

Lindsey Zeichner

The Language of the Face: The Substance and Science of Facial Communication

Universidade Fernando Pessoa  
Porto 2023



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“TODOS OS DIREITOS RESERVADOS”

Lindsey Zeichner

The Language of the Face: The Substance and Science of Facial Communication

Dissertation presented to Universidade Fernando Pessoa  
as a requirement to obtain the doctoral degree in Ciências  
da Comunicação, under the supervision of Prof. Dr. Jean-  
Marie Grassin.

## RESUMO

LINDSEY ZEICHNER: A linguagem do rosto: A substância e a ciência da comunicação facial (Sob orientação do Prof. Doutor Jean-Marie Grassin)

Esta tese tem como objetivo analisar o papel do rosto na comunicação humana em uma perspectiva multidisciplinar. Só recentemente é que os neurocientistas conseguiram reunir um esquema parcial para explicar a função facial. Atualmente, existem questões cruciais sem resposta relativamente à forma como a face humana é capaz de satisfazer necessidades essenciais de comunicação e relações sociais. Este estudo tem três objetivos: 1) preencher as lacunas de conhecimento atribuídas às desconexões interdisciplinares entre as ciências biomédicas e as ciências sociais, 2) realizar uma meta-síntese crítica da literatura diversificada nos campos e reunir a ciência fragmentada da comunicação facial, a fim de melhor elucidar os processos intrincados pelos quais os seres humanos se comunicam através de seus rostos, e 3) apresentar os resultados em um formato pedagogicamente consistente que torne os resultados acessíveis a académicos e profissionais provenientes das mais diversas áreas.

Este estudo utiliza uma metodologia meta-sintética em vez das ferramentas meta-analíticas mais comuns, porque a meta-síntese é mais adequada para lidar com o âmbito alargado das fontes de dados multidisciplinares.

Os resultados deste estudo oferecem várias perspectivas sobre a comunicação facial. Em primeiro lugar, a tese introduz o novo conceito de que a comunicação facial é uma "linguagem" composta por um extenso vocabulário. Esta "linguagem do rosto" tem pontuação, contexto, regras sociais (pragmática), sotaques e dialetos. Em segundo lugar, a investigação alarga o modelo clássico de processamento facial: os resultados deste estudo expandiram a conhecida rede neural distribuída para mais de cinquenta nós de processamento facial. Em terceiro lugar, esta tese relata uma nova observação neuroanatômica que coloca o sistema de neurónios-espelho no centro da patologia de quase vinte doenças analisadas neste

estudo. Em quarto lugar, este estudo faz avançar a nossa compreensão dos neuro correlatos do sorriso - uma expressão facial profundamente enraizada na comunicação humana.

A importância deste estudo reside no facto de ser um recurso interdisciplinar para académicos, investigadores e clínicos que precisam trabalhar em equipa para resolver o problema global da comunicação facial disfuncional.

Em conclusão, esta tese cumpriu os seus objectivos gerais de elucidar melhor os processos intrincados através dos quais os seres humanos se comunicam com os seus rostos, e os resultados levam a repensar as disciplinas médicas e as disciplinas humanísticas sobre a forma como se vê o papel do rosto humano.

## ABSTRACT

LINDSEY ZEICHNER: *The Language of the Face: The Substance and Science of Facial Communication* (Under the supervision of Prof. Doctor Jean-Marie Grassin)

This thesis aims to examine the role of the face in human communication from a multidisciplinary perspective. Only recently have neuroscientists been able to put together a partial schema to explain facial function. Presently, there are critical unanswered questions concerning how the human face is able to meet essential communication and social needs. This study has three objectives: 1) to fill the knowledge gaps attributed to interdisciplinary disconnects between the biomedical sciences and the social sciences, 2) to perform a critical meta synthesis of the diverse literature in the fields and put together the fragmented science of facial communication in order to better elucidate the intricate processes by which humans communicate with their faces, and 3) to present the findings in a pedagogically-sound format that informs a range of scholars and professionals coming from highly diverse backgrounds.

This study employs a meta-synthetic methodology rather than the more common meta-analytic tools because meta-synthesis is more suitable to cope with the expansive scope of the multidisciplinary data sources.

The findings of this study offer several insights into facial communication. Firstly, the thesis introduces the novel concept that facial communication is a “language” comprised of an extensive vocabulary. This “language of the face” has punctuation, context, social rules (pragmatics), accents, and dialects. Secondly, the research extends the classical model of face processing: findings from this study expanded the known distributed neural network to more than fifty face-processing nodes. Thirdly, this thesis reports a fresh neuroanatomic observation that places the mirror neuron system at the center of pathology for almost twenty diseases analyzed in this study. Fourthly, this study advances our understanding of the neurocorrelates of smiling—a facial expression deeply embedded in human communication.

The significance of this study is that it is an interdisciplinary resource for academics, research scientists, and clinicians who need to work as a team to address the global problem of dysfunctional facial communication.

In conclusion, this thesis met its broad objectives to better elucidate the intricate processes by which humans communicate with their faces, and the findings prompt a rethinking in the medical disciplines and the humanistic disciplines about how one views the role of the human face.

## RÉSUMÉ

LINDSEY ZEICHNER: Le langage du visage : La substance et la science de la communication faciale

(Sous la supervision du Prof. Dr. Jean-Marie Grassin)

Cette thèse vise à examiner le rôle du visage dans la communication humaine d'un point de vue multidisciplinaire. Ce n'est que récemment que les neuroscientifiques ont été en mesure d'élaborer un schéma partiel pour expliquer la fonction faciale. À l'heure actuelle, des questions cruciales restent sans réponse concernant la manière dont le visage humain est capable de répondre à des besoins essentiels en matière de communication et de socialisation. Cette étude a trois objectifs : 1) combler les lacunes de connaissances attribuées à la coupure épistémologique entre les sciences biomédicales et les sciences sociales, 2) réaliser une méta-synthèse critique des divers écrits dans ces domaines et rassembler le savoir fragmenté sur la communication faciale afin de mieux élucider les processus complexes par lesquels les humains communiquent avec leur visage, et 3) présenter les résultats dans un format pédagogique qui permette à un éventail d'universitaires et de professionnels venant d'horizons très divers d'avoir accès à l'information.

Cette étude recourt à une méthodologie méta-synthétique plutôt qu'à des outils méta-analytiques plus courants, car la méta-synthèse est mieux adaptée pour faire face à l'étendue des sources de données multidisciplinaires.

Les résultats de cette étude permettent de mieux comprendre la communication faciale. Tout d'abord, la thèse introduit le concept nouveau selon lequel la communication faciale est un "langage" disposant d'un lexique et d'une syntaxe étendus. Ce "langage du visage" comporte une ponctuation, un contexte, des règles sociales (pragmatique), des accents et des dialectes. Deuxièmement, la recherche étend le modèle classique du traitement des visages : les résultats de cette étude élargissent la distribution du réseau neuronal connu à plus de cinquante nœuds de traitement des visages. Troisièmement, cette thèse fait état d'une

nouvelle observation neuroanatomique qui place le système des neurones miroirs au centre de la pathologie pour près de vingt maladies analysées dans cette étude. Quatrièmement, cette étude fait progresser notre compréhension des neurocorrélats du sourire, une expression faciale profondément ancrée dans la communication humaine.

L'importance de cette étude réside dans le fait qu'elle constitue une ressource théorique et documentaire interdisciplinaire pour les chercheurs, les enseignants-chercheurs et les cliniciens qui doivent travailler en équipe pour résoudre le problème global de la communication faciale dysfonctionnelle.

En conclusion, cette thèse a atteint ses objectifs généraux, à savoir mieux élucider les processus complexes par lesquels les humains communiquent avec leurs visages, et les résultats incitent à repenser, dans les disciplines médicales et humanistes, la façon dont on considère le rôle du visage humain.

## **DEDICATION**

In dedication to my family, who encouraged me to keep going, even when the path forward seemed unending.

## **ACKNOWLEDGEMENTS**

An incredible thank you to my supervisor, Professor Jean-Marie Grassin, for his interest in my work and efforts to enable me to complete this thesis. My additional sincere thanks to Professor Ralf J. Radlanski, who has supported my research since day one, and provided valuable insight and assistance at every point along the journey. Thank you to Professor Samuel Zeichner for assistance both academic and personal over the course of this endeavor. Acknowledgements and thanks to Professor Jorge Pedro Sousa for enabling me to submit my thesis and share the fruits of this labor. I also would like to acknowledge Reitor Salvato Trigo for reading my thesis proposal and granting his time and advice to enable me to pursue this doctoral project at Universidade Fernando Pessoa. Finally, my sincere thanks to Pró-Reitora, Nadine Trigo, for her efforts to make my international enrollment less formidable.

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## LIST OF ABBREVIATIONS

- 5-HT – 5-hydroxytryptamine, serotonin
- ACC – anterior cingulate cortex
- ACh – acetylcholine
- AD – action descriptor
- AD – Alzheimer’s disease
- ADP – adenosine diphosphate
- AG – angular gyrus
- AP – acquired prosopagnosia
- aPFC – anterior prefrontal/frontopolar cortex
- AS – Angelman syndrome
- ASD – autism spectrum disorder
- ATP – adenosine triphosphate
- AU – action unit
- BA21 – Brodmann Area 21
- BA40 – Brodmann Area 40, the intraparietal sulcus
- BA45/46 – Brodmann Areas 45 & 46, the medial prefrontal cortex
- BA8/9 – Brodmann Areas 8 & 9, the inferior frontal gyrus
- BOLD – blood oxygenated level-dependent
- BPD – borderline personality disorder
- CDP – cognitive developmental prosopagnosia
- CFC – cognitive fear circuit
- CN III – cranial nerve III, oculomotor nerve
- CN VI – cranial nerve VII, facial nerve
- CNS – central nervous system
- dACC – dorsal anterior cingulate cortex
- DBS – deep brain stimulation
- DBS – deep brain stimulation
- dIPFC – dorsolateral prefrontal cortex
- dIPFC – dorsolateral prefrontal cortex
- dmPFC – dorsomedial prefrontal cortex
- DNN – distributed neural network
- DS – Down syndrome

DTI – diffusion tensor imagine  
DTI-DT – diffusion tensor magnetic resonance imaging with fiber tractography  
FACS – facial action coding system  
FFA – fusiform face area  
fMRI – functional magnetic resonance imaging  
GABA – gamma-aminobutyric acid  
GS – geniculo-striate  
GSA – general visceral afferent  
GVE – general visceral efferent  
HC – healthy control  
HD – Huntington’s disease  
hMNS – human mirror neuron system  
IFC – inferior frontal cortex  
IFG – inferior frontal gyrus  
IgA/IgG/IgM – immunoglobulins A, G, and M  
IOG – inferior occipital gyrus  
IPS – intraparietal sulcus  
LCSPT circuit – limbic-cortico-striato-pallidal-thalamic circuit  
LFC – lateral frontal cortex  
LFC – lateral fusiform gyrus  
LLSAN – levator labii superiores alaeque nasi  
MDD – major depressive disorder  
MEG – magnetoencephalography  
MFG – middle frontal gyrus  
ML – mesolimbic  
MNS – mirror neuron system  
mOFC – medial orbital frontal cortex  
mPFC – medial prefrontal cortex  
MRI – magnetic resonance imaging  
NAc – nucleus accumbens  
NK cells – natural killer cells  
NDD – neurodegenerative disease  
NIRS – near infrared spectroscopy  
OCD – obsessive compulsive disorder

OFA – occipital face area  
OFC – orbital frontal cortex  
OXTR – oxytocin receptor gene  
PAG – periaqueductal gray area  
PD – Parkinson’s disease  
PET – positron emission tomography  
PHG – parahippocampal gyrus  
pmOFC – prefrontal medial orbitofrontal cortex  
POMC – pro-opiomelanocortin  
pSTS – posterior superior temporal sulcus  
PUL – pulvinar  
PVC – primary visual cortex  
PVN – paraventricular nucleus  
RCTA pathway – retino-colliculo-thalamo-amygdala pathway  
RFC – reactive fear circuit  
rIFFA – right inferior frontal face area (repeated at ch3 pg 15)  
SMA – supplemental motor area  
SMAS – superficial musculoaponeurotic system  
SON – supraoptic nucleus  
SPECT – single-photon emission computed tomography  
SPFC – superior prefrontal cortex  
STG – superior temporal gyrus  
WS – Williams syndrome  
STS – superior temporal sulcus  
SVA – special visceral afferent  
SVE – special visceral efferent  
TBI – traumatic brain injury  
TLE – temporal lobe epilepsy  
TMA – transcranial magnetic stimulation  
ToM – theory of mind  
TPJ – temporoparietal junction  
TS – Turner syndrome  
vlPFC – ventrolateral prefrontal cortex  
vmPFC – ventromedial prefrontal cortex

VTA – ventral tegmental area

vTA – ventral thalamic area

## INTRODUCTION

### 0.0 Context of the Research

The principal and essential role of the human face is *communication* and *socialization* (Mehrabian, A. 2017). Yet, physicians and dentists, whose training concerns the face, are largely unaware of, and/or unfamiliar with, the disorders affecting facial communication. Correspondingly, psychologists, sociologists, communication scientists, linguists, or anthropologists, whose training is in communication, language, or culture, do not have the resources within their discipline to learn and understand the *medical* basis for how the face works as an organ of communication and socialization. Thus, there is an interdisciplinary disconnect in this vital field of study.

A review of the literature from 1990 to the present, revealed a fluid and, in many cases, an obscure body of scientific knowledge. In addition, the neuroscience underlying facial communication remains incompletely understood. Only recently have neuroscientists been able to put together partial schemata to explain facial function. Thus, in the current context, there are critical unanswered questions concerning how the human face is able to meet essential social needs that go beyond the capabilities of spoken or written language. This thesis, “The Language of the Face, the Substance and Science of Facial Communication”, sets out to address the interdisciplinary disconnect, and to unify the incompletely understood and fragmented science underlying facial communication.

### 0.1 The Problem

To date, the literature lacks a contemporary, comprehensive, and coherent explanation of human facial function. This is largely for two reasons: 1) the literature in this field of study is diverse spanning neuroscience, medical imaging, medicine, surgery, dentistry, psychology, anthropology, sociology, language, and communication sciences; thus, the scope is not easily appreciated by scientists within a single discipline and, 2) It is only recently that neuroscientists have been able to put together partial schemata to explain facial function. Consequently, the problem is that the neuroscience community lacks the full insight of the social science community into the critical social aspects of the face, while the social science

community lacks access to the scientific underpinnings of the medical aspects of the human face.

The primary problem addressed by this thesis is to better elucidate the intricate processes by which humans communicate with their faces by bringing together the fragmented, interdisciplinary science in order to add new insight into how the human face works. The secondary aim of this thesis is to present the findings in a pedagogically-sound format that informs a range of scholars and professionals coming from highly-diverse backgrounds. In this thesis, this author employs a novel methodology (meta synthesis) to collect, curate, and synthesize the data thus bringing together the findings of more than 500 scientific studies in order to advance the scientific understanding of the way in which the human face participates in communication and socialization.

## **0.2. The Specific Objectives**

The objectives of this thesis were:

- 1) to assemble and collate long-standing research, both from the Biomedical Sciences and the Humanities, on the subject of facial communication,
- 2) to perform a critical meta synthesis of the diverse literature in the fields, in order to synthesize the findings into a cohesive explanation of how the human face functions as an organ of communication and socialization, and
- 3) to present the findings in a pedagogically sound format that informs a range of scholars and professionals coming from highly diverse backgrounds.

## **0.3. The Methodology**

By means of a trimodal literature search of databases encompassing the biomedical, the humanities and social sciences, and the gray literatures, this dissertation assembles the underlying science to support, explain and illustrate some of the more interesting facets of human facial communication, as well as inter-species communication. For instance, how human infants communicate facially with other mammals; how post pubescent humans use their faces to attract a suitable mate; how humans telegraph the palatability of food via innate

facial expressions; how the mirror neuron system allows humans to know what a conspecific is thinking via fleeting exchanges of facial expressions; how activation of distinct muscles of facial expression enhance immunity and cardiovascular function, or how neuromuscular electrical transmission in the brain's face-processing system generates strong emotions when humans look at a face.

