.

Chronometric TMS studies of the face processing are especially useful because they can be used to causally track the processing speed of face perception across the nodes of the face network. Pitcher and colleagues have used this approach in two papers to trace the speed of facial expression recognition (Figure 5). In the first study participants performed a delayed match to sample facial expression recognition task while double pulse TMS (separated by 40 ms) was delivered over the right OFA and right somatosensory cortex (SC) (Pitcher et al., 2008). TMS was delivered at different latencies after presentation of the match stimulus ranging from 20–60 ms, 60–100 ms, 100–140 ms, 130–170 ms, 170–210 ms, and 210–250 ms (these latencies were chosen to target face-selective ERP components that peak at 100 ms and 170 ms).

Results showed TMS disrupted expression recognition at 60–100 ms only when delivered over the right OFA, and at 100–140 ms and 130–170 ms when delivered over the right SC. In a follow-up study (Pitcher, 2014) the same TMS protocol was repeated but the right OFA and the right posterior superior temporal sulcus (pSTS) were stimulated. Results showed the same impairment window at the right OFA (60–100 ms) and a similar early (but longer) impairment window at the right pSTS (60–140 ms). Taken together, the results of these studies causally demonstrate the speed at which facial expression recognition is processed from posterior to more anterior face areas in the human brain. Such timing information is essential when understanding the functional connections and the direction of these connections in brain networks (Figure 5).

Figure 5



TMS studies (Pitcher et al. 2008; Pitcher, 2014) can trace the causal time-course of facial expression recognition across multiple brain areas. In these studies, double pulse TMS (pulses separated by 40 ms) was delivered at different latencies after stimulus onset over the right occipital face area (OFA), right posterior superior temporal sulcus (pSTS) and the face area in the right somatosensory cortex (SC). Results show similar early latency impairments at the OFA and pSTS and a later latency impairment at the SC. Interesting the length of the impairment is longer in the higher brain areas (pSTS and SC) then in the OFA.

Interestingly, the duration of the impairment window in the pSTS and somatosensory cortex was almost twice as long as the impairment window in the OFA. This difference in the length of the TMS impairment window is consistent with physiological evidence from non-human primates showing that the response profile of neurons in higher cortical regions is longer than the response in earlier cortical regions (Kovacs et al., 1995). Human fMRI evidence also shows that cortical regions in and around the rpSTS show a longer temporal response window to movie clips than regions in early visual cortex (Hasson et al., 2008). Future chronometric TMS studies can further address this question to investigate whether TMS can be used to measure the duration of cognitive functioning in different brain areas.

While chronometric TMS results give precise timing information for the causal engagement of specific face-selective areas they also raise questions with respect to other experimental methods with precise temporal resolution. EEG and magnetoencephalography (MEG) studies of face perception report face-selective activity peaking at 100 ms and 170 ms (Bentin et al., 1996; Liu et al., 2002; Itier et al., 2006). These latencies are later than the TMS impairment windows observed at the OFA and pSTS (Pitcher et al., 2007; Pitcher et al., 2008; Pitcher, 2014) and only correspond to the later stages of the window at the somatosensory cortex. One possible explanation for this discrepancy is the fact that TMS studies are targeting a single face area while EEG and MEG studies are presumably recording the summation of activity from multiple brain areas. This summation may take longer.

A second possible explanation is the difference between the methods. TMS is disrupting a cognitive process, not recording the activity (from multiple brain areas) that contribute to that process. It is therefore possible that TMS delivered at the peak activity (corresponding with the EEG or MEG peak) is too late to have an effect because the corresponding processing has already occurred. However, TMS delivered while the neuronal activity that supports that cognitive process is building, may be sufficient to interrupt and impair performance on the concurrent behavioral task. There is nonhuman primate evidence to support this theory. Afraz et al. (2006) used microsimulation to disrupt face-selective cells in the inferotemporal cortex of macaques while they performed a face detection task. Results showed that stimulation delivered 50ms prior to the peak local field potential (LFP) activity (at 150 ms) produced a greater task performance impairment that stimulation delivered concurrently with that peak. This result, together with the human

TMS results, suggests that brain stimulation methods that seek to disrupt task performance should target latencies when the neuronal activity in the stimulated areas is building, not when the activity peaks.

Using TMS to Study Feedforward and Feedback Face Processing

Models of the face processing network propose that face-selective areas that preferentially process different cognitive functions share information related to the function being performed (Bruce and Young, 1986; Haxby et al., 2000). This necessitates the existence of bidirectional connections between face areas to facilitate the processing of incoming sensory information with information from areas performing other cognitive tasks. Chronometric TMS studies can be used to study the functions and timings of these feedforward and feedback processes.

