How does face processing occur to facilitate face perception?

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Abstract

Face perception is a critical and valued ability that humans have that allows us to be able to understand faces. Studies have shown that the uniqueness of face processing is due to the special nature of faces, a bias formed in infancy, which causes them to be processed dissimilarly to objects. Three main processes are responsible for this difference: first-order relational, second-order relational, and holistic processing. Specialised regions in the human brain have been studied to attempt to understand where and how the different processes occur, called the Fusiform Face Area, the Occipital Face Area, and the posterior Superior Temporal Sulcus Face Area. This has been made difficult as gender and hemisphere role specialisation has been found, possibly affecting processing across these regions. Models by Bruce and Young, and Haxby, are useful in visualising the process to aid in understanding the distinct pathways and the interlinked processes of face perception. The investigation should inform the readers on the basic processes behind face perception and provide an understanding of the need for further research in the field.

Introduction

We rely on a complex and specialised process to extract information about human faces, generalised as 'face perception'. It is how we understand and have an awareness of the human face; recognising and extracting its information like identity, gaze, race, and expression. It provides us with many advantages, such as the ability to detect the presence of faces in an environment and the ability to differentiate between variances in common configurations of faces so that we can identify individuals and comprehend changes in appearance. It facilitates our understanding and interaction with other members of our species, making it imperative for social behaviour in humans.

Understanding the processes behind face perception is of significant interest as it allows us to consider solutions for other related problems. In medicine for example, those with prosopagnosia and often those with schizophrenia, have impairments in being able to perceive faces, but by understanding exactly how those impairments occur within the brain could lead to treatments to reroute the brain processing system; leading to a better quality of life. A technological example is its use in creating and improving artificial systems that use computer vision. By understanding and reflecting processes and systems found the in the brain, it could inspire a biological-based computational system that can mirror brain processes to create an efficient and accurate face recognition systems.

The rationale for the choice of face processing is due to its ever-changing nature. The topic is constantly evolving as it is one that continues to be researched, with each new study seemingly finding new data that both advances our understanding and rejects old theories, keeping the scientific community on their toes. The vastness and complexity of the different brain systems means that new areas of research are constantly being found, making face perception an exciting issue to study. By investigating how we actually 'do' face perception and the processes behind it, means that when new research is published, a good understanding is had to enable complex ideas to be comprehended.

The aim of the investigation intends to address how face perception occurs through varying processes with the following question; 'How does face processing occur to facilitate face perception?' In attempting to answer, the investigation will outline main issues discussed in research such as why faces are processed differently to objects, the areas of the brain that are responsible, and the popular models used in demonstrating the sequencing of the processes. The investigation does not intend to cover any material outside the scope of the main issues mentioned, such as the use of memory, attention, or familiarity in face perception. Although there are further topics important in fully understanding how we process faces, they are not fundamental for basic understanding.

In the Discussion, the text firstly addresses how whether faces are special – explaining the contradicting arguments and the specific processes evidencing them, as well as discussing infant abilities for face processing. Secondly, face-selective regions in the brain are described and their roles detailed, with information on asymmetry in the two hemispheres during processing and speculative reasons for this. Thirdly, two cognitive and neurological models are explained and assessed against new research. The investigation then moves onto Outstanding Problems and

Future Directions, describing unanswered face perception and processing questions to then lead onto topic suggestions for research to focus on. The investigation ends with Conclusions segment, drawing together the topics addressed and summarising why face processing should continue to be researched.

Discussion
Are faces and their processing special?
Conflicting Theories
There are currently conflicting propositions on whether faces are special stimuli, however the most supported proposal is that faces *are* special (McKone & Robbins, 2011). In the Domain-Specificity hypothesis it is suggested that there is specificity to faces; requiring unique processing systems and mechanisms for determining information such as identity, which are not used for objects (McKone & Robbins, 2011). It proposes that faces are processed in the dedicated Fusiform Face Area in a category specific way. There is much evidence pointing towards this, for example the evolutionary studies using research of twins to show that face recognition and neural mechanisms can be inherited unlike with objects (Polk, et al., 2007). Evidence from a study by Riddoch et al. (2008) with a subject with prosopagnosia, a condition where they are unable to recognise people, showed that although the subject had poor face recognition they were still able to perform object recognition and learning.