#### **0.4. The Justification of the Problem Choice and Contribution**

This thesis problem is important for several reasons. Firstly, this problem merits investigation for both medical and societal reasons. In particular, it is not well appreciated in the medical community that three prevalent diseases account for profound facial communication deficits. For example, in a 2019 epidemiological study, we reported that autism spectrum disorders (ASD) and Parkinson's disease (PD) accounted for 175 million cases worldwide (Zeichner, Zeichner, and Kuhnle 2019). Moreover, the economic impact is far-reaching. For example, ASD is a social disease effecting not only patients, but also their families, friends, public schools, the workplace, and society. There is yet no established medical treatment.

Similarly, the impact of PD is significant. It is estimated that PD effects more than 8.5 million people worldwide and the prevalence is growing exponentially. The World Health Organization (WHO) considers PD to be pandemic. In the U.S. alone, yearly healthcare expenditures are estimated at \$52 billion.

Another example, our most recent unpublished findings point to yet another impactful disorder of facial communication that passes with little notice. Specifically, major depressive disorder (MDD) has been ranked as the third cause of the burden of disease worldwide in 2008 by WHO, which has projected that this disease will rank first by 2030 (Malhi and Mann 2018). In essence, there are highly prevalent facial communication disorders having significant medical and societal burdens that go untreated because physicians are largely unaware of the facial aspects of their patients' communication deficits.

Secondarily, the thesis problem merits attention because the science of facial communication lacks a unifying educational resource for the vast number of professionals who need to know this key information about how the human face functions. Whereas, *up-to-date* resources are scant, this thesis addresses the scholarly demand.

#### **0.5. The Potential Impact and Implications of this Study**

A key role of the unified data base resulting from this thesis project would be to form the groundwork for vital research in facial communication disorders to be utilized by the medical sciences as well as the human sciences. In short, this thesis contributes to the advancement of the knowledge in the fields of both the medical sciences and the social sciences.

## **0.6. Conclusions**

This dissertation highlights previously incompletely explored neural pathways involving the human face and their relationships to racial bias, sexual preference, and prosocial and antisocial behaviors. The thesis proposes new, or expands existing schemata, for neural networks involving self-identity, gender, race and age determination, and the recognition or generation of specific expressions of facial emotion. Additionally, the text explores possible mechanisms for heretofore unexplained or partially explained disease processes. The thesis also offers scientific insight into how the activation of specialized muscles in the face can act systemically on the rest of the body to moderate metabolism, immunity, cardiovascular health, and pain tolerance.

## **0.7. Readers' Guide/Chapter Outline**

This dissertation has four chapters: 1) The Language of the Face—what humans express via their faces including the vast “vocabulary”, linguistic elements, the social and cultural aspects of facial communication, 2) The Structure of the Face—the distinctive anatomy that makes facial expression possible, 3) The Physiology of the Face—how humans make and read faces, and 4) The Pathology of the Face—prevalent facial dysfunctions.

It is the intent of this writer to communicate with readers from diverse disciplines. Therefore, this thesis is richly footnoted to guide the readership in what might otherwise be an unfamiliar domain. The writing style clarifies medical terms for nonmedical readers and correspondingly the text explains terms used in linguistics, sociology, or psychology, that might be unfamiliar to surgeons, dentists, or neuroscientists. By design, there is little unexplained jargon.

## CHAPTER I – The Language of the Face

### 1.0 Introduction

Have you gone to the airport to meet a visiting friend? You can recognize the arriving travelers with no one to meet them: their gaze is unfocused; their facial expressions are neutral. The people expecting to be met look different. Their eyes are narrowed. Their lips anticipate a smile. Finally, your friend appears. Their face brightens as you come into view, granting you a smile. Without thinking, your face returns a pleasurable smile. No words were spoken, yet you had a meaningful conversation. Remarkably, we engage in facial exchanges like this thousands of times each day. Facial communication is critical. In fact, our survival depends upon these fleeting, split-second expressions (Blum 1998).

Since the first edition of Grey's Anatomy in 1858, medical anatomy books have instructed students of medicine that the primary function of the muscles of the face were "to act as sphincters and dilators of the facial orifices". Now, more than 160 years since the publication of the first edition of Gray's Anatomy, the 41<sup>st</sup> edition (Standring 2016) has not yet redefined the role of the facial muscles to conform with our modern understanding. Thus, today's physicians and dentists still are likely to view the facial muscles principally with regard to their role in modulating the eyes, nose, and mouth. But the face is not merely a container for the eyes, ears, nose, and mouth. Rather, it is a *principal* and *essential* mode of human communication and socialization.

Thousands of years ago, early humans functioned without language. They addressed urgent issues of self-preservation based on facial gestures. Early humans had to woo mates, comfort infants, bond to trustworthy faces, avoid offensive or deceitful faces, comprehend intentions, express emotions, and work cooperatively with other humans (Hoebel 1972; Keesing 1976). The brain is hard-wired to read faces and make facial gestures within milliseconds. Modern humans still rely on split-second fundamental social decisions based on faces (Blum 1998).

Indeed, facial expression remains a major mode of human communication. Facial communication is a rich language. The "linguistic" function of the face goes beyond the capacity of verbal or written communication. That is, the face signals feelings, needs and

desires—what speech or writing cannot express. (Ekman and Friesen 1978) and (Scherer 1982) catalogued a vast *nonverbal* “vocabulary” of more than 7,000 facial expressions, thus exceeding a typical adult’s active vocabulary of fewer than 5,000 words.

The human face plays a key role in the survival of individuals, and humankind as a species. The growth and development of facial structures in utero, and early postnatal development of neural mechanisms underscores this vital role. That is, we acquire the ability to “talk” with our faces beginning the seventh month in utero (Reid et al. 2017). Even earlier in development (at twenty gestational weeks), human fetuses can signal distress with facial expressions identical to those observed in full-term neonates (Dondi et al. 2014). Infants preferentially track faces within the first hour of birth (Johnson et al. 1991) and neonates can mimic facial expressions thirty-six hours after birth (Field et al. 1983). The centrality of facial communication to humans is decidedly expressed via the early and extensive development of this communicative and socialization system.

Humans exchange facial signals at lightning speed and over great distances<sup>1</sup>. The lift of the eyebrow, to acknowledge a friend, lasts only one sixth of a second. One can tell in milliseconds if a stranger’s face registers surprise or pleasure—even if they are fifty meters away. Humans detect smiles, an important part of communication, at 100 meters. The rapidity with which we recognize faces, facial expressions, and respond with facial signals suggests that subcortical<sup>2</sup> neural mechanisms are involved. That is, rapid facial communication takes place within the core of the human brain rather than involving the parts of the brain concerned with thinking or deliberation. Humans are hard-wired to “talk with their faces.”

This chapter, frames facial communication in the context of “language.” That is, the text describes the vast assortment of human facial gestures and how they are used to express thoughts, emotions and intentions using a “linguistic” metaphor. For example, facial expressions comprise a “vocabulary.” Researchers studying facial emotional expression, have codified the “words” into a “dictionary.” This “dictionary” is known as the facial action

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<sup>1</sup> Yet, chimpanzees and rhesus macaques can exchange facial signals faster than humans. Slower facial muscle movement is believed to be an evolutionary adaption to facilitate speech (Burrows et al. 2014).

<sup>2</sup> Subcortical refers to the regions of the brain beneath the outer cortex. The subcortex is where more primitive functions are processed.

coding system (FACS). Unlike a foreign language, there is a core of universally-expressed and universally-recognized facial displays. Nevertheless, there are numerous unique, culturally-dependent expressions that are not used globally.

Researchers have determined that “speakers” of this nonverbal “language” use regional “dialects.” They retain “accents” when they relocate to a different culture. Within cultures there are “display rules,” pragmatics<sup>3</sup>, that govern what one can express via the face depending upon age, gender, or stature. The “language of the face,” like verbal language, develops over time in humans. However, because of biological necessity, the development of facial language commences earlier than verbal language. In fact, development begins in utero so that humans can communicate from birth.

### 1.1 The Types of Facial Expression

The facial “vocabulary” hosts at least three types of expressions categorized as: 1) purely emotional displays, 2) paralinguistic/co-speech facial expressions, and 3) facial postures and movements (Fridlund 1994). Purely emotional facial displays are innate expressions that signify emotional states such as pain, surprise, fear, astonishment, joy, sadness, etc. Paralinguistic expressions are facial gestures that punctuate, articulate, or clarify speech. Facial postures and movements are facial gestures such as lip-licking, lip-biting, or yawning that convey an affective state, for instance anxiety, anticipation, boredom, etc.

Further, facial expressions can be subdivided into “universal displays”—expressions that are common across cultures, versus “culturally-specific” expressions that are particular to ethnicity, nationality, religion, or other demographic variables. Then, there are subtypes of culturally-specific facial expressions such as: gender-influenced facial communication (expressions used and recognized differently between men and women of the same culture), or age-specific expressions (unique facial expressions associated with infants, children, adolescents, or elderly of the same culture), or affilial facial displays associated with social groups, or even familial facial expressions (facial displays shared by members of a family). The aforementioned schema of “facial language” is illustrated in **figure 1**. The complexities of “facial language” will be discussed in greater detail, later in this chapter.

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<sup>3</sup> Pragmatics is a branch of linguistics concerned with the use of language in social contexts.

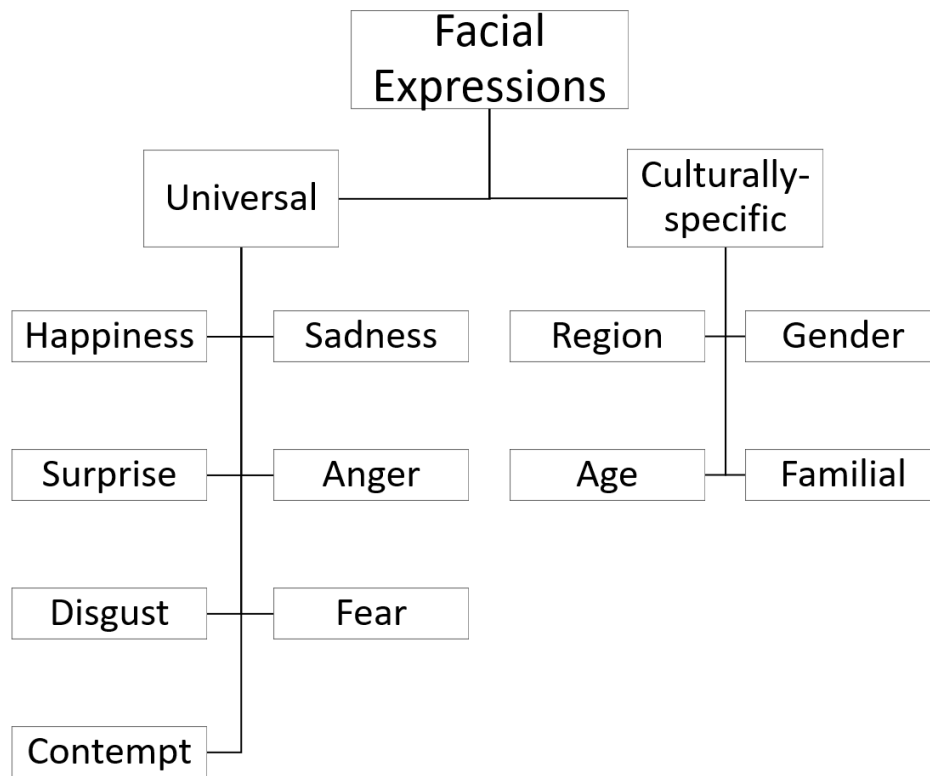


Figure 1. A structural schema for the types of facial expressions. Source: Author's original

## 1.2 Facial Display Rules

Facial “display rules” diversify facial “language” (Ekman and Friesen 1969). Display rules govern emotional facial expressions. That is, which emotions or facial displays can be used in public, which faces can be used in private, which facial displays are reserved for kin, and/or which facial expressions are appropriate for communication with humans of a higher or lower social status. Humans learn “display rules” when growing up. Additionally, cultural display rules modify facial emotional expression by amplification (e.g., amplifying feelings of sadness at funerals), deamplification (e.g., minimizing sadness at weddings), masking emotional expression (e.g., flight attendants interacting with unruly customers), or neutralization (expressing nothing, such as when playing poker) (Matsumoto and Hwang 2013). Thus, cultural “display rules” add intricacy to facial communication.

Facial “display rules” are profoundly influenced by culture. Cultural display rules explain how universal facial expressions of emotion are regulated according to social context

by people of different cultures (Ekman and Friesen 1969). Ekman's classic study of Japanese and American university students first demonstrated the existence of "display rules". Later, (Lee and Matsumoto 2011b) set forth how "display rules" modulated facial expression in the Japanese culture. In the Lee and Matsumoto study, Japanese subjects suppressed emotional facial expression in public, but not in private. Thus, it is noteworthy that facial expression is not determined solely by biology; facial displays are deeply influenced by culture.

### 1.3 Categorization of Facial Expressions

#### i. Universal facial expressions

As stated previously, emotional facial expressions may be characterized as universal or culturally-specific. Naturalist, Charles Darwin, in his book, *The Expression of Emotions in Man and Animals* (1872) proposed that a set of facial expressions, that he had observed and studied, were universal across cultures. Darwin further argued that human expressions of emotion were innate. In consonance with Darwin, psychologist, Paul Ekman (1972) theorized that there were six core facial expressions of emotion that were expressed and recognized globally, regardless of race, culture, nationality, religion, gender, or other demographic variables. These facial displays were: anger, fear, disgust, happiness, sadness, and surprise. In 1986, Ekman expanded the theory of universality to include a seventh emotional facial expression: contempt (Ekman and Friesen 1986). These seven core facial expressions of emotion are illustrated in **figure 2** along with a description of the principal features of each facial expression.



Figure 2. The Seven Universal Facial Expressions. The universal facial expressions with their principal features labeled. Source: <https://www.pantomime-popkultur.de/2016/04/micro-expression-the-facial-expressions-of-the-7-basic-emotions-at-a-glance/> Photos courtesy of pantomime-popkultur.

It is further believed that the universal expressions are innate because they are also found in congenitally blind persons (Matsumoto and Willingham 2009).

The exact number of core universal facial expressions has been in flux over decades. Recently, Cowen et al. (2020), asserted that there are sixteen facial expressions shared globally. In addition to Ekman's core expressions of anger, contempt, sadness, and surprise, Cowen extended the list of globally-expressed and universally-recognized facial displays to include: amusement, awe, contemplation, confusion, contentment, desire, disappointment,

doubt, elation, interest, pain, and triumph. Despite the apparent controversy, most researchers accept the concept of universality in facial communication.

## ii. Culturally-specific facial expressions

Notwithstanding the existence of core, global facial expressions, substantial research has shown that facial expressions are influenced by culture. In a classic study by Ekman and Friesen (1969), American and Japanese college students viewed stressful films showing explicit, gory surgeries. The Americans and Japanese experimental subjects displayed the same expressions of disgust, anger, fear, and sadness when viewing the films, but *only* when they believed they were unattended. However, when an authority-figure, wearing a white coat and carrying a clipboard, entered the room, there were significant differences. The faces of the Americans continued to show negative feeling. In contrast, many Japanese smiled. The researchers concluded that an element of Japanese culture prevented free expression of negative emotions in the presence of another person. The authors explained this disparity by differences in display rules in Japan and in the U.S. Whereas, the Japanese tend to conceal negative emotions in social settings in order to maintain collective harmony, individualistic cultures, such as in the U.S., tend to endorse emotion expression<sup>4</sup>.

The suppression of facial expression is acquired culturally rather than being present congenitally. This was established by Camras et al. (2007). Camras studied the reactions of European-American and Asian infants at age eleven months. In that study, a researcher lightly grasped the subjects by the arm. European-American, Chinese, and Japanese babies were similar in their negative facial expressions when restrained by the stranger. Remarkably, all infants in this study, showed no apparent inborn difference in their willingness to publicly express facial emotion. Taken together, the Ekman and Camrus studies suggested that humans learn to communicate with their faces according to what is appropriate in the society in which they were reared.

Japanese society is not the only culture that modulates facial emotional expression. Several societies constrain emotions. For example, Korean society also constrains emotional

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<sup>4</sup> Possibly, in 1979, these groups were clearer defined as homogenous groups in terms of cultural norms. In the modern, globalized world these differences are likely diminished.

facial expression. Lee and Matsumoto (2011) reported that in a sample of Japanese or Korean university students, the subjects shared the emotional display rules about facial expressions. However, Japanese subjects thought that they should suppress emotions more than Koreans did.

