c) Individuals may differ in their ability to recognize faces and to interpret emotions.

What can studies of typical and atypical development tell us about the origins of

these differences?

MSc Social Cognition: Research & Applications

PSYC0164 – Social Neuroscience

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Term 2

04/04/2022

Candidate Number: RDVT9

Word Count: 2993

Humans across cultures typically display the same configural features of faces and categorise emotions in similar ways (Ekman et al., 1969). Yet the accuracy of recognition and intensity of our responses to the same facial or emotional stimuli can vary substantially across individuals. People with developmental disorders such as autism, prosopagnosia and conduct disorder generally encounter deficits in recognising faces or emotions (Berenbaum & Prince, 1994; Duchaine et al., 2003; Fairchild et al., 2014; Uljarevic & Hamilton, 2013; Weigelt et al., 2012). Individuals without neurobiological impairments can also vary greatly in their abilities to recognise faces and emotions (Duchaine & Nakayama, 2006; Holder & Kirkpatrick, 1991). While individual variability has constantly been observed, there is still considerable debate regarding whether recognition abilities are genetically programmed (i.e., the role of nature) or acquired through experience and learning (i.e., the role of nurture).

Therefore, this essay will examine the processing of faces and emotions in both typical and atypical populations in order to identify potential sources of ability differences related to face recognition and emotion recognition. Rather than focusing on *what* ability differences are, we will be more concerned with *why* they exist. Firstly, prominent models for face and emotion processing will be introduced. The second and third sections will investigate genetic and environmental contributions to face recognition and emotion recognition respectively.

Processing Mechanisms

Before discussing the origins of ability differences, it is important to first present the basic mechanisms of face and emotion processing. In the field of face perception (including both

face and facial emotion recognition), Bruce and Young's (1986) cognitive model and Haxby et al.'s (2000) neuro-anatomical model provide arguably the most influential theoretical frameworks. Bruce and Young (1986) postulated that face processing involves distinct information dimensions. According to their model, a face firstly undergoes a structural encoding process through visual detection. Then, if the face seen can be matched to a face previously-stored in face recognition units in memory, it is regarded as a familiar face, and identity-specific information is subsequently retrieved. Unfamiliar faces are processed via a separate pathway labelled as "directed visual processing" that allows us to remember them. Aside from face recognition, other systems responsible for the analyses of facial speech (i.e., lip and tongue movements) and facial expressions apply to both familiar and unfamiliar faces.

Haxby et al. (2000) identify face recognition units in Bruce and Young's (1986) model as the core system that deals with *invariant* aspects of faces, whereas *changeable* aspects of faces including expression, lip movement and eye gaze are processed in an extended system. Within the core system, the fusiform face area is recruited in recognition of familiar faces and discrimination of facial identities. Emotion processing, on the other hand, belongs to the extended system, where different brain areas are involved for different emotions (e.g., amygdala for fear conditioning) (Calder & Young, 2005). Overall, Haxby et al.'s (2000) model is compatible with Bruce and Young's (1986) model, the only difference being the way in which expressions are coded: either by a system specific to expressions (Bruce & Young, 1986), or by a system that codes expression alongside other changeable configural features (Haxby et al., 2000). Divergence between the two models lays the groundwork for our discussions regarding

origins of emotion recognition ability.

Despite extensive research into facial emotion recognition, understanding of emotion recognition from other visual stimuli, such as bodily or auditory cues, remains rudimentary. Nonetheless, the case of a patient with bilateral amygdala lesions who demonstrated comparable deficits in identifying vocal and facial emotional expressions suggests that emotion recognition mechanisms may be shared across sensory modalities (Scott et al., 1997). For the purposes of this essay, facial expression recognition is viewed as representative of emotion recognition.

Both models regarding face processing mentioned above make a distinction between recognising facial identity and facial expressions, which can be supported and extended by a plethora of clinical observations and behavioural studies. Prosopagnostic individuals with abnormalities in the fusiform gyrus either congenitally (developmental prosopagnosia, DP) or due to brain injury (acquired prosopagnosia, AP) may have severe difficulties recognising face identity, but still have normal performance in recognising facial expressions (Duchaine et al., 2003; Humphreys et al., 2007). In contrast, amygdala lesions oftentimes impair recognition of facial expressions, particularly fear, while preserving recognition of face identity (Adolphs et al., 1994, 1995).