The other proposal is that faces are *not* special. There are suggestions such as the Within-Class Discrimination Hypothesis, which predicts that objects engage the face-selective mechanisms and undergo the same processing that is used with faces. Other evidence that is believed to point towards faces not being special is the Expertise Hypothesis. It states that expertise is used in face-selective mechanisms, where experts with strong experience in specific objects should show the same types of processing for both faces and those objects (Rivolta, 2014). The hypothesis proposes the Fusiform Face Area is used in processing objects of expertise, and is not a dedicated module for face processing. Expertise is thought to make face stimuli seem special due to the amount of experience humans have in discriminating between faces, and that this could be applied to objects if they had the same amount of experience (McKone & Kanwisher, 2005).

There have recently been many studies that have popularised the proposal that faces are special over the proposal that they are not. Many studies comparing the response in the brain for both objects and faces have been able to evidence faces as special. Face-selective regions like the Fusiform Face Area and the Occipital Face Area respond more strongly to faces than objects. A stronger reaction for faces is also seen in ERP, where the N170 response has greater amplitude for faces than objects, disproving the Within-Class Discrimination Hypothesis (McKone & Robbins, 2011). A study that is thought to have discredited the Expertise Hypothesis itself is by Robbins and McKone (2007), where they used subjects that were experts in various dog breeds. Through inversion of dog and human faces, and other experiments such as the composite paradigm, the study demonstrated that although the subjects had great experience for dog breeds, they were still highly more responsive to facial stimuli, showing no face-specific processing for dogs (Robbins & McKone, 2007).

Face Perception in Infants
One of the key pieces of evidence that faces are special stimuli is the ability for infants to perform basic face processing from 2 days old after being born (Johnson, et al., 1991). It is believed that their behaviour from such a young age, such as the preference seen for face stimuli over other stimuli, and the imitation of the face movements of others, is thought to suggest that there is a mechanism that influences the infant's attention; ensuring that there is a steady supply of facial input (Johnson, 2011). This inclination of infants for faces predicts that the human face knowledge and processing system is likely to be innate. Research with 3 month old infants has shown that they prefer viewing faces that were intact than if they were jumbled, which proves against attentional bias later in life when the processing system has developed further (Turati, et al., 2002). Because of the later preference, it is believed that the face processing systems are continually developed, with estimates that it matures around 5-6 years to match the abilities of adults (Crookes & McKone, 2009).

The mechanism for this attention to faces in infants was proposed in the 'two-process' model of face perception by Johnson et al. (1991). The two processes are Conspec and Conlern. Conspec is a face-specific subcortical mechanism that was responsible for the tendency for infants to orient towards faces; used in detection and prioritisation of faces (Johnson, 2011). Conlern is a domain-relevant cortical circuit that provides an organised system responsible for other aspects of face processing and heavily relies on face experience (Simion & Giorgio, 2015). It is suggested that the Conspec mechanism influences the infant's attention towards face input to ensure that the cortical circuitry is progressively specialised for face stimuli. Conspec is affectively a "tutor" to Conlern by providing it with the knowledge and experience it needs (Johnson, et al., 2015).

There has been much research into the extent of which an infant can perceive faces and their facial expressions. A study by Hoftsten et al. (2014) used images of facial expressions that likely corresponded to the properties of an infant's visual abilities and showed them to adults at varying distances. They proposed that as adults could determine the facial expressions with the visual effects, infants would likely be able to do the same when viewing faces. Their results showed that infants could be thought to have capabilities to reasonably discriminate facial expressions; however there would be a large constraint due to their underdeveloped visual system and its ability for distance. The results suggested that there is likely to be capability for face perception; otherwise an infant's ability for discriminating face expressions should be more inadequate than the results of the study presented (Hofsten, et al., 2014).

As infants start to progress into adults, it is predicted that there are developments in their brain to provide more advanced face processing skills. An example of a study that shows the development of an infant's face processing ability is one by Pascalis et al. (2005). It demonstrated when an infant is exposed to non-human faces of macaque monkeys between ages of 6 months and 9 months, the infants had the ability to discriminate between the different macaque faces; but showed that the ability stops at 9 months of age. This is thought to show the increasing specialisation and improvement of face processing towards human faces during the early stage of an infant's life (Pascalis, et al., 2005). Further to the Domain-Specificity hypothesis, research has shown that the regions of the Fusiform Face Area and the associated cortical regions mature and become more specialised to provide greater face-

specific cognitive function (Johnson, 2011). However further research is needed to confirm any localised function differences between the face-selective regions adult and infant brain, due to the size of the regions in infants and the limits in technology (Pascalis, et al., 2011).