Eastern cultures are not the sole cultures to down-regulate facial expression. The British are known for a “stiff upper lip”, whereas the Finnish equivalent, “sisu,” is embedded in Finnish culture. A well-known example of constrained facial expression of emotion in the UK is “the Prince Charles Smile” (a.k.a., the “royal smile”) **figure 3**.



Figure 3. A smile can be culturally-specific. The illustration on the left is King Charles, III of England. Modified from Daily Mail 2009. The illustration on the right is the American actor, Seth Gamble. Reproduced under CC license. © Glenn Francis, [www.PacificProDigital.com](http://www.PacificProDigital.com). Reproduced under CC license. © Glenn Francis, [www.PacificProDigital.com](http://www.PacificProDigital.com).

The royal smile exemplifies upper class civility and situational control (“Divided by a Common Grimace: Steepholm — LiveJournal” n.d.). This facial display is characterized by restricted activation of the zygomaticus muscle<sup>5</sup> while using the risorius muscle to pull the lips sideways to show minimal teeth. This contrasts with the American smile (a.k.a., Hollywood smile) that extends the lips upward to show the upper teeth. It signifies likeability and allure to North Americans. The Finnish face is characteristically blank during discourse (“How to Spot an Angry Finn and Understand Finnish Facial Expressions” n.d.).

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<sup>5</sup> The zygomaticus major muscle is the muscle that moves the corners of the mouth upward during a smile. The risorius muscle is the muscle that moves the corners of the mouth outward.

#### 1.4 “Accents” and “Dialects”: the Nuance in Facial Communication

Further refining cultural specificity in “the language of the face,” are what Marsh, Elfenbein, and Ambady (2003) termed “nonverbal accents”—cross-cultural variations in the appearance of basic facial expressions. Marsh showed photographs of nine native Japanese plus nine photographs of Americans of Japanese ancestry to an experimental group of observers who identified as Americans. The photographs displayed various facial expressions of emotion, or neutral faces. The authors measured the observers’ ability to discriminate facial expressions belonging to the Japanese people who spent their lives immersed in Japanese culture, from those belonging to Japanese immersed in American culture. The naïve American observers, of varying ethnicities, accurately discriminated the nationality of the Japanese faces in the photos. The observers tended to determine nationality more accurately from expressive faces than from neutral faces. The study demonstrated people’s sensitivity to subtle differences in the appearance of facial expressions across cultures.

In 2007 (Marsh, Elfenbein, and Ambady 2007) ran a similar study, but this time they used pictures of Australians’ and Americans’ facial expressions. Once again, Americans were able to guess the nationality of the person pictured based on their smile. The ability disappeared when people were shown neutral expressions. This investigation suggested a fascinating intricacy of facial communication. That is, not only do humans communicate with their faces in accordance with their culture, but also when they adapt to a new culture, they retain a nonverbal accent of their former culture that can be discerned by natives of the culture to which they assimilated.

In addition to facial communication “accents,” researchers have reported facial expression “dialects”—regional variations in facial expressions. For example, Elfenbein et al. (2007) found substantial differences between facial expressions in university students in French-speaking Quebec compared to matched students in French-speaking Gabon. Moreover, consistent with prior research, the sample showed within-group advantage (i.e., the subjects more accurately interpreted the facial expressions from within their own culture, while showing lower cross-cultural recognition of emotional expressions).

The literature reflected numerous examples of culturally-specific facial expression. Saha et al. (2015) reported that distinct AUs (facial action coding units) came into play when coding the universal expressions of emotions in Indian, Japanese, or Euro-American subjects.

Not only is facial communication culturally specific, but also humans better communicate in the facial dialect of peers. In an interesting study, Tsikandilakis et al. (2019) examined facial communication within and among four cultures (Britain, Chile, New Zealand, and Singapore). They found that participants in each culture detected and recognized own-culture expressions more accurately than other-culture expressions. This supported prior ontogenetic arguments<sup>6</sup> (see Elfenbein and Ambady 2002b; 2002a) of own-cultural facial recognition advantage and confirmed that own-culture faces have increased sociobiological value for communication. Even when subjects were shown own-cultural faces for merely thirty-three milliseconds, they discerned the facial expressions more accurately than other-culture expressions. The rapid processing of the facial stimuli suggested subcortical<sup>7</sup> recognition of facial expressions attuned to in-group contacts.

Human facial expressions go beyond *cultural* specificity. Unique facial displays extend to *subcultures*. For example, young African-American groups have evolved a vocabulary of facial expressions to signify “attitude.” These are aggressive facial poses (“grittin”/“mean muggin”). In this subculture, these facial displays denote having “swag”, “being hard”, being “hyped” (“gettin crunked”), “being pumped”, “being fierce”, being very serious (about what they are doing), and/or being “for real” (“Pancocojams: Branding & Mean Mugging (Grittin) In Omega Psi Phi, Inc. & In Some Other Historically Black Greek Letter Organizations” n.d.). African-American culture incorporates an historical dance tradition called “steppin”. It can be seen in entertainment (e.g., in iconic unison choreography of African-American doo-wop musical groups such as The Four Tops and The Temptations, (Traiger 2002)), in sports, and in African-American gangs, sororities or fraternities. To show “attitude”, the steppin incorporates mean facial gestures. **Figure 4** is an illustration of subcultural facial expressions.

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<sup>6</sup> Developmental psychologists refer to ontogenetic adaptations as biological adaptations that serve an adaptive function at a specific time in development.

<sup>7</sup> The cortical (or outer regions of the brain) involve analysis, discrimination, deliberation, judgement, etc. Subcortical regions (regions deep within the brain) involve rapid, reflexive, unmoderated responses to stimuli.



Figure 4. Subcultural facial expressions in African Americans. Note in the top illustration, the “attitude” facial displays in a step-team in Mississippi, USA “grittin” before a crowd. Source: LookOut504, “Spelman Freshman Step Team Alum Battle.” The bottom illustration is a group of fraternity brothers at Alabama State University showing aggressive facial displays (“bein’ hard”). From mrchangeurlife. “Omega Psi Phi Que Doggs.”

African-American subculture is not the only group to use aggressive facial displays to show “attitude”, fierceness, or to display dominance. Sports are noted for “mean mugging” by both players and fans. For classic examples of “hard” or “hyped” facial displays see (Angieri 2019; “Bucks Fans Show Their Best ‘mean Mug’ for Game 2 of the NBA Finals [PHOTOS]” n.d.).

Thus, not only is there a core of universal facial expressions, but also facial communication is highly culturally-specific. Humans within regions of the globe use distinctive facial displays. Moreover, societies employ cultural “display rules” to up-regulate or down-regulate facial communication depending on the society’s values and traditions. Accents and dialects distinguish regional variations. These expressions are more comprehensible to ingroups than outgroups, and unique facial displays extend to subcultures. That is, there are subgroups within a culture that generate unique facial expressions common only to their peer group.

In short, there are three types of facial expressions and able to be divided further into universal and culturally specific. Display rules are influenced by culture. Societies regulate emotions. Accents and dialects distinguish regional variations. These expressions are more legible to ingroups than outgroups and unique facial displays extend to subcultures.

### **1.5. Paralinguistic Expressions**

Paralinguistic or “co-speech” expressions are non-emotional facial expressions employed in facial communication. They tend to be culturally-specific. Common examples in Western cultures are: nodding the head in agreement, conversational signals such as looking down to signal one has finished speaking or looking up to signal that an answer is expected from one’s conversational partner, etc.

Ekman (2004) subdivided paralinguistic facial expressions into two relevant types: facial illustrators and facial emblems.

- 1) *facial illustrators* provide emphasis or syntax to speech. Facial illustrators are facial signals acting as question marks or exclamation points. For example, raising or lowering one’s eyebrows signify a question, interest, or surprise. Some facial illustrators provide emphasis to particular words as they are spoken.
- 2) *Facial emblems* are expressions that signal specific messages whose meanings are particular to a group or culture (Knapp and Hall 2010). Facial emblems can be used in place of a word(s) or when words cannot be used. Emblem vocabularies vary by country and, often, differ between regional groups within those countries. In the US, two commonly seen examples of facial emblems are "winking" to indicate a shared understanding and the "one-eyebrow-raised-in-skepticism" expression. Another familiar facial emblem is an eyebrow flash to indicate “hello.” In Germany, a

common facial emblem is “blinking” upon arrival to say hello to a group of social acquaintances (**figure 5-left**). Another characteristic German facial emblem is intense eye contact or stare to signify that “I am seriously listening to your ideas.” (**figure 5-right**) (While polite to Germans, the attentive stare is unnerving in other cultures). (“7 Videos of German Facial Expressions That Need Explaining – DW – 01/10/2018” 2018).

Figure 5. German facial emblems



Figure 5. German facial emblems. The left photograph illustrates the German facial display corresponding to the “wink-hello” greeting. The right photo illustrates the German “stare” signifying interest and respect for the speaker.

Calbris (1990) described two French facial expressions they considered to be emblematic: “*faut se le farcir !*” (an asymmetric smirk plus raised eyebrows with eyelids partially covering the iris), and “*Mon Dieu, qu’il est bête !*” (eyes lifted). The former is emblematic for “What a pain!” and the latter, “My God, he is stupid!” Another common French facial gesture is “*faire la moue.*” *La moue* shows discontent, distaste, or another negative emotion. The lips are puckered and pushed forward. The eyes squint. One might use this gesture when standing in a queue for too long. (“The Top 10 French Gestures” 2023). A characteristic French facial gesture uses the buccinator muscle (this muscle almost never takes part in facial expression). This facial display of annoyance, *is formed by pursing the lips and blowing forcefully out, with a slight raise of the eyebrows. Another emblematic expression, “Ah bon?” (Oh, really?) is formed by raising the eyebrows, opening one’s eyes wide and pursing or forming an “O” shape with one’s mouth. It is most often used when one*

*has heard a surprising fact or bit of gossip, or when one has been told they are wrong about something* (“Interpreting the French Face | Les Blogs” n.d.) **figure 6.**

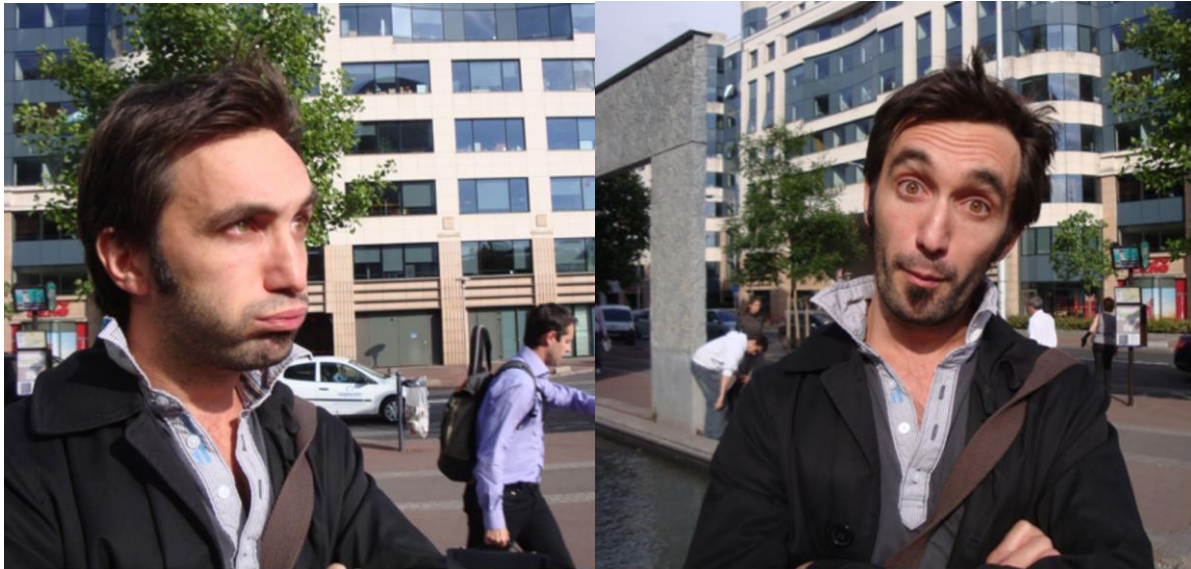


Figure 6. Emblematic French facial displays. Figure 6a (on the left) is the bilabial trill or the French “raspberry”. This facial display signifies annoyance. Figure 6b (right) is the emblematic expression, “Ah bon ?” This is used when one has heard a surprising fact. Source: France 24. Interpreting the French Face | Les Blogs.” Published Fri, 05/20/2011 <http://inparis.blogs.france24.com/article/2011/05/20/interpreting-french-face-0.html>.

Facial emblems involving the lips and tongue can be found in several cultures. An unusual facial emblem was studied and reported by (Ortega-Santos 2016). Ortega-Santos described Latin-American “lip-pointing,” pouting the lips accompanied by lateral movements to indicate direction. In some instances, slight head movements and eyebrow raising accompanied the lip movement. The author described this facial expression in regional cultures of Chile, Columbia, Guatemala, or Honduras. A second function of lip-pointing is to substitute for a pronoun. So, in Columbia, the question, *¿Quién va a venir?* (Who is coming?) might be answered with a lip-point in place of the words “she/he/, him/her, or they/them.” In addition to Latin American cultures, Enfield (2001) noted that lip-pointing was present in other cultures (e.g., Laos, certain Australian, African, and Native American cultures) with slight variations (or dialects) involving lip positions. In the Philippines, the lip-point, known as “*doon*” in Tagalog, (over there) is used to indicate direction. Another culturally-specific facial emblem is the tongue-bite in South Asian cultures (Eastern India) to signify embarrassment (or “*lajya*” in modern Oriya language) for having made a mistake (Keltner and Haidt 1999).

## 1.6. Gender Specificity in Facial Communication

Many investigators have reported gender differences in perceiving facial expressions. Erwin et al. (1992) addressed the issue of gender differences in perceptions of affective state. In an experiment that tested men's and women's abilities to discriminate happy or sad facial expressions in photographs of men or women, they found that men were better at detecting sad emotions in men, compared with women's sensitivity to sad emotions expressed by women. Further, they showed that women better perceived emotional expression in men than in women, while men were specifically insensitive to sad expressions in women.

Not only are there gender differences in *perceiving* emotions in faces, but also there are gender differences in *expressing* emotions in faces. In a large-scale analysis of gender differences in facial expression, (McDuff et al. 2017) reported that women expressed facial actions more frequently than men, and in particular, expressed more positively-valenced actions (smiles). Men more frequently expressed negatively-valenced actions (anger). The sample population consisted of 2106 male and female subjects between the ages of sixteen and eighty-two from five countries (UK, France, Germany, US, China) to adjust for possible cultural differences. The subjects viewed videos in order to elicit emotional facial responses.

In a recent neuroimaging study, Zhang et al. (2022) compared the brain activity of nulliparous women<sup>8</sup> (ages twenty-four to thirty-two) to men while the subjects viewed photos of infants displaying happy, neutral, and sad faces. The authors reported that the brains of women and men reacted differently to infants' faces. They found that infant facial expressions preferentially activated the brain regions in women critical for preparation for communicative, interactive, and nurturing behaviors. The authors further observed elevated neural interconnectivity between these regions. These regions consisted of the face-processing areas, and included the fusiform gyrus, cingulate cortex, parahippocampal gyrus, precuneus and inferior parietal lobe.

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<sup>8</sup> Nulliparous refers to women who have not given birth.

In short, within a culture, there are gender differences in facial communication. The differences include:

- 1) gender-specific interpretation of facial expressions,
- 2) gender-specific production of facial expressions, and
- 3) gender-specific neurophysiology for facial communication.

### i. Is There a Female Advantage in Facial Communication?

Women's capacity to express themselves by means of facial expression appears prominently in the lay literature (see **figure 7**). But can this notion be supported scientifically?



Figure 7. Twelve gender-specific female facial expressions. Women demonstrate considerable subtlety of facial communication compared to men. Women are capable of decoding some facial expressions superior to men. This is a satirical illustration. Source: modified from (Adjabi et al. 2020) CC BY license.