In other words, face recognition and emotion recognition mechanisms overlap but encompass distinct aspects respectively. In this essay, face recognition is defined as the ability to discriminate face identity, whereas emotion recognition is concerned with the ability to label facial expressions.

Face processing

a.   Role of nature

It has long been documented that human neonates preferentially track face-like stimuli compared to scrambled faces and blank stimuli (Goren et al., 1975; Johnson et al., 1991), indicating experience-independent abilities to perceive faces. However, rigorous attempts to consider face recognition ability as an inborn predisposition have mainly been made in the last two decades. A genetic component to face processing would suggest that ability differences in face recognition are heritable.

The potential heritability of face recognition ability was first proposed given the unusual family clustering of DP. Pedigree research found that both Caucasian (Dobel et al., 2007; Kennerknecht et al., 2006) and Chinese (Kennerknecht et al., 2008) DP subjects without other neurological dysfunctions (e.g., autism) had at least one to three first-degree family members with the same face-recognition deficit. The high familial occurrence of DP seems to indicate a high likelihood of genetic causes to impaired face processing. However, as these studies mainly relied on self-reported questionnaires and famous faces tests for the diagnosis of DP, alternative explanations besides genetics were not excluded. Specifically, self-reported measures may not be reliable since people only have moderate insights into their face recognition abilities (Bobak et al., 2019; Palermo et al., 2017). In fact, many self-identified prosopagnosics do not show impaired face recognition in further testing (Duchaine et al., 2007). Moreover, poor performance in recognising famous faces may simply reflect a familial environment that lacks exposure to celebrities.

To tackle the reliability issue and establish an explicit relationship between genes and face recognition abilities, researchers have conducted twin studies. Theoretically, given that monozygotic (MZ) twins and dizygotic (DZ) twins normally share the same family environment but different proportion of their genes (100% versus 50%), we can infer that genes account for individual differences if the correlation scores are significantly greater between MZ than DZ twins. Using the twin design and the highly reliable Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006), Wilmer et al. (2010) reported that the MZ correlation score (0.70) was more than twice as large as the DZ correlation (0.29) in healthy Australian adult twin samples, suggesting a strong genetic basis of family resemblance for face recognition abilities. Concurrently, Zhu et al. (2010) assessed face recognition ability among typical Chinese juvenile twins (age 7–19) and found significantly stronger correlations in face recognition between MZ twins than DZ twins. Taken together, the two studies consistently demonstrated the heritability of face recognition abilities in both WEIRD (Western, educated, industrialised, rich, democratic) and non-WEIRD populations, regardless of age. However, the credibility of twin studies has been challenged recently. Notably, researchers claim that MZ twins do not necessarily share identical genes, and that MZ twins are reared in a much more similar environment than DZ twins (Charney, 2012). Consequently, the true effect sizes in twin studies may be smaller than demonstrated, and therefore, genetic differences alone may not fully elucidate ability variability in face recognition.

b.   Role of nurture

It seems that genetic factors may explain much of familial resemblance in face

recognition ability. There are, however, at least two rationales why environmental factors also play a role in ability development: namely, wide ability variations across typically developing individuals, and perceptual narrowing during postnatal development.

First, from an evolutionary perspective, given the importance of a strong face recognition ability for social interactions, it is expected that genes regulating the enhanced ability would be strongly preferred in natural selection, thus reducing genetic variations in this respect (Plomin et al., 2013, as cited in Wilmer, 2017). However, even among neurologically intact individuals, the ability of face recognition can vary greatly. For the same CFMT tasks, the scores of typical subjects ranged widely from 43 to 72 out of 72 (Duchaine & Nakayama, 2006). In sharp contrast to DPs, who sit on the lower end of the ability spectrum in face recognition, there are also adolescent (Bennetts et al., 2017) and adult (Russell et al., 2009) "super-recognisers" who consistently reach full or nearly full marks on CFMT tasks and are able to recognise famous faces even based on childhood images.