Types of processing of Faces
As the face is most likely to be special stimuli, it is suggested the cognitive processing of correctly orientated faces use a dedicated face-specific neural architecture, such as holistic mechanisms. It is thought that these mechanisms are engaged by faces regardless of the processing type (Yovel & Kanwisher, 2004). Researchers Maurer et al. (2002) suggested that there were three types of processing for faces; first-order relational processing for the detection of the main features of the face, second-order relational processing for the space distances between the features, and holistic processing for the processing and association of facial features (Bate, 2013). These different processes are thought to be separate, but may depend on each other in a specific order (Maurer, et al., 2002).

First-order relational processing is when the basic facial configuration is processed, such as the position of the mouth below the nose or the eyes above the nose. As this generic facial arrangement are found in the majority of the humans, additional processing is needed to analyse the variations of the features, such as eye size or nose shape, to help towards determining the identity of the face. This further processing, and the spatial relations between the face features, is performed in the second-order relational processing. Both these processing types, providing information on the individual features and their configuration, are required for face recognition as they help to discriminate between identities (Zhaoac & Bentina, 2011).

The Holistic mechanism is a significantly studied part of face perception; it is the processing of features and configuration of a face into a perceived whole rather than as individual, independently processed facial features, also referred to as 'configural processing'. Yin (1969) was able to find that when unfamiliar objects and faces were inverted, the test subjects were able to learn and remember faces better than they could objects; named the face-inversion effect (Rivolta, 2014). It demonstrated that the brain identifies and extracts relationships between facial features in the form of holistic processing, but that it can only be used for upright facial processing, with an increasing amount of errors in subjects for identifying face manipulations with the greater rotation of the stimuli (Schwaninger & Mast, 2005).

Further experiments with manipulating facial features, such as those done by Tanaka and Farah (1993), were able demonstrate that the identification of features is more accurate when features are shown in a face rather than as a separate isolated image of the feature, called the part-whole effect, but that this effect is significantly reduced with inverted faces and objects (Taubert, et al., 2011). This evidenced holistic processing as the method used with correctly orientated faces, thought to be due to the easier recognition of facial features when upright. Moreover it was able show a different processing method called featural processing, where all the different features are put together to form a recognised object, was likely used with objects and inverted faces instead of holistic processing (Rivolta, 2014). Holistic processing allows for the whole face structure and spatial information to be integrated together

which is thought to provide more information than could be gathered from featural processing (Bate, 2013).

Face Selective Regions that Perform Face Processing
Associated Roles
In a study by Gross (1969) using macaque monkeys and single unit recordings, they found that when they were looking only at faces there were groups of neurons within the temporal cortex firing that did not when they were looking at other objects, such as food or tools (Rivolta, 2014). The neurons responded to different areas of faces; such as facial features, side profiles, or recognised faces. Since this important study into face perception, research has now found important areas in the human brain that play a role for facial perception, with neighbouring cortices that also respond to facial stimuli. They are located in both hemispheres of the brain, however right-hemisphere dominance with greater performance and size of the areas are seen in comparison to the left-hemisphere (Levine et al. 1988; Bukowski et al. 2013)

A deeply studied region is Fusiform Face Area (FFA) in the inferior temporal lobe. Kanwisher (1997) used fMRI to demonstrate that when people were shown faces and other stimuli, the region on the temporal lobe showed a strong result for faces than it did for objects. It was thought to be involved in the representation of invariant aspects of the face (Haxby, et al., 2000), however newer studies reported sensitivity of the region to facial expressions. In a study by Ganel et al. (2005) using fMRI, they found the FFA had a high response to facial expressions, and in other studies that the FFA was activated more for intense emotion than for neutral faces (Winston, et al., 2003) Current research shows that the FFA responds similarly to dynamic and to static faces, likely showing that it does not gather motion information from dynamic faces but rather the form information of faces such as identity (Furl, et al., 2015). Parvizi et al. (2012) in an ECoG and fMRI study determined that there are two regions of the FFA, and when electrical charges were administered to these areas, the subject of the study stated of there was a distortion and 'warping' to facial features, rendering the person's identity unrecognisable for the duration. When repeated with objects there were only slight distortions (Parvizi, et al., 2012).