Reviewing the scientific literature generally affirms that women are more expressive than men (Wallbott 1988; Dimberg and Lundquist 1990; Briton and Hall 1995; Krumhuber, Manstead, and Kappas 2007), as well as being better than men at sending nonverbal signals

(Buck, Miller, and Caul 1974; Wallbott 1988). Numerous studies suggest that women are superior to men in facial expression processing (see Kret and De Gelder (2012); Hall (1978) for review). Other studies suggest that women are better at recognizing subtle expressions of emotion than are men (Hoffmann et al. 2010). In fact, a “female advantage” in facial expression processing is even thought to be present in young children: three and a half-year-old girls are as accurate as five-year-old boys in facial expression recognition (Boyatzis, Chazan, and Ting 2012). It is believed by some researchers that female sensitivity to emotional faces is present at birth. Infant girls gaze at faces for signs of emotional expression shortly after birth and seem to comprehend a particular look or touch. When they view a face without emotion, a girl will turn her face to others nearby that are more expressive. Mutual facial gazing will increase by over 400 percent in the first three months of life, whereas this response will not increase at all in boys during this time. Brizendine and Hulle (2006). Brizendine believes that women are born wired with a finely tuned ability to read emotions in faces. Whereas Brizendine concluded that women are born wired with a finely tuned ability to read emotions in faces, this conclusion does not distinguish between a biological-driven advantage and one caused by differing gender socialization by parents and caregivers to account for this distinction.

## **1.7. Age-dependent Facial Expressions**

### **i. Facial Expression in Infancy**

The ability to make facial expressions begins in utero. The capacity to make, interpret and recognize faces develops sequentially from infancy through adulthood. For example, Johnson et al. (1991) showed that thirty-minute-old infants can distinguish faces from non-faces, and by one-week, post-natal newborns recognize their mother's face (Bushneil, Sai, and Mullin 1989; Pascalis et al. 1995). At approximately five to six months, infants develop the capacity to distinguish various emotional expressions (Leppänen and Nelson 2006; Walker-Andrews 1997; De Haan and Nelson 1997).

Human infants, like their adult counterparts, exhibit universal facial expressions of emotion. However, these infant facial displays are distinct to their age cohort. **Figure 8** illustrates the distinctive core facial expressions of infants (Donadon, Martin-Santos, and Osório 2019).

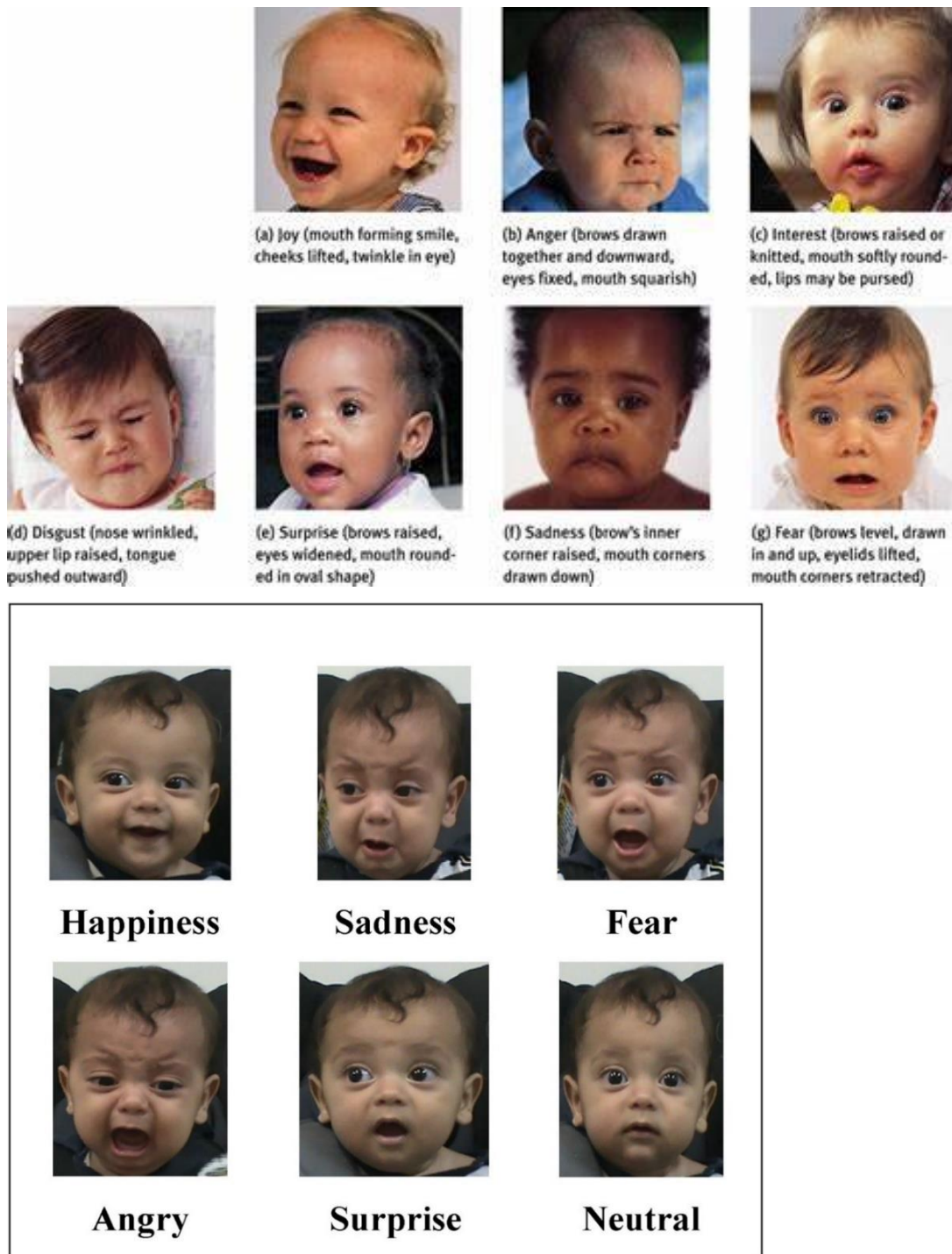


Figure 8. Universal facial expressions of emotions for infants. The distinct facial expressions of infants. Source: Donadon, et.al, (2019) “Baby Faces: Development and Psychometric Study of a Stimuli Set Based on Babies’ Emotions.” *Journal of Neuroscience Methods* 311 (January): 178–85. With permission of the publisher.

ii. **Facial Expression in Childhood**

The capacity to identify faces and discern facial expressions of emotion continues to develop throughout childhood and adolescence. In studies of preschool children, Philippot and Feldman (1990); Boyatzis, Chazan, and Ting (1993) showed that emotion recognition accuracy improved with increasing age. Childrens' ability to recognize different emotions emerged at distinct times. The ability to recognize happiness emerged earlier than other emotions such as anger, fear, and surprise (Gross and Ballif 1991; Smith and Walden 1998). Differential discrimination of emotional categories continues through middle childhood (Gao and Maurer 2009; Herba et al. 2006). Chung and Thomson (1995) showed that facial identity processing skills gradually improve with increased age throughout middle childhood. Gross and Ballif (1991) showed the same improvement with facial emotion recognition. A defining study by Romani-Sponchiado et al. (2022) of children between the ages of six and eleven years revealed a chronological course for which they develop the capacity to recognize facial expressions of emotion. The results indicated that happiness was the first emotion to be recognized, followed by neutral faces and disgust. Next, surprise, anger and fear and, lastly, sadness. Specifically, younger children—the six- to seven-year-old group—presented low accuracy scores, while children close to puberty—the ten- to eleven-year-old group—showed higher levels of accuracy.

Children, like infants, display characteristic age-associated facial expressions. For example, there are common infant “feeding faces” that caregivers learn to recognize. (see **figure 9**) (“The Nine Faces of Weaning, Piccolo’s Family Guide - Piccolo” n.d.).



Figure 9. Common infant feeding faces. Typical infant facial expressions responding to feeding stimuli. Top row corresponds to dislike. Middle row signals flavors (from left to right—sweet/savory, bitter, sour). Bottom row signifies like vs. dislike (from left to right—yes, maybe, no). Reprinted with permission Piccolo Foods Ltd, London, UK.

### iii. Facial Expression in Adolescence

In humans, the facility to recognize a face, or to distinguish a facial expression, develops during adolescence (age eleven to sixteen years) and continues to mature into adulthood (Fuhrmann et al. 2016). Interestingly, the facial expressions signaling courtship (i.e., responding to a flirtatious face) (Haj-Mohamadi, Gillath, and Rosenberg 2021) or other mature social behaviors, do not develop until after puberty. Hormonal stimulation at puberty is required to form the necessary neural networks (between the limbic system and the prefrontal cortex of the brain) to execute these particular forms of facial communication (Page et al. 2022). Neurons within the brain sit dormant for twelve or more years waiting to become biologically relevant.

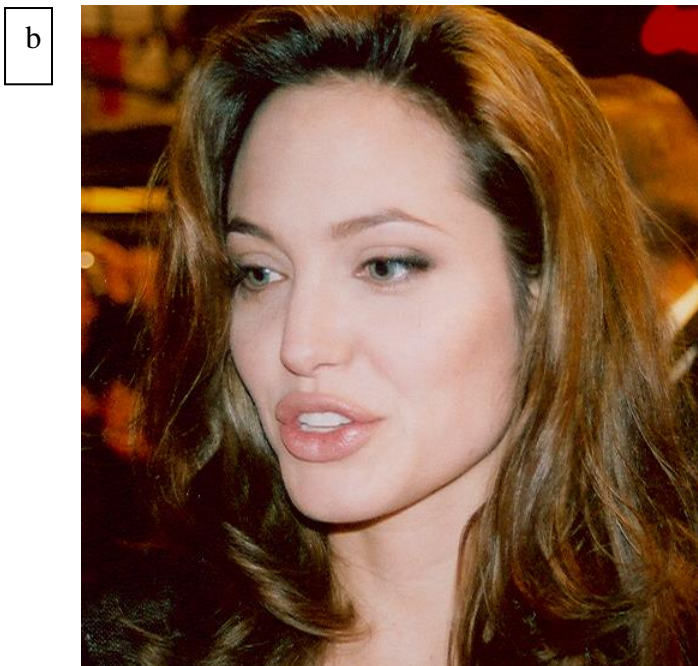
Thus, young girls do not form flirtatious facial gestures and young boys cannot decode such facial signals until they are able to reproduce. Similarly, young boys do not recognize aggressive facial signals (e.g., anger) until they are of sufficient physical stature to respond to an aggressor. Humans cannot decode profound sadness in a conspecific's face until they have had sufficient life experience to comprehend sadness.

Whereas there are ample published studies describing adolescents' capacity to recognize and interpret facial expressions, a literature search revealed a paucity of scientific studies related to the unique facial gestures that comprise Western teen culture. Nonetheless, there are many grey literature references to culturally-specific adolescent facial expressions. A perusal of the social media venue, TikTok, revealed several trending teen facial expressions ("TikTok Selfie Faces Are Everywhere - Vox" n.d.). For example, the "nose-scrunch with a wiggle" signifies "I am going to do a TikTok dance." "Fish lips", a.k.a., "duck face," sucking in the corners of the lips and pouting to look like a fish, was symbolic of ideal feminine facial features and is considered a flirtatious signal of teenage girls **figure 10a** ("TikTok Selfie Faces Are Everywhere - Vox" n.d.). "Duck face" fell out of vogue among teens. It was replaced by the "fish-gape" to signify "I am sexy." "Fish-gape" consisted of a relaxed jaw showing a slight amount of teeth accompanied by half-lidded eyes **figure 10b** ("Duck Face Is Over. The New Selfie Face Is Fish Gape." n.d.; "New Selfie Face - Fish Face - How Take Selfie | Teen Vogue" n.d.). It means "I am sexy like a celebrity."

Figure 6. Adolescent facial expression.



Duck face intended to be an alluring display. Creative Commons Attribution-ShareAlike License 3.0



Angelina Jolie fish-gape pose. Creative Commons Attribution-Share Alike 3.0 license.

#### iv. Facial Expression in Aging

As humans age, there is an age-related decline of facial expression decoding in older adults. Correspondingly, as faces age, the facial expressions of the elderly are more difficult

for an observer to decode. Olderbak et al. (2019) reported that performance in emotion recognition peaked in young people aged fifteen to thirty, with progressive decline after the age of thirty. Also, in a series of experiments, Calder et al. (2003) showed six facial expression pairs to participants between the ages of eighteen and seventy-five years old. They asked the subjects to identify the correct emotions (happy, sad, anger, fear, disgust, or surprise). The experiments demonstrated that with increasing age, participants less accurately recognized facial signals of fear, and to a lesser extent sadness and anger. In a meta-analysis Ruffman et al. (2008) looked at data sets of younger and older adults. Similarly, Ruffman found that older adults were significantly worse than young adults when recognizing facial expressions of anger, happiness, and sadness. Later, Isaacowitz and Stanley (2011) performed another meta-analysis of data sets of young and old adults. Unlike Ruffman, Isaacowitz included data sets containing dynamic facial displays (videos) rather than static photos. The authors concluded, aged individuals had difficulty recognizing sadness, fear, and anger, but not happiness. They suggested that previous reports of diminished recognition of happy faces in older populations could be attributed to short gaze time when static images were used in the experiments. Nonetheless, elderly subjects could compensate because additional cues such as facial movement facilitated the recognition of happy faces. In general, the literature reflected that aging is accompanied by the decline in the ability to correctly recognize many types of emotional facial expressions.

Not only is the recognition of emotional facial expression impaired in the elderly, but also facial communication is disrupted with aged humans because it is difficult for observers, of any age category, to decode the faces of older members of their social group. For example, Malatesta et al. (1987) measured the accuracy of interpreting videos of emotional facial expression in a sample of young, middle-aged, and older women. Not only did they find that older women decoded facial expressions less accurately than younger woman, but also, they reported that decoders of any age better recognized the facial expressions of peers within their corresponding age category. This observation underscored the disadvantage of older adults to successfully communicate. Not only do older adults less accurately recognize facial expressions in faces of all age categories, but also elderly faces are more difficult to interpret by all humans in any age category.

In a variation of Malatesta's study, Borod et al. (2004) measured the accuracy and confidence of younger or older participants to recognize emotional facial expressions in

photographs of young, middle-aged, and older women's faces. They found that the older women rated emotional facial expressions less accurately and with less confidence than younger women.

In a related study, Riediger et al. (2011) evaluated the performance of young, middle-aged, and older observer/raters to judge correctly the emotional facial poses (neutrality, happiness, anger, disgust, fear, and sadness) of young, middle-aged, and older posers. The authors reported that facial expressions of old posed faces were more difficult to interpret than in young posed faces. They observed also that older raters were less accurate in recognizing anger, disgust, fear, and sadness, but did not show significant differences from younger raters for neutrality and happiness.

Ebner, He, and Johnson (2011) investigated how age of faces and emotion expressed in faces affected young and older adults' eye gaze and accuracy of interpretation when viewing facial expressions. Subjects viewed photographs of Caucasian faces of three different age groups, each age-group displaying each of six expressions. The authors measured the subjects' accuracy of facial expression identification. They found both young and older participants were better at identifying expressions in young than older emotional faces. Furthermore, they reported that old faces required longer gaze to improve accuracy of interpretation.

Several possibilities have been discussed in the literature to explain why there is greater difficulty of identifying expressions in older than younger faces. Fölster, Hess, and Werheid (2014) summarized the explanations and social implications: "It may be due to age-related changes in physical features (e.g., wrinkles), that may make it harder to read emotions in older faces. Another interesting possibility is that it may be that prototypes of facial expressions are more likely to be young faces. For example, emotion schemas may be developed in childhood from the relatively young faces of parents, and from TV and movie depictions of facial expressions (where older individuals are underrepresented; Signorielli, 2004). Additionally, perhaps due to age-related changes in flexibility and controllability of muscle tissue, intentional display of facial emotions may become less successful, and displays of unintended blended emotions may become more likely (Radlanski and Wesker 2015).

Accurately identifying expressions is crucial for social interactions and environmental adaptation in everyday life (Carstensen, Gross, & Fung, 1998). The fact that older faces' expressions may be more likely to be misinterpreted than young faces, by both young and older adults, has potentially important implications for many life situations, such as in discussions with doctors, lawyers, and in social interactions in general.”