Pitcher et al. (2012) delivered double pulse TMS (pulses separated by 10 ms) over the right OFA at different latencies after stimulus onset ranging from 20 ms up to 150 ms while participants performed face and body discrimination tasks. Results demonstrated that TMS delivered at 40/50 ms impaired the discrimination of both faces and bodies, while TMS delivered at 100/110 ms impaired the discrimination of faces only. This suggests that the OFA contributes to early face recognition (early meaning in the first 100 ms) during two temporally and functionally distinct processing phases. The initial stage is domain general, and may reflect a very rapid feedforward pass of information into the visual system. This is followed by a later category-selective phase during which the face network selectively processes face information. Such processes are consistent with models of the primate visual system proposing that activity in higher cortical areas alters the activity in lower cortical areas via feedback processing mechanisms (Lamme and Roelfsema, 2000). Mattavelli and colleagues provided evidence consistent with this hypothesis in a combined TMS and EEG study of face processing (Mattavelli et al., 2013). TMS delivered over the medial prefrontal cortex 100 ms after participants viewed faces with different facial expressions (happy, fear, and neutral) reduced the face-selective P1 and N1 components recorded from the occipital electrodes.

Combining TMS and EEG offers a powerful experimental method for studying the temporal effects of disruption across the face network during feedforward face processing. Sadeh et al. (2011) delivered double pulse TMS (at 60 and 100 ms) over the right OFA as participants viewed faces and bodies while simultaneously recording EEG. Results showed that TMS delivered over the OFA selectively enhanced the face-selective N1 component for faces, but had no effect on the N1 component for bodies. This result suggests that disruption of the OFA, the earliest stage of the face processing network, had a subsequent impact on face-selective areas at higher stages of the face network that are thought to contribute to the N1 component such as the FFA and the pSTS (Henson et al., 2003; Horovitz et al., 2004). Mattavelli and colleagues also used a combined TMS and EEG methodology to investigate conscious and unconscious face perception (Mattavelli et al., 2019). They again demonstrated that TMS delivered 60ms after stimulus onset had an effect on the N1 component and extended this result by demonstrating face specific effects in the EEG signal lasting up to 300ms after faces were detected.

TMS Studies of Face Perception in the OFA

TMS has also been used to study other aspects of face processing besides identity and expression recognition. The OFA is located in the lateral occipital cortex making it earliest region in the ventral visual processing stream that responds more to faces than to other stimulus categories. Network models propose that the OFA represents the more primitive, local, and stimulus-driven components (e.g., the eyes and the mouth) while the FFA represents invariant and global features that contribute to identity discrimination (Haxby et al., 2000; Taylor et al., 2010). This functional dissociation between the OFA and FFA was demonstrated in an fMRI adaptation study that compared the responses to physical changes in a face that changed the identity percept (Rotshtein et al., 2005). While the FFA responded only when the changes contributed to an identity change the OFA responded to physical changes in a face regardless of whether those changes contributed to participants perceiving a different facial identity.

Several TMS studies have demonstrated how the OFA is causally engaged in processing low level facial features. For example, Kietzmann et al. (2015) demonstrated that TMS delivered over the right OFA impaired judgments of viewpoint angle when faces were presented in the contralateral (but not the ipsilateral) visual field. The same study also demonstrated that TMS delivered over the right OFA impaired judgements of facial viewpoint symmetry in both visual fields. This causal role of the right OFA in facial symmetry detection was also demonstrated in a TMS study by Bona et al. (2015).

Mooney faces are black and white images that can be recognized as faces despite lacking any distinguishable local facial features. The fact that participants perceive Mooney faces as faces is taken as evidence that faces are processed using holistic mechanisms that integrate all the component parts of a face. Bona et al. (2016) demonstrated that TMS delivered over the right OFA impaired the discrimination of Mooney faces and Mooney objects. The authors interpret these results as demonstrating that the OFA plays a causal role in holistic recognition that is not specific to faces. This may be the case, but is also important to note that TMS studies that disrupt face recognition in the OFA typically use face stimuli in which facial features (e.g., the eyes and the mouth) have been altered (Pitcher et al., 2007; Dilks et al., 2013) and these local features are not apparent in Mooney faces. The face inversion effect, in which faces are more difficult to recognize when they are inverted, is also taken as evidence for the holistic processing of faces (Yin, 1970). TMS delivered over the right OFA has also been shown to disrupt recognition of face parts even when faces are inverted (Pitcher et al. 2011b) again demonstrating that the OFA is engaged in processing face parts.

Conclusion

The aim of this chapter has been to report the different brain areas and exciting approaches that have been used in TMS studies of face processing. A chapter published 9 years ago in the *Oxford Handbook of Face Perception* reported on the five TMS papers that had been published on face processing up to that date (Pitcher et al. 2011d). The current chapter covers 40 papers, demonstrating the growth of this area. Moreover, the past 10 years have also seen studies that have combined TMS with EEG (Sadeh et al. 2011; Mattavelli et al. 2019) and TMS with fMRI (Pitcher 2014; Pitcher et al. 2017; Handwerker et al. 2020) to study disruption across the extended face network. It is hoped that future TMS studies will continue to produce exciting and innovative insights into face processing in the coming years.

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