The Occipital Face Area (OFA) in the lateral inferior occipital gyri is thought to have a functional role in early visual perception. It is able to recognise and represent the main facial features of the eyes, nose, and mouth, but not necessarily the space between them; however this is still being debated through conflicting results (Pitcher et al., 2011; Rotshtein et al. 2007). Recent fMRI and TMS studies suggest that the OFA outputs to other regions and is used in representing facial features in later processing in higher cortical regions that processes more complex facial features (Pitcher, et al., 2011). Like the FFA, it has similar responses to both dynamic and to static face stimuli, and shows sensitivity to changes in the facial form. This may show it is used in extracting form information of faces, and hence is thought to contribute to identity discrimination (Furl, et al., 2015). This is further backed up by a study where TMS was used to disrupt the OFA, which found that the subjects were still able to categorise between normal facial stimuli and face stimuli that were jumbled, but unable to distinguish between face identities and had no effect with object stimuli (Solomon-Harris, et al., 2013).

Another important region is the posterior superior temporal sulcus face area (pSTS-FA). Similar to the FFA, research has shown that the region becomes active when viewing facial expressions; with stronger response to emotional faces than with neutral faces (Engell and Haxby 2007). However it is suggested that the roles of the FFA and the pSTS-FA in facial expressions differ through the types of information the extract, where the pSTS-FA is more sensitive to faces that conveyed valence (positive or negative emotion) information, but the FFA was indifferent. Research has shown that the pSTS-FA responded much more intensely to dynamic stimuli of moving faces than to static, unlike the FFA that showed similar results for both stimuli (Bernsteinan & Yovel, 2015).This shows that the pSTS-FA may extract additional material from the motion of the dynamic stimuli, such as the recognition of actions performed (Gilaie-Dotan, et al., 2015). The region also extracts changeable information from faces, such as emotion and gaze (Kanwisher & Yovel, 2006).

In an fMRI study by Liu, Harris and Kanwisher (2009), they showed that the FFA, pSTS-FA, and OFA were all individually significant in facial perception. In one part of the study, they measured the response of the regions by providing stimuli of real face features of the eyes, nose, and mouth, and compared the response to stimuli of unnatural black oval shapes in the same locations of the face features. They found that all three regions, the OFA, FFA, and the pSTS-FA, showed sensitivity to the real facial features. In the other part of the study, they provided stimuli of the human spatial organisation of the facial features, and compared the response to the unnatural locations of facial features. The results from the fMRI showed the FFA was also sensitive to the real spatial configuration, but that the OFA and pSTS-FA was not. (Liu, et al., 2010)

Furthermore, due to the results of the FFA being responsive to both facial features and facial organisation, they conducted additional research using the data from their results to determine that the FFA engages in integrating facial features and facial organisations into a unified or 'holistic' representation, rather than having distinct neural populations for processing the two stimuli cases (Liu, et al., 2009). The results were consistent with the idea that the position of the regions has an effect on the stages of facial processing; the OFA begins earlier in the process due to its posterior position to the FFA (Liu, et al., 2002). Their study was able to provide findings that could be used in future research on the differences and separation of roles that the three regions play and their connection between each other.

Recent studies have found further face-selective areas, such as in the anterior temporal sulcus (aSTS-FA). Research using fMRI (Watson, et al., 2014), demonstrated activation of the region by both faces and voices through clips of different stimuli, such as voices-alone or faces with sounds. Future study is required to pinpoint the exact role of this region, but it points towards carrying a "multimodal representation of people" (Duchaine & Yovel, 2015). Another face selective area is found in the anterior temporal lobe (fATL), and is thought to be used in identity processing and representation (Anzellotti & Caramazza, 2014) This was deduced from an fMRI study by Yang (2014) that found that there were stronger responses to two images of different celebrities than there were for two different images of the same person with varying features. The face selective area of the inferior frontal gyrus (IFG-FA) was found to have stronger responses to dynamic faces than static

faces (Fox et al., 2009, Pitcher et al., 2011). It has been suggested to have a role in the processing of eye-gaze movements and identity representation (Guntupalli, et al., 2016; Chan and Downing 2011).