#### v. **Family-specific Facial Expressions**

Even finer nuance in facial expression was demonstrated by Peleg et al. (2006). The authors reported that *families* have characteristic facial expressions. In an elegant experimental design, Peleg compared the repertoires of facial movements of congenitally blind persons with those of their sighted relatives. The subjects were induced to produce emotional facial expressions of joy, anger, surprise, sadness, disgust, and think-concentrate. The findings revealed unique “signature” facial expressions within families suggesting that facial expressions may be inherited and genetically controlled.

### **1.8. Cross-cultural, Pan-gender, and Omni-generational Facial Displays**

Some facial displays, while not universal, span the globe. One unusual example, the linguo-bilabial fricative appears ubiquitously. It is commonly called "blowing raspberries" in the UK or "the Bronx Cheer" in regions of the United States. There are two variations with separate, complex meanings. If the tongue is inserted between the teeth while expelling air from the oral cavity with the buccinator muscle<sup>9</sup>, then the sound of flatulency is expressed. This is a true linguo-bilabial trill. The meaning of this is derisive, but it is not a totally offensive gesture because of the comedic value of the "fart". Flatulence is fundamentally funny (Spiegel 2013). The second variation, without a tongue extended between the teeth, is designated a bilabial trill. When air is expressed, it produces the “pffffff” sound. This expression in many societies and subcultures signifies exasperation or annoyance.

### **1.9. Codification of Facial Expression: The Facial Action Coding System**

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<sup>9</sup> The buccinator muscle is the cheek muscle that pulls the cheeks inward to hold food within the mouth during feeding, and allows the cheeks to expand during blowing or whistling.

The facial action coding system, FACS, is a scientific tool to catalogue facial movements. The FACS is widely used by psychologists, animators, and marketers of consumer products (Clark et al. 2020) to recognize and label the movement of muscles of the face. This system, was introduced by Ekman and Friesen (1978) and later updated with large contributions by Joseph Hager (Ekman et al. 2002). Using the FACS, human coders break down individual muscle movements into action units (AUs). These AUs describe specific anatomic muscle movements that make up facial expressions. These action units can be modified by duration and intensity, and combined with other units in order to produce descriptions of thousands of unique facial expressions.

Thus, AUs are the basic actions of individual muscles or groups of muscles. The AUs are organized according to five grouping codes: 1) main codes, 2) head movement codes, 3) eye movement codes 4) visibility codes and 5) gross behavior codes. (Refer to **Table 1** in the appendix for a description of the specific codes for facial expressions.)

Intensities of the action units are annotated by appending letters A–E (for minimal-maximal intensity) to the action unit number (e.g., AU 1A is the weakest, almost imperceptible, trace of AU 1, and AU 1E is the strongest intensity possible).

- A - Trace
- B - Slight
- C - Marked or pronounced
- D - Severe or extreme
- E – Maximum

In addition to action units and intensities, the FACS uses “action descriptors” (ADs). ADs are movements that may involve several muscles together such as, AD19, tongue show (various muscles depending on the movement), or AD29 jaw thrust (pterygoids and masseter muscles). In all, FACS 2002 specifies nine action units in the upper face and eighteen in the lower face. Additionally, there are fourteen head positions and movements, nine eye positions and movements, five miscellaneous action units, nine action descriptors, nine gross behaviors, and five visibility codes. ADs are tabulated also in **Table 2**.

s

Supplementary to the above-mentioned codes, there are other modifiers present in FACS codes, for example, directional modifiers such as "R" which represents an action that occurs on the right side of the face and "L" for actions which occur on the left. An action which is unilateral (occurs on only one side of the face) but has no specific side is indicated with a "U" and an action which is unilateral but has a stronger side is indicated with an "A".

Multiple AUs can come together in combinations to form more than the 7,000 combinations of unique facial expressions described by Scherer (1982).

It should be mentioned that manually coding of facial expressions requires extensive training of coders and many man-hours to decode a short segment of facial movement video (sixty to ninety minutes to decode sixty seconds of facial video). Thus, in recent years, there has been an emphasis on computer-coding using artificial intelligence (Hamm et al. 2011).

Further noteworthy is that the Ekman-Friesen-Hager FACS was formulated for Caucasian/European/North Americans and thus has limitations for culture-specific facial expression studies. Subsequently, several additional culture-specific facial expression databases have been introduced. Lyons, Kamachi, and Gyoba (1998) and (Matsumoto (1988) developed sets of Japanese emotional expression stimuli. Yang et al. (2020); Gao et al. (2008); Chen and Yen (2007); Ma et al. (2020) have developed Chinese databases. Kim et al. (2017) developed Korean Facial Expression stimuli set for use in psychological and clinical studies of emotion in Korea. The system for German facial expression coding is MPI (Kaulard et al. 2012).

## **1.10. Summary/Conclusions Chapter I**

In summary, facial communication is critical: it is a principal and essential mode of human communication and socialization. Humans communicate with their faces innately. Facial communication in humans begins in utero, then undergoes extensive development from infancy to old age. This chapter introduced the metaphor that compares facial gestures to a "language" that has a vast "vocabulary," a "dictionary" that codifies the "words", "punctuation", "dialects", "accents", and social rules or "pragmatics". The facial "dictionary" has three types of expressions: 1) purely emotional displays, 2) paralinguistic/co-speech

facial expressions, and 3) facial postures and movements. Facial expressions can be further subdivided into “universal displays”—expressions that are common across cultures, versus “culturally-specific” expressions.

Research has shown that facial expressions are substantially influenced by culture. Several societies constrain emotional facial expressions. Additionally, there are cross-cultural variations in the appearance of basic facial expressions termed “nonverbal accents”. Also, there are facial expression “dialects”—regional variations in facial expressions. Humans better communicate in the facial dialect of peers. Unique facial displays extend to subcultures such as ethnic youth.

In addition to purely emotional facial displays, humans use paralinguistic facial expressions to communicate with peers. Paralinguistic or “co-speech” expressions are non-emotional facial expressions employed in facial communication. These are known as facial *illustrators* that punctuate a sentence or provide emphasis as words are spoken, and facial *emblems*. Facial emblems signal specific messages whose meanings are particular to a group or culture.

Also, there are gender differences in perceiving facial expressions and in expressing facial emotions. The literature reflected that there may be a female advantage in facial communication. Facial communication is disrupted with aged humans, both because the elderly have limited ability to interpret faces of others and because it is difficult for observers, of any age category, to decode the faces of older members of their society. This has broad social implications worth knowing.

Chapter I gives social context to this thesis. The chapter frames the biology and neuroscience for the chapters that follow. The subsequent chapters will describe the various components of the facial communication system and how they work together to enable humans to fulfill complex and essential psychological and sociological tasks such as recognizing one’s self, conceiving of one’s identity, choosing a desirable mate, feeling positive about the faces of friends and aversive to the faces of strangers, recognizing kin,

feeling parental love for one's offspring, feeling romantic love toward one's mate, attributing beauty to faces, and even moderating one's sexual orientation.

## **CHAPTER II – The Structure of the Face**

### **2.0. Introduction**

The anatomy of the face has long been studied. Whereas much has been written about the anatomy of the muscles of facial expression from the medico-surgical perspective, there is a paucity of material from the broader perspective of other disciplines such as psychology, sociology, anthropology, linguistics, or semiotics. The human face is a major part of a person's identity, social and cultural interactions, psychological status, and provides the unique means to communicate on an emotional level (Radlanski 2016). This chapter approaches facial anatomy from a broad humanistic perspective, rather than from the medico-surgical perspective. From this viewpoint, the author addresses the distinctive anatomic features of the muscles of facial expression, and the structure of the human face that allows it to serve its principal role in communication, socialization, and identity. Thus, the aim of this chapter is to describe the anatomical details of the human face in an alternative context that prepares the reader for a humanistic understanding of facial communication and emotional expression.

### **2.1. The Configuration of the Human Face**

The face is constructed of multiple layers (Prendergast 2011). The concavities and convexities of the facial bones and skull comprise the framework upon which the muscles of facial expression overlie. That is, the facial skeleton is the foundation that multiple layers of soft tissue cover. The muscles of facial expression are enclosed in an envelope known as the superficial musculoaponeurotic system (SMAS). It was only in 1976, that Mitz and Peyronie (1976) published their description of this fibrofatty superficial facial fascia. This system, or network of collagen fibers, elastic fibers, and fat cells, connects the mimetic muscles to the overlying dermis (skin) and plays an important functional role in facial expression (Prendergast 2013). Superficial to the plane of the superficial musculoaponeurotic system, there are multiple compartments of superficial fat, called fat pads.

A network of sinuous septae separate the fat pad compartments. The septae converge to form the facial retaining ligaments (Radlanski and Wesker 2015). See **figure 11**.

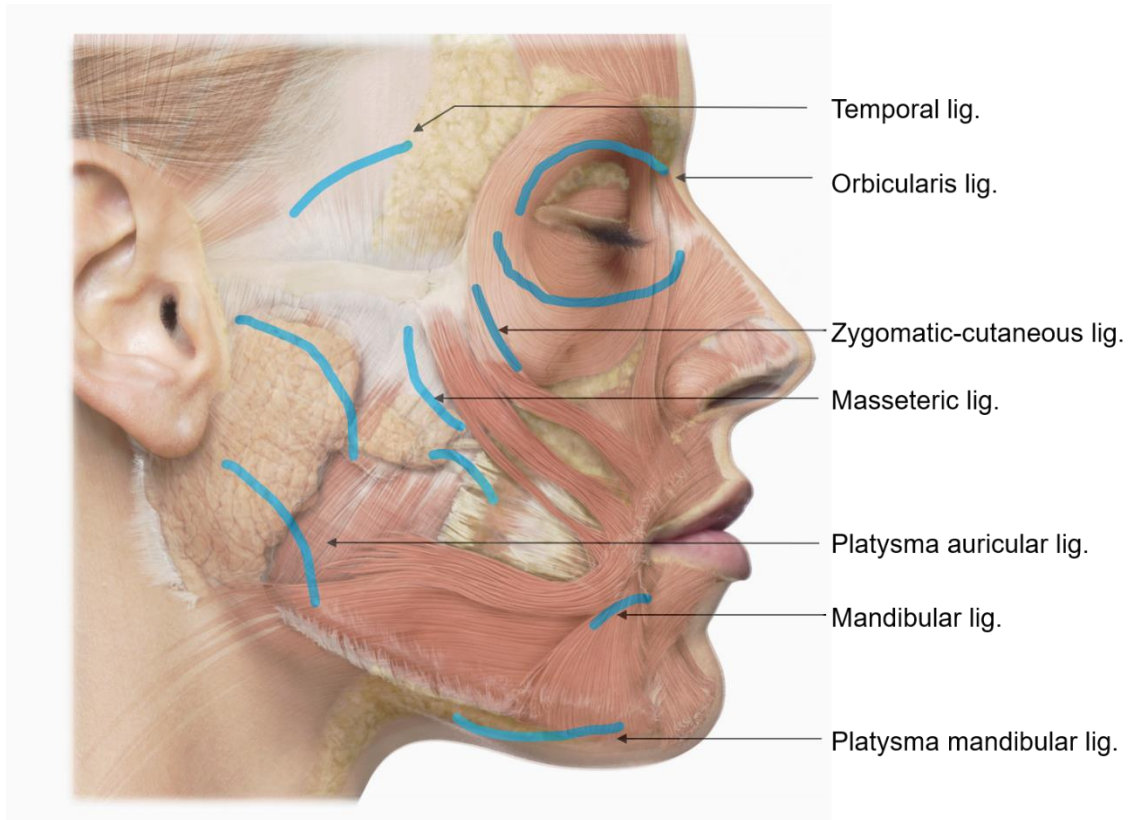


Figure 7. The Facial Retaining Ligaments of the Superficial Musculo Aponeurotic System. Facial retaining ligaments are shown in blue. (Modified from Radlanski & Wesker, 2012, with permission of publisher).

They are named retaining ligaments because at their termini, they insert into the facial skeleton holding the SMAS, the mimetic muscles, the dermis, and other contents to the bony skeleton, like a cargo net. Thus, the face is configured to allow the muscles of facial expression and skin to move fluidly and change shape over the underlying rigid skeleton while still remaining attached. The configuration of the human face constitutes a remarkably well-engineered signal system for communicating: given that the face sits at the highest point of a bipedal creature that stands upright (Hockett 1973).

## 2.2. Anatomic Distinctions of the Muscles of Facial Expression

### i. The General Structure of Skeletal Muscle

Before one can address the distinct anatomical features of the muscles of facial expression, one must appreciate the general structure of skeletal muscles. The muscles of facial expression structurally resemble other skeletal muscle, however there are several

distinctions that make them uniquely-suited to their specialized purpose. These distinctions are noted in the following section.

Like other skeletal muscles, the muscles of facial expression are analogous to the “cables-within-a-cable” design of support cables for suspension bridges: each cable contains hundreds of small cables running in a parallel direction. In the instance of skeletal muscle, there is a hierarchy of cylindrical cables: five in total (**figure 12**). The outermost cylinder constitutes the muscle. Deep<sup>10</sup> to the muscle are a multiplicity of fascicles. Within fascicles are multiple fibers (also termed the muscle cell). Fibers contain a multiplex of fibrils (a.k.a., myofibrils). Finally, within myofibrils are thin strands of contractile protein termed filaments.

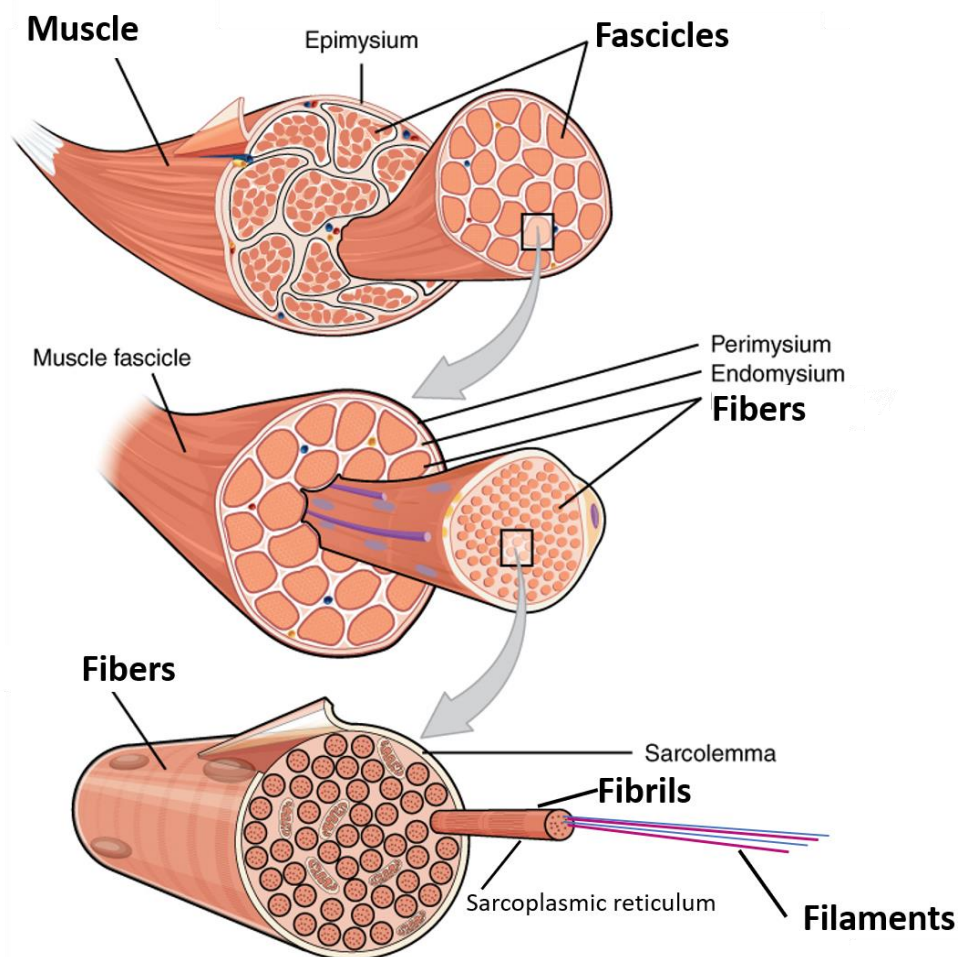


Figure 12. The five components of skeletal muscle. Modified after (Anatomy & Physiology. Biga et. al. 2019). Via Creative Commons 4.0 license.