Second, if face recognition ability is solely derived from gene sequences, we would expect face recognition performance to remain about the same or even improve with age as cognitive systems mature (Susilo et al., 2013). A strong counter-example lies in the development of own-race bias. While adults exhibit significantly better performance in memorising and distinguishing faces within their own racial groups (Bothwell et al., 1989; Meissner & Brigham, 2001), both Caucasian and Chinese 3-month-old infants demonstrated equivalent recognition levels to ingroup and outgroup faces (Kelly et al., 2007, 2009). The ability to discriminate outgroup faces began to disappear at 6-months-old groups; and 9-months-old infants could only

recognise own-race faces. The findings among more than three hundred infants in two cultures consistently suggest that experience of facial input during the first year of life plays a crucial role in shaping face-processing systems and determines the face prototypes we recognise more easily later in life. Perhaps the main limitation of the studies above is their cross-sectional methodology. It is possible that abilities to discriminate outgroup faces may naturally fade over time rather than as a result of exposure to homogeneous environments.

Fortunately, prior longitudinal research in cross-species contexts could parallelly validate the role of early experience in face recognition. Six-month-olds could discriminate both human and monkey faces (Pascalis et al., 2002), but 9-month-olds and adults could only discriminate between human faces. Nonetheless, if exposed to monkey faces during a 3-month training period, 6-month-olds retained the ability to distinguish monkey faces when they reached 9 months old (Pascalis et al., 2005), with the effect being stronger when monkey faces were labelled individually rather than categorically or not labelled (Scott & Monesson, 2009). In contrast, experiments with monkeys revealed that the ability to distinguish faces of the non-exposed species could be permanently lost after one-month selective exposure to either human or monkey faces following six-to-24-month deprivation of face exposure (Sugita, 2008). Similarly, human patients deprived of visual experience until 2-6 months old demonstrated lasting deficits in configural face processing even after years of recovery (Le Grand et al., 2001). The findings consistently indicate that within-category face recognition is highly sensitive to the experience of face exposure during infancy. Combined with the minimal effect of face recognition training in adulthood (Tree et al., 2017), it seems clear that normal perceptual development during infancy

is critical to ensure unimpaired face recognition abilities later on.

Emotion processing

a. Role of nature

Divergence between theories regarding how emotion-related brain systems develop may justifiably reflect how genetics and environment interact to influence emotion recognition. One possibility corresponds to Bruce and Young's (1986) model, that innate genetic polymorphisms might regulate the reactivity of emotion-specific brain circuits through the modulation of neurotransmitter systems (Nelson & De Haan, 1996). Considering that contributions of genes and environment to emotion recognition ability have been nearly inseparable in empirical research (Pollak et al., 2000), the role of nature and nurture here refers to their respective greater influences in gene-environment interactions.

Associations between genes and amygdala activation may well buttress the genetic account. Studies have shown that amygdala damage would impair the recognition of emotions, especially fear (Adolphs et al., 1994). At the genetic level, one or two copies of the long-allele (LL) 5HTT promoter polymorphism may lead to decreased levels of amygdala activity in its carriers (Hariri et al., 2002; Munafò et al., 2008). Therefore, one would expect individuals with amygdala-related functional polymorphisms to demonstrate atypical recognition of fear; and the deficits should be heritable. Studies have shown that boys with conduct disorder and callous-unemotional traits (CD/CU+), a psychiatric disorder characterised by low empathy and often aggression behaviours, displayed lesser right amygdala activity to fearful faces and greater

difficulties identifying them compared to typically developing controls (Jones et al., 2009); meanwhile, higher levels of CU traits were reported to be associated with the LL genotype (Widom et al., 2020). In a recent study among Caucasian twins, Moore et al., (2019) further demonstrated that genetic influences could fully account for CU traits and deficits in recognition of fear and sadness. Based on studies mentioned above, we may (at least partially) deduce that genetics largely contribute to ability variability in emotion recognition through the modulation of emotion-related brain systems.

However, despite supporting evidence, systematic meta-analyses have demonstrated that extant studies examining associations between genotype and aggression have overall produced highly mixed results that lack replicability and statistical power (Vassos et al., 2014; Widom et al., 2020), which calls into question the validity of our conclusion above. A likely explanation for the inconsistencies is that gene studies generally rely on *a priori* inferences of limited gene sequence(s), whereas complex behaviours like aggression might involve interactions among a myriad of genes. In addition, the relatively small sample sizes in gene studies might have resulted in the general lack of statistical power. Thus, gene studies mentioned earlier would have been more convincing if they had investigated genome-wide associations in larger samples.