Dominance in the Hemispheres
Many studies have proposed a right-hemispheric dominance in face processing, thought to be due to its ability for processing visuospatial and configural information (Rhodes, et al., 1993). However, newer research by Prete et al. (2015) proposed that the dominance may be due to the commonness of right-handed humans or attributed to social interactions (Prete, et al., 2015). Conflicting research has found the right-hemisphere dominance may not always be the case. Kanwisher et al. (1997) found evidence that the FFA activation in their subjects was varied, half of the subjects had bilateral activation and the other half had only right hemisphere activation. A study using repetition of face stimuli has shown left hemisphere dominance with regards to face identification; suggesting that this was due to the processing of matching of faces with the correlated identity information (Pourtois, et al., 2005).

In a study by Proverbio et al. (2006), they investigated the proposed right-hemisphere dominance for gender variances. Using 40 right-handed subjects, evenly gendered, they measured the responses to different emotional faces. They concluded that for face processing in perception females showed bilateral activation of the regions, with a slight tendency for the left hemisphere rather than any hemispherical dominance, whereas the males tended to show a dominant right-hemisphere and hence greater asymmetry than seen in the females (Proverbio, et al., 2006). The left hemisphere tendency in females over the asymmetry seen in men could be due to many reasons, such as females using more local information for encoding identity or that the left hemisphere is more specialised for face encoding (ESGM, 2013). The results might go towards explaining the varying results of research on hemispherical dominance, as their results were able to evidence that there was likely a difference in the processing for each gender.

Some researchers believe that both hemispheres are utilised and specialised for different purposes within face perception. They suggest that the right-hemisphere is attributed to holistic systems that integrate features of the face, and that the left-hemisphere is specialised in analytical processing, such as feature processing. A study that was able to show these specialised roles was one by Bourne et al. (2009). By showing the subjects normal faces, blurred faces, and displaced features at different areas of the screen, but centring their vision at the centre of the screen, they were able to present them to the two different visual fields. Their results showed differences in priming effects of the manipulated and un-manipulated faces for each visual field, and the data was able to evidence that their right hemisphere was used for configural information and the left hemisphere for featural (Bourne, et al., 2009).

Models for understanding Face Processing
Cognitive Model
A dominant model for cognitive face processing was proposed by Bruce and Young (1986). It suggests that each stage of the process occurs segregated from each other, occurring through successive processes that follow the hierarchy. This means that the stages have to follow a set order, so earlier stages always have to be completed before later stages can take place (Bate, 2013). It proposes that the wider

cognitive system may be involved in mediating various stages like facial speech analysis and for facial recognition. For example, face recognition is thought to use various factors gathered from the model to decide whether a face is completely recognised or whether the face resembles someone (Bruce & Young, 1986). The separate stages were evident in a study by Lui et al. (2002) using MEG; they were able to determine there was a M100 MEG response after face stimuli was seen, with a larger amplitude for facial features; demonstrating it was only used in face categorisation. A M170 amplitude response was triggered for both categorisation and for identification of faces, although the M170 was more responsive to face configuration. They proposed their results showed there were two separate stages of processing in face perception (Liu, et al., 2002).

One of the most significant processes that occur when a face is seen is structural encoding. This uses both the 'view centred descriptions' and 'expression independent descriptions' stages to form a basic view-independent representation of the face stimuli (Bate, 2013). Although the identity of the person is unknown, the brain is still able to extract information on the basic features of the stimuli so it can be used to further determine characteristics such as age or gender. The 'view centred descriptions' represent the primary facial information, such as light intensity and contrast that affects how the face looks. The 'expression independent descriptions' represent abstract facial features and their configuration on the face, independent of facial expression or appearance (Rakover & Cahlon, 2001). This structural encoding is used for other processes within the model, such as 'face recognition' and 'directed visual processing' making it a crucial part of the model.