<sup>10</sup> In anatomic terminology, “deep” or “deep to” means beneath or from the underside of an anatomic structure.

Each “cable” has an overlying connective tissue cover or jacket. Superficial to the muscle, is a connective tissue cover called the epimysium. Surrounding each fascicle is the perimysium. The fibers (the muscle cell) wear two jackets: the endomysium and deep to that, the muscle cell membrane known as the sarcolemma. (Neural motor endplates, the source of stimulation for muscle contraction, rest on the sarcolemma, and the cell nuclei lie just deep to the sarcolemma.) Finally, the fibrils are surrounded by a net-like covering called the sarcoplasmic reticulum. Channels known as t-tubules weave within the sarcoplasmic reticulum.

The features that distinguish the muscles of facial expression from other skeletal muscle are both gross and microscopic anatomical distinctions. The noteworthy distinctions of the muscles of facial expression are of nine types—grouped as “three groups of three”. The first category are purely structural distinctions. The second category constitute connective tissue-related particularities, and the third category relates to unique innervation.

The three *structurally*-related distinctions of muscles of facial expression compared to general skeletal muscle are:

- 1) The mimetic muscles have thinner muscle fibers,
- 2) The bundles vary in fiber diameter, and
- 3) The motor endplates are dispersed.

The three *connective tissue*-related differences are that mimetic muscles have:

- 1) No overlying fascia or epimysium,
- 2) More abundant perimysial collagen, and
- 3) Insert into skin or adjacent muscle rather than attaching to bone.

The three distinctions pertaining to *innervation* are that the muscles of facial expression have:

- 1) No proprioceptors<sup>11</sup>,

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<sup>11</sup> A proprioceptor is a receptor within neurons located within muscles, tendons, and joints that informs the brain about the position of the body and muscle movements.

- 2) A greater proportion of fast twitch fibers and
- 3) Receive polyneuronal innervation.

These nine unique features of the muscles of facial expression are explained in greater detail below.

## **ii. Gross Anatomical Distinctions**

Gross anatomic distinctions are observable in the muscles of facial expression without microscopy. The muscles of facial expression are the only somatic<sup>12</sup> muscles originating in bone or fascia and inserting to skin (excepting the obiculares oculi and oris that have no bony attachments) (Cattaneo and Pavesi 2014). This anatomic configuration is suited to molding the overlying skin to precisely-defined shapes and furrows—what we recognize as emotional expression.

## **iii. Microscopic Anatomical Distinctions**

The microscopic anatomy of the muscles of facial expression also is unique. For example, muscles of facial expression differ from limb muscles in how muscle fibers interrelate with adjacent connective tissue. That is, facial muscles do not have an overlying fascia or epimysium (except for the buccinator) (Cotofana et al. 2016). Additionally, in facial muscles, the perimysial collagen is much more abundant than in limb muscles (Nelson and Blaivasf 1991). This benefits muscle action by providing considerable mobility for the muscle to contract or extend by diminishing friction and allowing smooth movements (Kurose et al. 2006).

Further, on the microscopic level, facial muscle fibers are thinner than fibers found in limb muscles. Their diameter is reported to be in the twenty to fifty  $\mu\text{m}$  range—approximately half that found in limb muscles (Happak et al. 1997). Moreover, within single muscles, there are bundles of varying fiber diameter. These account for distinctive subtlety of movement. That is, the variations in fiber diameter between single fascicles of the same facial

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<sup>12</sup> By “somatic muscle” the author denotes muscle of the external skeleton in contrast to “visceral” muscle that lines the gut or other internal organs.

muscle suggest that each of the single fascicles fulfills a different function. Thus, the muscles of facial expression are not single functional units, but rather are composed of varying subunits with functional specialization (Radlanski and Wesker 2015).

The innervation of the facial muscles is also distinctive. There is a high proportion of myofibers receiving polyneural innervation<sup>13</sup> (Happak et al. 1997). It is thought that the polyneuronal innervation enables the facial muscles to perform the fine adjustments necessary for emotional expression.

Unlike limb muscles, where motor endplates are concentrated in bands in the middle, the motor endplates of facial muscles are dispersed. The significance of this patchy distribution of motor endplates is believed to allow fascicles within a facial muscle to be recruited separately, thereby enabling subtle movements (Happak et al. 1997).

The distribution of Type I and Type II (fast twitch/slow twitch) fibers in the muscles of facial expression is distinctive. That is, the muscles of facial expression contain a much higher proportion of Type II (fast twitch) fibers to Type I (slow twitch) than that found in limb and trunk musculature (Freilinger et al. 1990; Stål et al. 1990; Schwarting et al. 1982). Type I fibers are slow to contract but have a high level of endurance, thus fatigue slowly. Type I fibers predominate in muscles that do not need to contract quickly, such as postural muscles. In contrast, Type II fibers are present in high proportions in muscles that require rapid contraction. This unique attribute may support the production of spontaneous facial expressions comprising quick muscle contractions that last less than a second (so-called “micro expressions”) (Burrows et al. 2014; Schmidt, Cohn, and Tian 2003; Ekman and Friesen 1982).

Yet another interesting distinction is that there are no proprioceptors in the muscles of facial expression (Cobo, et al. 2017). Thus, the muscles of facial expression appear to lack a mechanism to inform the central nervous system about their static and dynamic status. However, this is but an anatomic curiosity. Because of the aforementioned tight association of a muscle of facial expression with the skin, the microreceptors in the skin serve to provide

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<sup>13</sup> Polyneural innervation is when a single muscle is supplied by more than one motor neuron.

sensory feedback. Using the method of microneurography, Johansson et al. (1988) showed that the mechanoreceptors in facial skin avidly respond to facial muscle movement. Additionally, neuroanatomical studies have demonstrated that facial proprioceptive impulses travel via branches of the trigeminal nerve to the central nervous system (Cobo et al. 2017). Whereas this proprioceptive distinction is anatomically trivial, it is highly relevant clinically. That is, face surgeons need to be aware of the communicating nerve branches between the trigeminal nerve and the facial nerve because transecting a nerve will undermine the already restricted proprioceptive capacities of the muscles of facial expression.

In short, the distinctive anatomy of the muscles of facial expression is an archetypal example of form dictating function. The muscles of facial expression perform their function by contracting in recognizable and interpretable patterns<sup>14</sup>. The mechanism is summarized in the following paragraphs:

### **2.3. The Mechanism of Muscle Contraction:**

The function of muscles relates to its structure. Skeletal muscles are comprised of subunits. At the periphery of a typical skeletal muscle there is a connective tissue membrane called fascia. The fascia surrounds the muscles and thickens at the ends, anchoring the muscles to bone. Deep to the external fascia are multiple bundles of muscle called fascicles. The fascicles are covered by a connective tissue layer called epimysium. Within these fascicles are multiple fibers, each containing multiple myofibrils. The myofibrils contain contractile units called sarcomeres. The sarcomeres contain alternating thick and thin protein filaments (actin and myosin). The muscle contracts when the filaments slide past each other. Muscle fibers will contract when they receive chemical signals from the nervous system. This takes place at the neuromuscular junction, and there may be many of these junctions, concentrated at the ends. In facial muscles, they are dispersed so as to enable fine movements (“patchy” movements). At the terminus of an axon at the neuromuscular junction, the terminal end of an axon is a bulbous grape-like structure called a synaptic bulb. The bulb contains neurotransmitter chemicals, such as acetylcholine, that can be released to stimulate receptors on the adjacent motor endplate region of the sarcomere (**figure 13**).

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<sup>14</sup> A cogent description of the general mechanism by which skeletal muscles contract can be found at <https://basicmedicalkey.com/physiology-of-the-muscular-system>.

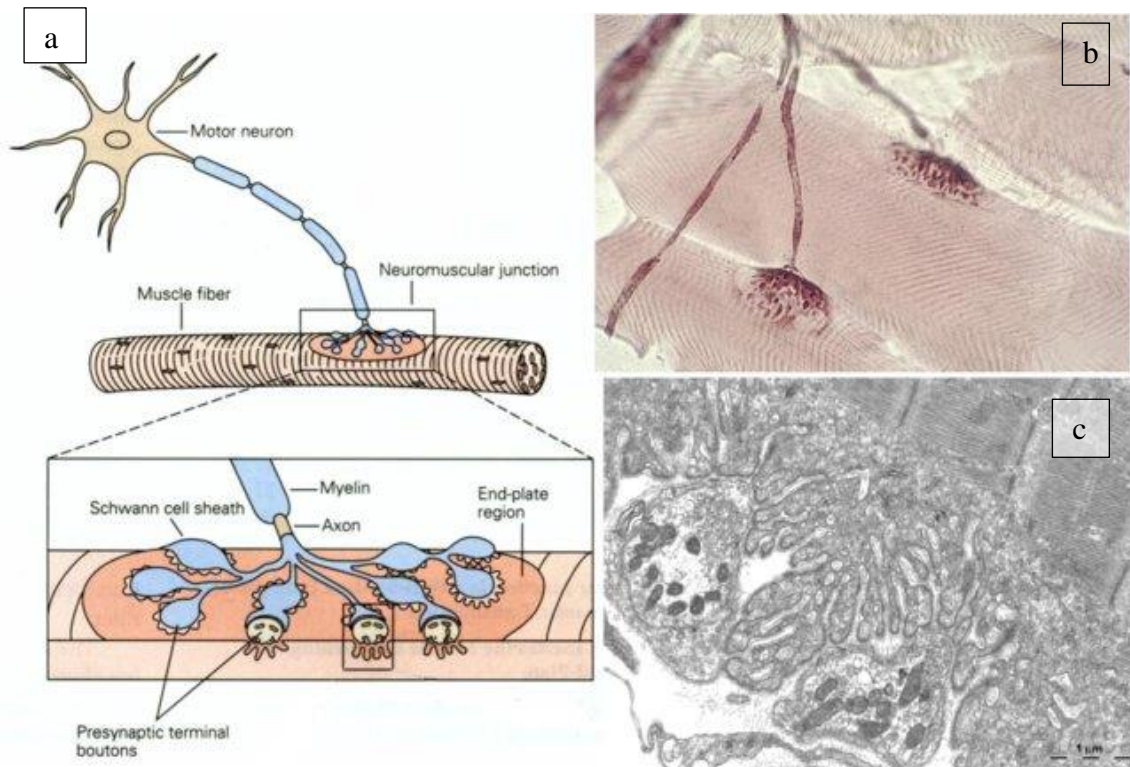


Figure 13. a) Sketch of neuromuscular junctions. The distal end of a motor neuron fiber forms a synapse, or “chemical junction,” with the adjacent muscle fiber. This region, the motor endplate, has a bulbous grape-like structure called a synaptic bulb. Neurotransmitter molecules (acetylcholine, or ACh) are released from the synaptic vesicles and diffuse across the synaptic cleft. There they stimulate receptors in the motor endplate region of the sarcolemma. b) Photomicrograph of skeletal muscle and motor neurons. c) Electron microscopy of motor end plates. From Boncompagni, S. (2012). Severe muscle atrophy due to spinal cord injury can be reversed in complete absence of peripheral nerves. *European Journal of Translational Myology*. 22. 10.4081/ejtm.2012.1799.] via CC license 4.0.

The thick filaments are called myosin. The thin ones are actin. Myosin is anchored in the center of the sarcomere on the m-line<sup>15</sup>, and represents the microscopic appearance of myosin. Actin connects in a band at the end of the sarcomere on what is microscopically called the z-line. When actin filaments slide along the myosin filaments, the sarcomere shortens (**figure 14**).

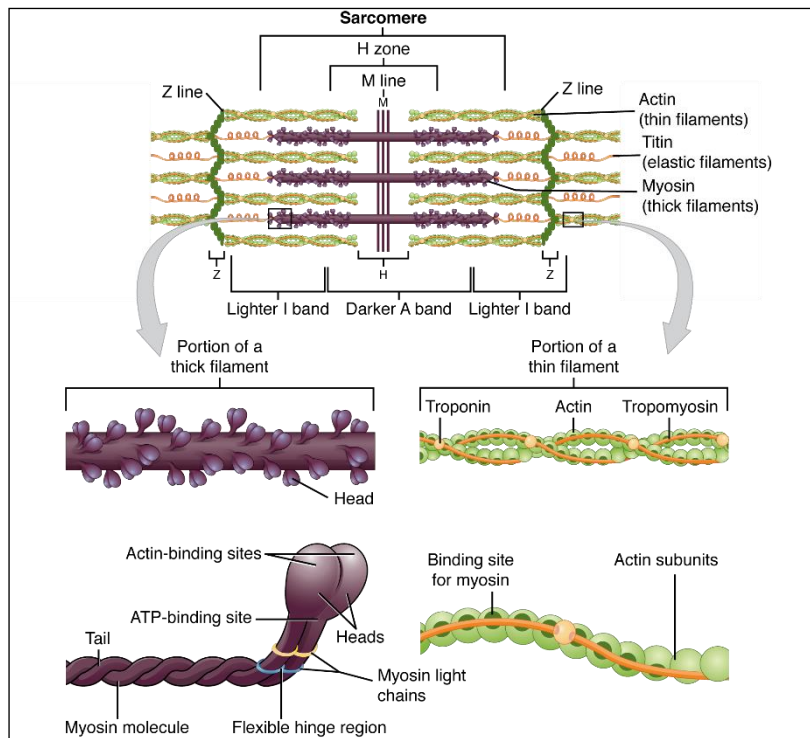


Figure 14. a) The filamentous components of the sarcomere. b) Muscle contraction. From [Anatomy & Physiology. Biga et. al. 2019 via Creative Commons 4.0 license]

When the actin slides over the myosin in the process of muscle contraction, the cross-bridges of the myosin filament grab the actin binding site and pull. This contraction requires chemical energy. ATP (adenosine triphosphate), a chemical compound that supplies energy, attaches to the myosin filament and releases a phosphate, turning into ADP (adenosine diphosphate), enabling the myosin to move. The myosin remains attached to the binding site until another molecule of ATP can supply the energy to release the cross-bridge.

<sup>15</sup> The m-line is in the middle of the sarcomere (the functional unit of a muscle cell).

Muscle contractions are modulated by the actions of calcium. When the muscle is relaxed, regulatory proteins called tropomyosin and troponin cover the binding sites on the thin actin filament. When calcium levels are high enough, calcium binds to the troponin and displaces the tropomyosin to expose the binding sites in the presence of ATP.

Calcium ions are stored in the sarcoplasmic reticulum. To activate them, neurotransmitters are released from the synaptic vesicle, binding to the sarcolemma and depolarizing the membrane. This impulse travels down the t-tubules, opening the calcium channels and releasing calcium ions, which reach the myofibrils (Schmidt and Thews 1977).

## **2.4. The Muscles of Facial Expression and their Actions**

There are forty-four muscles of facial expression: twenty-one paired symmetrically plus two unpaired muscles situated at the midline (procerus and obicularis oris) (Radlanski and Wesker 2015). Embryologically, the muscles of facial expression are derived from the mesoderm of the second pharyngeal arch (Sperber and Sperber 2018). Accordingly, the facial nerve, the nerve of the second arch, supplies all the muscles of facial expression except for the levator palabrae superioris, which is supplied by the oculomotor nerve (cranial nerve III).

### **i. Descriptive Anatomy**

It is instructive to categorize the facial muscles by anatomic region.

- 1) Periauricular—pertaining to the ear
- 2) Orbicular—pertaining to the eye
- 3) Nasal—pertaining to the nose
- 4) Oral—pertaining to the mouth
- 5) Other (Orphans)—unrelated to an anatomic region.

2)

As a mnemonic, consider the muscles of facial expression following a “rule of threes”. Each of the five groups contains three muscles except for the Oral Group that contains ten muscles (three groups of three organized in a hub and spoke pattern around the central orbicularis oris muscle). The accompanying tables illustrate this organizational

scheme (**Tables 3-7**). The tables also show the individual or grouped muscles responsible for specific facial expressions.

**a. The Periauricular Group**

There are three auricular muscles: 1) the anterior, 2) the superior, and 3) the posterior auriculares (**figure 15**).