A subtler way to detect genetic effects on emotion recognition ability is to compare neurologically typical and atypical populations who share similar experiences. Studies have shown that adverse childhood experience (e.g., maltreatment) is predictive of high CU traits (Dackis et al., 2015) and a tendency to identify neutral faces as displaying anger or sadness (Pollak et al., 2000). The liability is not definite, however, as not all maltreated subjects

demonstrated CD/CU+ or inaccurate emotion recognition. Although participants in these studies may have experienced maltreatment in different familial environments, individual sensitivity and neurological response to adverse events may likely be influenced by biological factors. Indeed, Reif et al. (2007) reported interesting results about how serotonergic genes interact with childhood environment to predict aggressive behaviours in adulthood. Specifically, the authors found that adverse childhood experience only predicted adulthood violence in carriers of short-allele 5HTT genotype. An important strength of this study is that an independent investigator blindly rated each subject's level of adverse childhood environment based on relevant items, thereby making genetic contributions across subjects comparable and reducing the observer bias. Importantly, the inconsistent associations reported between 5HTT genotype and CU traits by Reif et al. (2007) and Widom et al. (2020) may have again prompted genome-wide research.

b.   Role of nurture

An alternative theory explaining the development of emotion recognition ability corresponds to Haxby et al.'s (2000) model, that systems underlying emotion processing are not restricted to expressions, instead, they only become specialised with exposure to species-typical configural features that represent different emotions (Leppänen & Nelson, 2006). In other words, people learn to interpret facial expressions based on their early experience of observing emotions in relevant contexts.

Comparison between the emotion recognition ability between typically developing children and maltreated children may testify to this account. If exposure to facial expressions contributes to emotion recognition ability, then more experience with specific facial expressions

may lead to enhanced sensitivity to them, whereas less experience may result in diminished sensitivity. Research has shown that, compared to typically developing controls, neglected children had marked difficulties in matching facial expressions to pertinent emotional situations and in distinguishing discrete emotions (Pollak et al., 2000). In contrast, although physically abused children had difficulties discriminating between sadness and disgust, they performed equally well at identifying anger compared to non-maltreated controls (Pollak et al., 2000). It is highly likely that impaired emotion recognition ability in maltreated children results from adverse experiences: neglected children generally have less exposure to the full range of facial expressions, whereas abused children might encounter angry parents frequently in familial environments. Furthermore, research on adults who had early abuse experience found consistent attentional bias for anger, indicating early abuse may facilitate cortical specialisation for selective emotions and continue to affect individuals' ability to recognise emotions later in life (Gibb et al., 2009).

A recent large-scale study across twelve countries offers compelling evidence of the socialisation of emotion recognition (Quesque et al., 2020). In particular, females consistently performed better at labelling facial emotions compared to males. The cross-cultural experimental design also allowed the authors to rule out the possibility that women are biologically more sensitive to emotions than men, since the magnitude of gender differences varies widely across countries. A plausible explanation would be that, in most cultures, women are expected to care for other people's feelings, and mothers are usually the ones who tend to emotional needs of the whole family. Even as early as preschool age, observing and imitating parents' behaviours

contribute to girls' enhanced level of emotional competence (Denham et al., 2010), which may motivate them to attend to expressions and engage frequently in social communications, amplifying gender differences in emotion recognition ability as adults.

Conclusion

Review of literature in typical and atypical development suggests an interplay between nature and nurture as origins of ability differences in recognising faces and emotions. Genetic predispositions may determine general processing patterns and individual potential for abilities, whereas exposure to sufficient environmental stimuli during postnatal development are crucial for the direction and degree of gene expression. Despite empirical difficulties in separating the contributions of nature and nurture and inconsistent results due to methodological limitations, there is a consensus that biological and experiential factors both contribute to human abilities to recognise faces and emotions, resulting in wide ability variations. Further research will need to adopt more reliable measures for testing the magnitude of ability variations and respective contributions of nature and nurture.

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