One of the sub-processes the model describes is for face recognition. The structural encoding stimulates the Face Recognition Units (FRU) and the representation of the face is compared with stored representations and data on familiar people in the FRU. If there is a match between the representations, the Person Identity Nodes (PIN) linked with the individual are activated to get information on the person and the relevant name information unit is retrieved (Bate, 2013). These sub-processes have been proven to be independent and performed in hierarchical way. Research using subjects with prosopagnosia, as their ability to recognise familiar faces was absent, showed the subjects were still able to interpret and recognise individual facial features (Bodamer, 1947). This provides evidence towards the Bruce and Young segregated process, as Bodamer's research was able to show that damage to one area of the model does not fully impair others (Bate & Bennetts, 2015).

Neurological Model
There are currently two popular models for the organisation of neural systems for facial perception that focus on the system as distributed rather than having a specialised module. The first is the Haxby model that proposes two main neural systems called the Core System and the Extended System. The Core System is made up of visual extrastriate regions such as the OFA, FFA, and pSTS-FA and nearby cortices that perform visual analysis. The Extended System is made up of the other various neural systems working with the Core to extract material about faces (Haxby, et al., 2000). The second model is the O'Toole model that is based on the Haxby model, but extends and modifies it to allow for dynamic face processing. One of the modifications proposed by the O'Toole model is that the pSTS-FA is an

important part of the face perception process, as it processes dynamic identity information extracted from motion of familiar faces (Bernsteinan & Yovel, 2015).

The Core System uses the hypothesis that there are distributed processes using multiple regions in the brain that show large responses to facial stimuli compared to non-face stimuli. The core system is used for analysing the visual appearance of a human face, and utilises the separate and individual roles of the face-specific regions. The model suggests that the OFA performs the early perception of facial features, through processing and visual encoding of the basic details of the face. The FFA is responsible for processing non-changeable or 'invariant' information from the face, such as unique identity and gender. The pSTS is used for processing changeable information from faces, such as the perception of expression, eye gaze, and lip movements (Bate, 2013; Haxby & Gobbin, 2011). In the extrastriate cortex, there are further visual areas that show responses to faces that are not part of the three face-selective areas. For example, research by Grill-Spector et al. (2004) was able to show an area outside the FFA in the ventral temporal cortex correlated with face identification success (Haxby & Gobbin, 2011).

The Extended System interacts with the core system through various neural structures to access person-specific information and to represent emotion (Bate, 2013). The Person Knowledge sub-system is suggested to be used in interaction with the FFA for identity processing and the immediate retrieval of information on familiar people, such as personality and intentions related to that person (Haxby & Gobbin, 2011). The sub-system is made up of the medial prefrontal cortex (MPFC), temporoparietal junction (TPJ), anterior temporal cortex, and the precuneus. The Emotion sub-system is used for emotion representation and state, as well as processing emotional response to familiar individuals. The regions that make up the sub-system are the amygdala, insula, and the striatum (Bate, 2013). The last sub-system is Motor Simulation, which is made up of the inferior parietal and frontal operculum, and the intraparietal sulcus and frontal eye fields. The system is used for processing eye gaze, and extracting the meaning of facial expressions using regions of the human mirror neuron system (hMNS) to provide motor representations for producing face expressions (Montgomery & Haxby, 2008).

The models make many assumptions that have since been disproven by newer research. An example was the assumption that the FFA is insensitive to expressions, which has now been shown that it extracts information both from static and changeable faces, including face expressions (Arsalidou, et al., 2013). Another assumption is that neural connections for face processing were thought to originate from the OFA as the point-of-entry for information (Haxby, et al., 2000). Research using patients with prosopagnosia has showed that there are more likely to be multiple pathways. In studies (Rossion et al. 2003) with a patient with a damaged right OFA and left FFA, the patient still showed responses in the right FFA and right pSTS-FA which evidenced that face-sensitive information was still being networked without the use of the OFA. In research by Gschwind et al. (2012) using DTI for the face-selective regions, they found evidence of connections between the OFA and the FFA, but none from the OFA and FFA to the pSTS-FA. They showed the early visual system had direct pathways to both the FFA and the OFA, but that the OFA had stronger connections (Gschwind, et al., 2012).