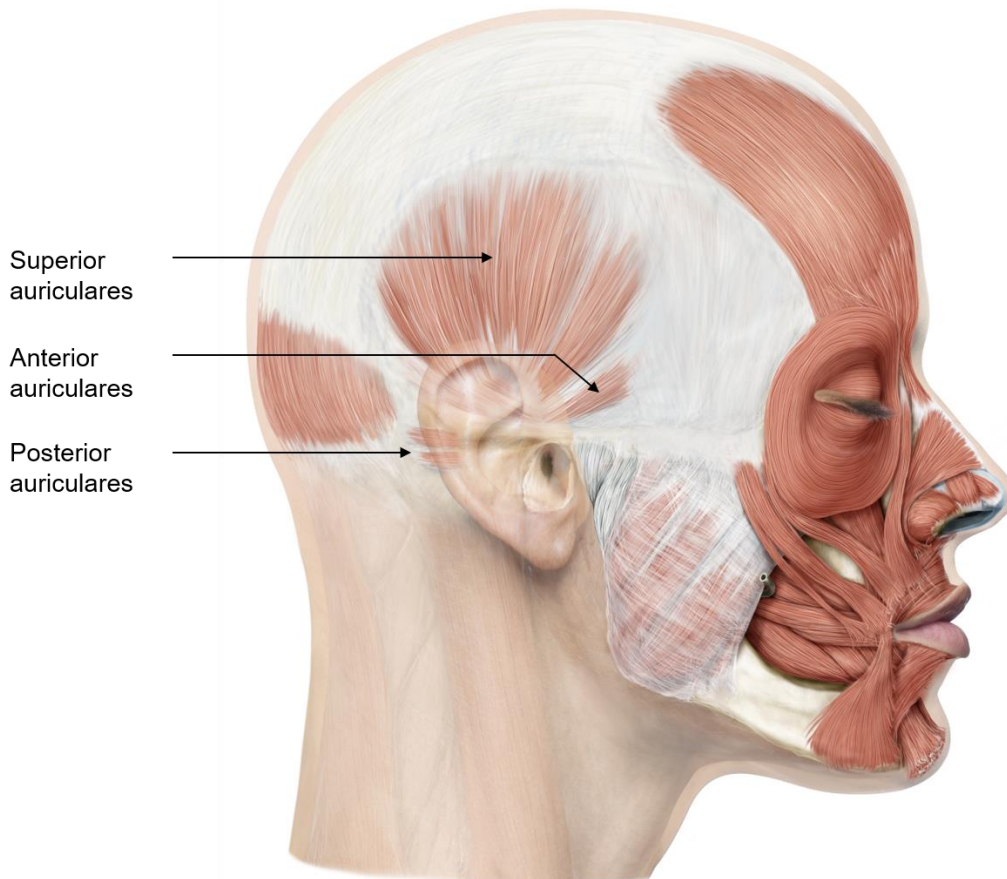


Figure 15. The periauricular muscles. The three auriculares muscles are labeled. (Modified from Radlanski & Wesker 2012 with permission of publisher.)

These muscles are intended to swivel the auricle in the direction of interesting sounds. In humans, they are underdeveloped and do not effectively produce motion of the ears. Nonetheless, the reflex (the auricular blink), is present in normal subjects. In response to a punctate (short and abrupt) sound, the posterior auriculares muscle contracts and the eyes swivel in the direction of the sound. The posterior auricularis muscle serves via reflex to draw our attention to important events. Curiously, the reflex is intensified by positive emotion. Erotica and food seem to be the most potent potentiators of the magnitude of the

postauricular reflex in modern humans (Benning 2018). Thus, in modern humans, although the auriculares muscles are no longer well developed, their primal function remains intact.

The anterior auricular muscle, the smallest of the three auriculares muscles, is thin and fan-shaped. It arises from the lateral edge of the galea aponeurotica<sup>16</sup>, and its fibers converge to insert into a projection on the front of the helix (Standring 2016). The superior auricular muscle, the largest of the three auriculares muscles, is also thin and fan-shaped. Its fibers arise from the galea aponeurotica, and converge to insert by a thin, flattened tendon into the upper part of the superior surface of the auricle. The posterior auricular muscle consists of two or three fleshy fasciculi<sup>17</sup>, which arise by short aponeurotic fibers from the mastoid portion of the temporal bone. They are inserted into the lower part of the cranial surface of the concha. The primary action of the auricularis superior is to draw the auricula of the ear upward and backward. The action of the auricularis anterior is to draw the auricula forward and upward. And, the auricularis posterior serves to draw the auricula backward. The temporal branch of the facial nerve innervates all three auricularis muscles.

## **b. The Orbicular Group**

The Orbicular Group also consists of three muscles: 1) the orbicularis oculi, 2) corrugator supercilii and 3) levator palpebrae superioris (Guyuron and Kinney 2012). The orbicularis oculi muscle is a circumferential muscle that surrounds the eye. It lies within the eyelid and causes the eye to close or blink. At the same time, it compresses the nearby lacrimal gland, aiding the flow of tears over the surface of the eye. The orbicularis oculi is innervated via two plexi<sup>18</sup>: a superior one, formed by the union of the temporal and superior zygomatic branches of CN VII, and an inferior one, usually formed by the union of the inferior zygomatic and superior buccal branches of CN VII (Ouattara et al. 2004). This dual plexi innervation is thought to explain why there is no palpebral (eyelid) deficit when the zygomatic branch is transected during zygomatic fracture fixation or when the temporal branch is transected in frontal or temporal facelifts. Consistent with “the rule of 3s”, the

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<sup>16</sup> Aponeurotica refers to an aponeurosis, a flat sheet or ribbon of tendon-like material that anchors a muscle.

<sup>17</sup> Fasciculi here refer to bundles of muscle fibers.

<sup>18</sup> In neuroanatomy, a plexus (from the Latin term for "braid") is a branching, intertwined network of nerves.

orbicularis oculi muscle is comprised of three concentric sub-portions (pars) 1) the pars orbitalis, 2) *the pars palpebralis* and 3) the pars lacrimalis (**figure 16**).

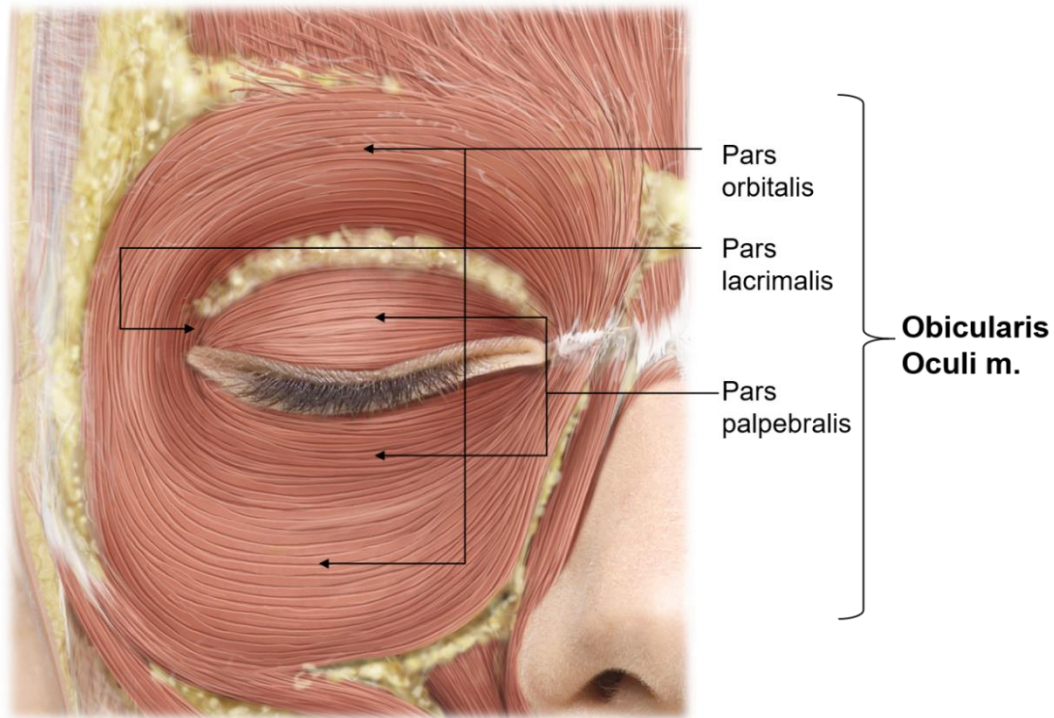


Figure 16. The three parts of the orbicularis oculi. The parts of the orbicularis oculi are labeled here. (Modified from Radlanski & Wesker 2012 with permission of publisher.)

The pars orbitalis of the orbicularis oculi comprises the outermost ring. It closes the eyelids firmly. It is controlled by voluntary action via the facial nerve. This muscle segment arises from the frontal and adjacent maxillary bones. It forms circular fibers that wrap around the eye and blend with various neighboring muscles on all sides of the orbit (Guyuron and Kinney 2012). In the lower lids, this orbital portion of the orbicularis facilitates the forceful closure of the eyelid during squinting and acts in concert with other mimetic muscles during facial expression.

The pars palpebralis comprises a more centric ring of muscle. It closes the eyelids gently in involuntary or reflex blinking. The palpebral part arises from the medial palpebral ligament and adjacent bone. The palpebral fibers cross both the upper and lower eyelids to blend with each other on the lateral side of the eye. It should be noted that the pars palpebralis also reflects the “rule of threes”. That is, the pars palpebralis of the orbicularis oculi muscle is further divided into three concentric segments: the outer preseptal portion, the

more central pretarsal portion, and the most central ciliary (eyelash) portion (a.k.a., muscle of Riolan/gray line) (**figure 17**).

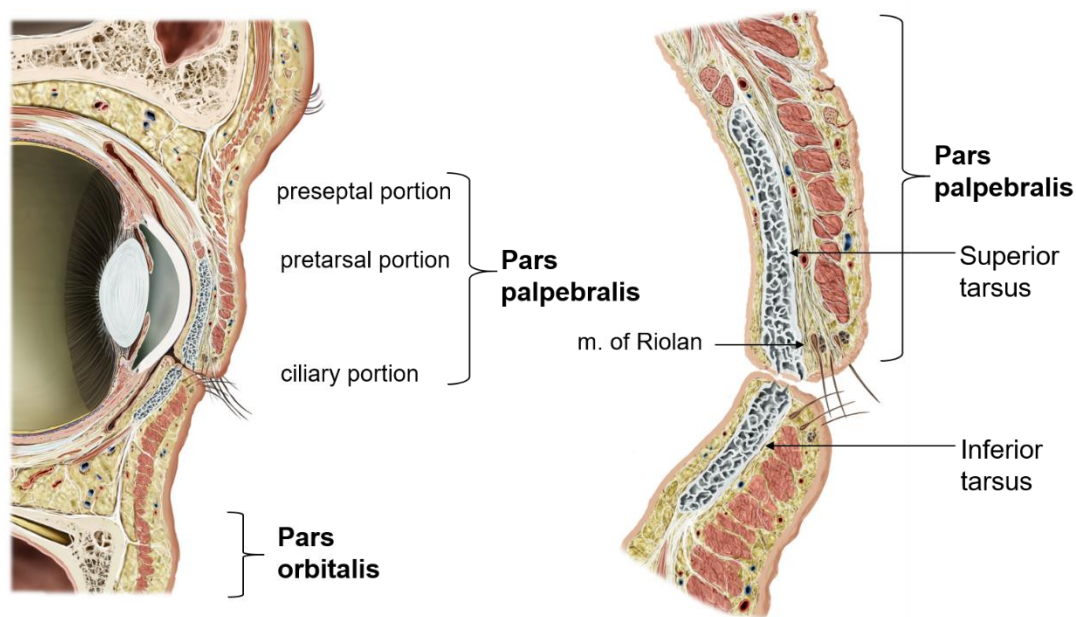


Figure 17. The three portions of the pars palpebralis of the obicularis oculi muscle. The muscle of Riolan (Gray line) is within the ciliary portion of the pars palpebralis. This muscle is the smallest striated muscle in the body. (Modified from Radlanski & Wesker, 2012 with permission of the publisher).

The pre-septal segment extends from the medial canthal tendon to the lateral raphe<sup>19</sup> overlying the lateral canthal tendon. It has superficial origins from the anterior limb of the medial canthal tendon. The deep heads of the muscle, originating from the lacrimal fascia overlying the lacrimal sac, contribute to the lacrimal pump mechanism (Townsend 1989). The pretarsal muscle segments from both the upper and lower eyelids fuse laterally, forming the lateral canthal tendon that inserts onto Whitnall’s orbital tubercle. The medial canthal tendon is composed of two heads. The more prominent superficial head attaches to the anterior lacrimal crest, whereas Horner’s muscle, the smaller, deeper head, attaches to the posterior lacrimal crest. The canaliculi<sup>20</sup> are positioned just beneath the superficial head of the medial canthal tendon (Hester, Codner, and McCord 1996). The third portion of the pars palpebralis, known as the ciliary segment or “muscle of Riolan”, is situated at the lid border. “It is known as the smallest striated muscle in the body” (Guyuron and Kinney 2012).

<sup>19</sup> A raphe (from Greek ραφή, "seam") is a ridge where two anatomic components join together.

<sup>20</sup> The lacrimal canaliculi are the small channels that transport tears.

The pars lacrimalis of the orbicularis oculi compresses the lacrimal sac, which receives tears from the lacrimal ducts. The compression directs the tears into the nasolacrimal duct. The lacrimal part arises from the lacrimal bone and sends fibers to the tarsi of the superior eyelid and blends with fibers on the lateral side of the eye. The remaining muscles of the orbicular triad are the levator palpebrae superioris and the corrugator supercilia (**figure 18**).

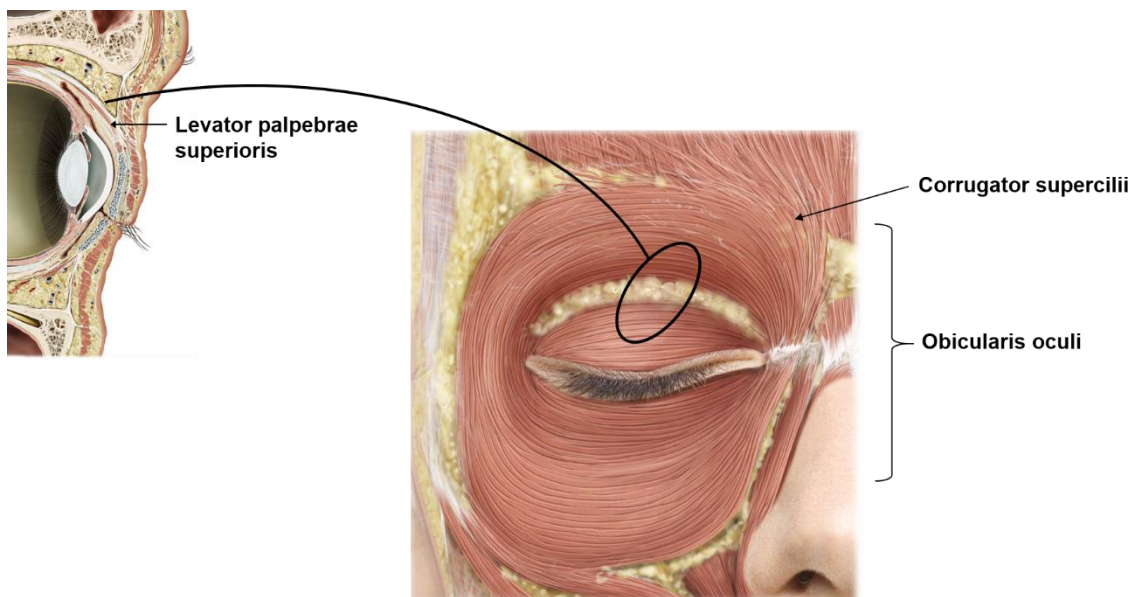


Figure 18. The muscles of the orbicular triad are: the obicularis oculi, the levator palpebrae superioris and the corrugator supercilia. (Modified from Radlanski & Wesker 2012 with permission of publisher.)

The levator palpebrae superioris is the primary muscle involved in raising the superior eyelid. It originates from the lesser wing of the sphenoid bone within the orbit. The muscle then travels anteriorly in the superior orbit until reaching Whitnall's ligament, where it is redirected inferiorly and anteriorly. It continues inferiorly into the eyelid to insert on the anterior surface of the superior tarsal plate (Radlanski and Wesker 2015).

Unlike the other facial muscles, the levator palpebrae superioris does not develop from the second pharyngeal arch. (It receives general somatic efferent innervation—motor fibers from the spinal cord). Thus, as a testament to its embryological origin, it is not innervated by the facial nerve, but instead by the oculomotor nerve (CN III) (Ng et al. 2013).