A key theory that is thought to amend and create depth for face perception is the Two-Stream hypothesis; where different forms of information come from the visual system using ventral and dorsal streams, but through pathways that can interact together. Both the Haxby and O'Toole model suggest expressions are processed using the dorsal pathway, but do not take into much account of the ventral stream. The ventral stream is linked with the recognition of object and representation of form; extracting form information from faces and hence used for processing dynamic faces (Duchaine & Yovel, 2015). The face selective regions are found in the Two-Streams; in the dorsal stream is pSTS-FA, IFG-FA, aSTS-FA, and the ventral is OFA, FFA, and fATL (Pitcher, et al., 2011). The pathway begins at the OFA and projects to the fusiform gyrus. The dorsal stream pathways start at the OFA to the STS, and is linked with action guidance and the spatial recognition of objects; thought to be used in extraction of information for dynamic faces (Mishkin, et al., 1983).

An overall view of face perception can be realised by using both neurological and cognitive research, such as by integrating the Bruce and Young (1986) model into the Haxby model. One of the ways the Bruce and Young model has been addressed is through the suggestion of there being distinct, separate pathways for identity recognition and face expression. Research using macaques by Hasselmo et al. (1989) is able to provide evidence towards this assumption, where single-unit recordings showed that identity and expression responsive neurons were located in different areas, making it likely that a similar separation was likely in the human face-selective regions also (Haxby & Gobbin, 2011). It was further proved through the differing in roles of the face-selective regions; the FFA is used for extracting form information of faces for determining identity and the pSTS in extracting information on changeable features (Furl, et al., 2015; Engell and Haxby 2007). A key difference between the models is that the Haxby model proposes a broader, more integrative system for processing, rather than the independent stages as suggested in the Bruce and Young model.

Outstanding Problems and Future Directions

How are faces encoded in the brain?
As proposed in the Bruce and Young model (1986) for face perception, there is a process that encodes face information to represent the identity later on; although it does not specify any neurobiological information on how this is done. Research has suggested that neurons in the inferotemporal (IT) cortex transmit information about identity, with much complex processing taking place from the retina to the cortex (Brincat & Connor, 2004). Because of the complexity of the processing system, we are currently unable to decode the representations carried by the IT neurons which would have allowed us to see a presentation of the object represented by the neurons and allow predictions IT neuron responses to different objects and faces.

A radical new study by Chang and Tsao (2017) investigated the neural 'code' of face representations in macaques. They were able to find that each face-selective neuron in the IT cortex represented facial features along specific axes within multidimensional space, called the 'STA' axis. The STA axes can be combined in many different ways allowing us to perceive any face. Using fMRI and monitoring the neurons in certain areas of the IT cortex, they were able to develop an algorithm that could decode the face projection on these axes, so when showing the macaque an

image they could use the readings to recreate the neuron representation (Chang & Tsao, 2017). Further work should take place to mirror this research in human brains to provide greater depth and understanding of how faces are processed in humans, and to provide an approach for recognition in artificial intelligence.

Can we treat prosopagnosia?
Prosopagnosia is a condition that affects the ability of a person to recognise faces. The condition can be *developmental* where it is present from birth or *acquired* from brain damage; and can affect the ability to determine facial expressions, gaze, and other areas of face processing. Recent studies have looked into increasing face recognition skills using the neuropeptide oxytocin, thought to modulate face processing activity, which has shown to increase face processing in healthy patients (Westberg, et al., 2016). A study by Bate et al. (2014) showed that when subjects with developmental prosopagnosia inhaled oxytocin, they temporarily performed better on both face memory and matching identity tests. Their research could be used to develop more permanent affects for those with developmental prosopagnosia, and could be applied to other disorders such as anxiety and depression (Bate & Bennets, 2014).

Conversely, those with acquired prosopagnosia have seen limited improvements from treatment. It was suggested that this could be due to the distinct, highly specific functions of the face-selective areas, where an injury to one area could cause disrupt to the entire processing system as necessary sub-processes by the regions cannot occur (DeGutis, et al., 2014). Wilkinson et al. (2005) used galvanic vestibular stimulation to activate the face-selective regions. Through using electrical stimulation, their acquired prosopagnosia subject was able to match faces more accurately (Wilkinson, et al., 2005). The results however could be due to enhancing attention of the subject, rather than from improved face processing in the regions (DeGutis, et al., 2014). Further direction should be undertaken to investigate more solutions into treating acquired prosopagnosia, with deeper investigation into the electrical stimulation of the various face-selective regions.

Can face processing be recreated using artificial systems?
Basic computer models have been created to attempt to replicate how visual processing occurs within the human brain; however there are currently no algorithms that can match the complexity and performance (Navlakha & Bar-Joseph, 2011). A study by Tsao and Livingstone (2008) looked at how face processing may be recreated using mechanisms found in the brain, and proposed that there should be distinct processes in this artificial system, detection and recognition. The study suggests that detection should take place before recognition to act as a filter between face and non-face stimuli, making the process more efficient and domain-specific as it would be in the human brain (Tsao & Livingstone, 2009).

An efficient algorithm for holistic face recognition is the Viola and Jones (2004) algorithm. It uses a cascading system made up of filters and detectors that gradually became more complex, ensuring that that filtering is only performed on the parts of the image that match what the filter or detector is looking for at that point (Viola & Jones, 2004). A popular algorithm for face recognition is the Eigenface algorithm, created by Turk and Pentland (1991). It is based on the common configuration of facial features, and assesses face identity by how much variance there is from an

average face. An issue with the algorithm is that the faces must be scaled and positioned correctly to their template (Tsao & Livingstone, 2009). Future direction should be focussed on greater understanding of the 'logic' behind face processing within the human brain so that algorithms can become more efficient and new ideas created on what can be reproduced for an artificial system.

Conclusions

Face processing is an important part of perceiving and understanding the human faces; without it we would neither be able to identify nor interpret the sensory information provided by our eyes when seeing a face. The complexity of face processing is slowly being unravelled by researchers to discover the processes behind it; what they are, how they work, areas of the brain responsible, and whether they follow a set process or model. Many studies have looked at the differences between faces and objects, comparing and contrasting the data on the processes undertaken by the brain to perceive both stimuli. Much of the evidence points towards the uniqueness of the processing of faces, which have led to the conclusion that unlike objects, faces are special stimuli. The specialisation of the face stimuli is thought to happen during infancy, where unique processes of Conspec and Conlern ensure that neural circuits in the brain becomes progressively biased towards faces.

After maturity, faces undergo three distinct types of processes; first-order relational, second-order relational, and holistic processing. They are carried out by the different roles of the Fusiform Face Area, the Occipital Face, and the posterior Superior Temporal Sulcus face area; although new smaller areas are being found that also play a role in face perception. It was generally thought that the three regions showed right-hemisphere dominance, but it has been recently shown that gender and hemisphere role specialisation affect how faces are processed across the brain. How faces are processed in the brain can be explained with the Bruce and Young cognitive model and the Haxby neurological model, and their integration with the Two-stream hypothesis for visual information. They predict that each stage of face perception is separate and hierarchical, and that there may be distinct neural systems for the different processes required that can interact with each other.

The work was limited by the scope of the investigation, with many more topics within face perception that could be discussed. Had there been more opportunity to write more, the investigation would have covered topics such as recognising race, familiar and unfamiliar faces, and further analysis into facial expression and gaze. This would have allowed the reader to follow a broader overview of the topic. It would have also gone into more detail about each of the topics mentioned in the text, identifying more studies and experiments to better explain each of the ideas covered in the investigation to ensure the reader can have a deeper understanding.

Future research in the face processing field should go towards better understanding the roles of the face-selective regions, in particular focusing on the role of the Occipital Face Area. The OFA has conflicting research on its role within face processing, with some researchers believing it has an early functional role as the point of entry, along with being used in recognition and presentation of face features to other brain regions later on in processing. This is conflicted by research using a subject with prosopagnosia from a damaged OFA, which has shown there is still information being circulated to the other face selective regions determining that it is

unlikely it is the only way for information to enter the processing system. This is important to determine as it would require the Haxby model to be updated, as it specifies the OFA as entry for information, and would overturn the common opinion on how the process starts and how the regions network with each other.

Research into how face processing occurs in both adulthood and infancy allows us to investigate various questions: how our neural architecture develops over time and why we see a difference in perception between objects and faces. It will determine why we have the ability to differentiate between a large number of people, but not many objects, and why we see differences in reactions of the brain regions to non-face stimuli. Without the research, we would not know why we can recognise friends and relatives from those we do not know. It is crucial research to develop our understanding to lead onto advances such as enhancing treatment for those with prosopagnosia, increasing our own recognition skills for jobs in security, and the development of artificial systems. The research into the different questions and aspects of face perception is important for our existence, without it, we would not be able to comprehend the basis of human social interaction.

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