Curiously, from the perspective of facial communication, the levator palpebrae superioris has a small segment of fibers that are innervated sympathetically (involuntary). This segment is known as the muscle of Müller. These fibers contain  $\alpha_2$ -adrenergic receptors that respond involuntarily to sympathetic stimulation, such as fear or surprise, to retract the superior eyelid, thus communicating a facial expression.

The last muscle of the orbicular group is the corrugator supercilii. The corrugator draws the eyebrow downward and medially. It is called the "frowning" muscle. The corrugator is considered the principal muscle expressing suffering. It also contracts to block sun glare, pulling the eyebrows toward the bridge of the nose, making an awning over the area above the middle corner of the eye and creating typical forehead furrows (Di Petrillo and Guareschi 2014). It originates from the nasal process of the frontal bone and extends obliquely over the supraorbital rim, where it interdigitates with fibers from the frontalis and orbicularis muscles and inserts into the deep surface of the skin (Tan et al. 2011). The temporal branch of the facial nerve supplies the corrugator muscle.

### c. **The Nasal Group**

The Nasal Group is another collection of three muscles: 1) the centrally-located nasalis, 2) the procerus, which opposes it superiorly and 3) the depressor septi nasi, which opposes it inferiorly (**figure 19**) (Standring 2016).

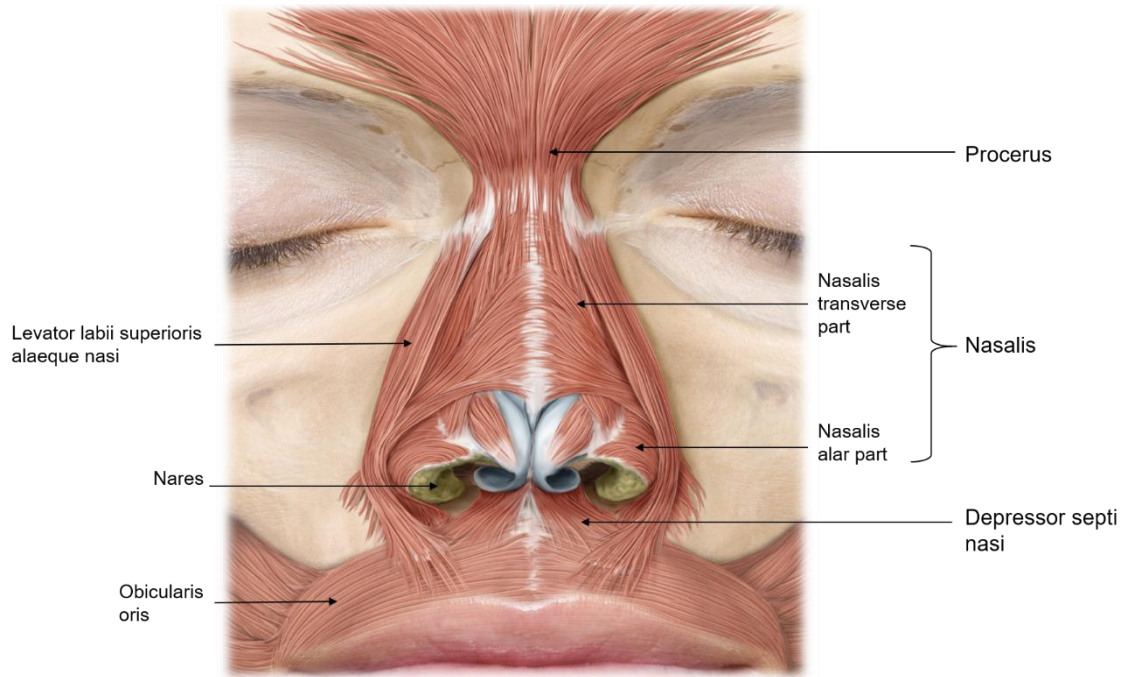


Figure 19. The nasal muscle group (Modified from Radlanski & Wesker 2012 with permission of publisher.)

The nasalis muscle, also known as the nasalis compressor, is located in the nose. It has two parts: the transverse and alar parts. The transverse part arises from the alveolar process of the maxilla, just superior to the incisor teeth on each side, and covers the bridge of the nose. The transverse part merges with its opposite muscle, the procerus, and inserts in an aponeurosis<sup>21</sup> over the nasal bone. The alar part also arises from the alveolar process and inserts to the greater alar cartilage, which is situated between the fibro-fatty tissue of the nostril and the lateral cartilage. The transverse fibers of this muscle compress the nasal alar cartilages to close the nasal openings, while the alar fibers of the muscle draw the nasal alae downward and laterally to help open the external nares. This flexing and retracting within the nose, called nostril flaring, appears during respiratory distress. From the facial communication perspective, the nasalis produces facial expressions, such as anger and lip pursing. The buccal branch of the facial nerve innervates the nasalis muscle.

Superior to the nasalis is the procerus muscle. It is the pyramid-shaped muscle extending from the lower part of the nasal bone to the forehead between the eyebrows. As its Latin name signifies, it is tall and slim. More specifically, it arises from the periosteum of the

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<sup>21</sup> An aponeurosis is a flat sheet or ribbon of tendon-like material that anchors a muscle.

lower portion of the nasal bone, the perichondrium of the upper lateral nasal cartilage, and from the aponeurosis of the transverse nasalis muscle. The medial portions of each procerus muscle often fuse in the midline with its contralateral counterpart, forming a single central belly over the nasal dorsum, which is why it is often identified as a single muscle of facial expression, rather than paired (Dutton 2011). The muscle then passes vertically between the brows and separates into its paired heads, which interdigitate with the medial border of the frontalis muscle. At its most distal extent, the procerus muscle inserts onto the skin over the lower forehead, between the frontalis muscles. Contraction of the procerus muscle draws the medial angle of the brow downward and produces transverse wrinkles over the nasal bridge. Its role in facial communication conveys disdain. It contributes with the adjacent corrugator supercillii, to express sadness.

The procerus, like the aforementioned orbicularis oculi, receives dual innervation from branches of the facial nerve. A nerve from the buccal branch supplies the procerus muscle (Hwang et al. 2006), after having received a contribution from the zygomatic branch (Caminer, Newman, and Boyd 2006).

The depressor septi nasi arises from the incisive fossa of the maxilla. Its fibers insert into the nasal septum and back part of the alar portion of the nasalis muscle. The depressor septi is a direct antagonist of the other muscles of the nose, drawing the ala of the nose downward, and thereby constricting the aperture of the nares. The contraction of the depressor septi shortens the upper lip during smiling. It is more involved with speech than facial expression. The depressor septi receives innervation via the buccal branches of the facial nerve.

#### **d. The Oral Group**

The oral group contains ten muscles (three groups of three organized in a hub and spoke-like pattern around the central *orbicularis oris* muscle) (**figure 20**).

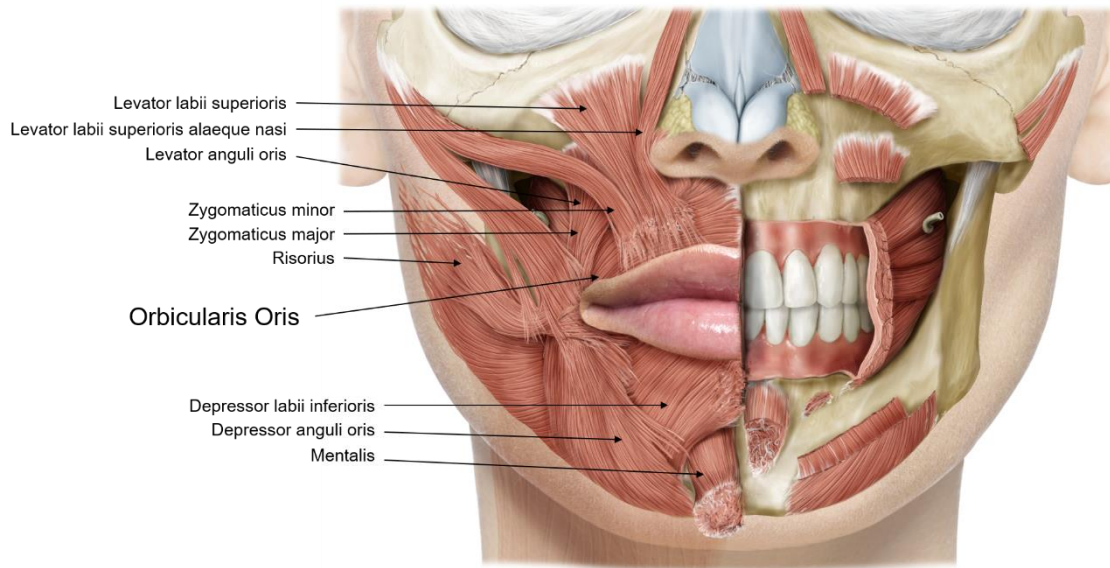


Figure 20. The oral muscle group. (Modified from Radlanski & Wesker 2021 with permission of the publisher).

The orbicularis oris is a circle-shaped muscle arranged in concentric rings around the mouth (Nicolau 1983). The primary actions of the orbicularis oris are to close the mouth and pucker the lips. The latter activity earns the orbicularis oris muscle the appellation “the kissing muscle”. This muscle consists of two well-defined parts—deep and superficial. The superficial portion is subdivided further into two muscle fiber bundles (thus, the orbicularis oris muscle is yet another representation of the “rule of threes”). The distinction coincides with function. The deep portion is sphincter-like and relates to feeding. The superficial part relates to facial expression and the precise movements of the lips needed in speech. The deep orbicularis oris muscle originates from the modiolus (the nexus at the corners of the mouth where seven muscles join the orbicularis oris) and inserts into the contralateral modiolus. That is, its continuous horizontal fibers pass from one oral commissure to the other. This deep portion abuts the inner mucosal surface. When the fibers shorten to close the lips, the margins flatten in a scissor-like motion to seal the angles of the mouth.

The superficial orbicularis oris has an upper and lower bundle. The lower (nasolabial) bundle derives from fibers of the depressor anguli oris. The superficial fibers then extend from the commissures toward the midline of the upper lip. The shorter fibers of this bundle

do not cross the midline, but rather extend to the ipsilateral philtral ridge<sup>22</sup>, where they insert into the skin. The longer fibers of the lower bundle extend beyond the midline and insert into the skin of the contralateral philtral ridge. The upper (nasal) bundle represents the common insertion of the fibers of the zygomaticus major and minor, levator labii superioris, levator labii superioris alaeque nasi, and transverse portion of the nasalis. These fibers insert into the anterior nasal spine, the septo-premaxillary ligament (Latham 1970), and the nostril sill passing deep to the alar base.

The orbicularis oris muscle receives innervation from three separate branches of the facial nerve: 1) the superior aspects (upper lip) come via the zygomatic branch. 2) the labial angular regions are supplied by the buccal branches, and 3) the lower lip is supplied via the marginal mandibular branches (Hwang et al. 2006).

Consistent with the “rule of threes”, two triads of muscles radiate superiorly from the centrally-positioned orbicularis oris muscle. These muscles elevate the lip. They are named “the levators” and the “smile muscles” respectively. The third group of three muscles are inferior to the lip and depress the lip. These are termed, “the depressors”.

The “levators” are comprised of: levator labii superioris, levator labii superioris alaeque nasi, and the levator anguli oris.

The levator labii superioris muscle is situated lateral to the nose. Its primary function is in raising the upper lip. It’s role in facial expression is to express distaste or retching (vomiting). The levator labii superioris originates near the medial aspect of the infraorbital rim and inserts into the upper lip. The buccal branch of the facial nerve (cranial nerve VII), along with some fibers from the zygomatic branch, innervate the levator labii superioris (Bloom and Appaji 2019). A hyperactive levator labii superioris muscle results in an unaesthetic gingival display known as a “gummy smile”. This condition, if it deems to be too serious for the patient, may be treated surgically by means of a LeFort I osteotomy, by myotomy with lip repositioning, by recurrent injections of botulinum toxin-A or by infiltrating hyaluronic acid.

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<sup>22</sup> The philtrum (Greek: φίλτρον = love charm) is a vertical groove in the midline portion of the upper lip bordered by two lateral ridges or pillars. (Ancient Greeks considered the philtrum to be one of the most erogenous spots on the human body.)

The second muscle of the “levator triad” is the levator labii superioris alaeque nasi. The levator labii superioris alaeque nasi (LLSAN) has the distinction of having the longest anatomic name in the medical dictionary. Consequently, it has come to be known by its nickname, “The Elvis” muscle—the iconic unilateral lip curl or snarl, made famous by the King of Rock and Roll, Elvis Presley. This muscle, situated immediately adjacent to the nose, raises the upper lip and wrinkles the nose when it contracts. This muscle’s nickname is but an interesting sidelight. The levator labii superioris alaeque nasi is reported to serve an indispensable function for human survival: This muscle (in coordination with its neighbor, the levator labii superioris,) functions to protect the body from contamination, poisoning, or illness resulting from food (Thulkar, Kehri, and Ingle 2019). Humans and animals use the levator labii superioris alaeque nasi muscles to reject or detect unpleasant odors and to open the mouth to expel the unpalatable foods. This essential function of this muscle of facial expression is underscored by research demonstrating that infants as early as two days ex-utero exhibit this muscle activity in response to unpalatable stimuli (Steiner 1973). The LLSAN receives its innervation from the buccal and zygomatic branches of the facial nerve.

The last muscle comprising the levator triad is the levator anguli oris. The levator anguli oris is the most lateral of the three levator muscles. It originates at the anterior surface of maxilla below the infraorbital foramen. Its fibers insert into the corner of the mouth. The levator anguli oris elevates the corner of the mouth participating in the complex process of smiling. The levator anguli oris receives its innervation from the buccal branch of the facial nerve (Chapman et al. 2017). Each muscle has a dedicated function. The levator labii superioris alaeque nasi, the muscle closest to the nose, responds to pathogens by wrinkling the nose. The laterally adjacent levator labii superioris responds to toxins by elevating the lip in a manner to assist the ejection of the offending stimulus once it is tasted. The levator anguli oris likewise responds to gustatory stimuli. It raises the corner of the mouth to smile in response to positive smell or taste. Thus, without language, humans both recognize a safe food supply and signal it to other humans via facial expression. The levator labii superioris alaeque nasi signals pathogens or disease with the facial display we recognize as “disgust”. The levator labii superioris signals poison with the facial expression we recognize as “distaste” and the levator anguli oris signals palatability with a facial display that characterizes pleasure. The communication function extends beyond response to active stimuli. Humans form the expressions of distaste, disgust and palatability when thinking

about past stimuli. Moreover, humans make the “disgust” display not only for immediate, feeding-related stimuli, but also in response to moral disgust such as contemplating the concept of dishonesty, or death, disease, or culturally-unacceptable sex acts (Chapman et al. 2009; Cannon, Schnall, and White 2011; Whitton et al. 2014).

The second cluster of three muscles that radiate superiorly from the orbicularis oris are collectively known as the “smile muscles”. Individually, they are the risorius, the zygomaticus major and the zygomaticus minor.

The risorius is the most laterally positioned of the three “smile” muscles. The risorius is generally believed to arise in the fascia near the parotid gland and masseter muscle and inserts into the skin at the angle of the mouth (Bae et al. 2014). It retracts the corner of the mouth laterally to produce a characteristic wide smile known as a “false” or “insincere” smile. A “true” smile (also known as the Duchenne smile) recruits the neighboring smile muscles, the zygomaticus major and minor, that draw the corners of the mouth upward to produce wrinkles around the eyes, which we interpret as an expression of warmth and sincerity (**figure 21**). The risorius muscle, like its companion mimic<sup>23</sup> muscles is innervated by the facial nerve. The buccal branch of the facial nerve supplies the risorius. There is considerable variation in prevalence of this muscle. In a study of fifty North American cadavers, Pessa et.al. (1998) observed the risorius muscle in 6% of cadavers. Farahvash et al. (2010) reported a prevalence of 30.8% in Persian cadavers. In contrast, Bae et al. (2014) observed a 98% prevalence of the risorius in a Korean population.

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<sup>23</sup> “Mimic” muscles is alternative terminology for “muscles of facial expression”. The terms are used interchangeably in this thesis.

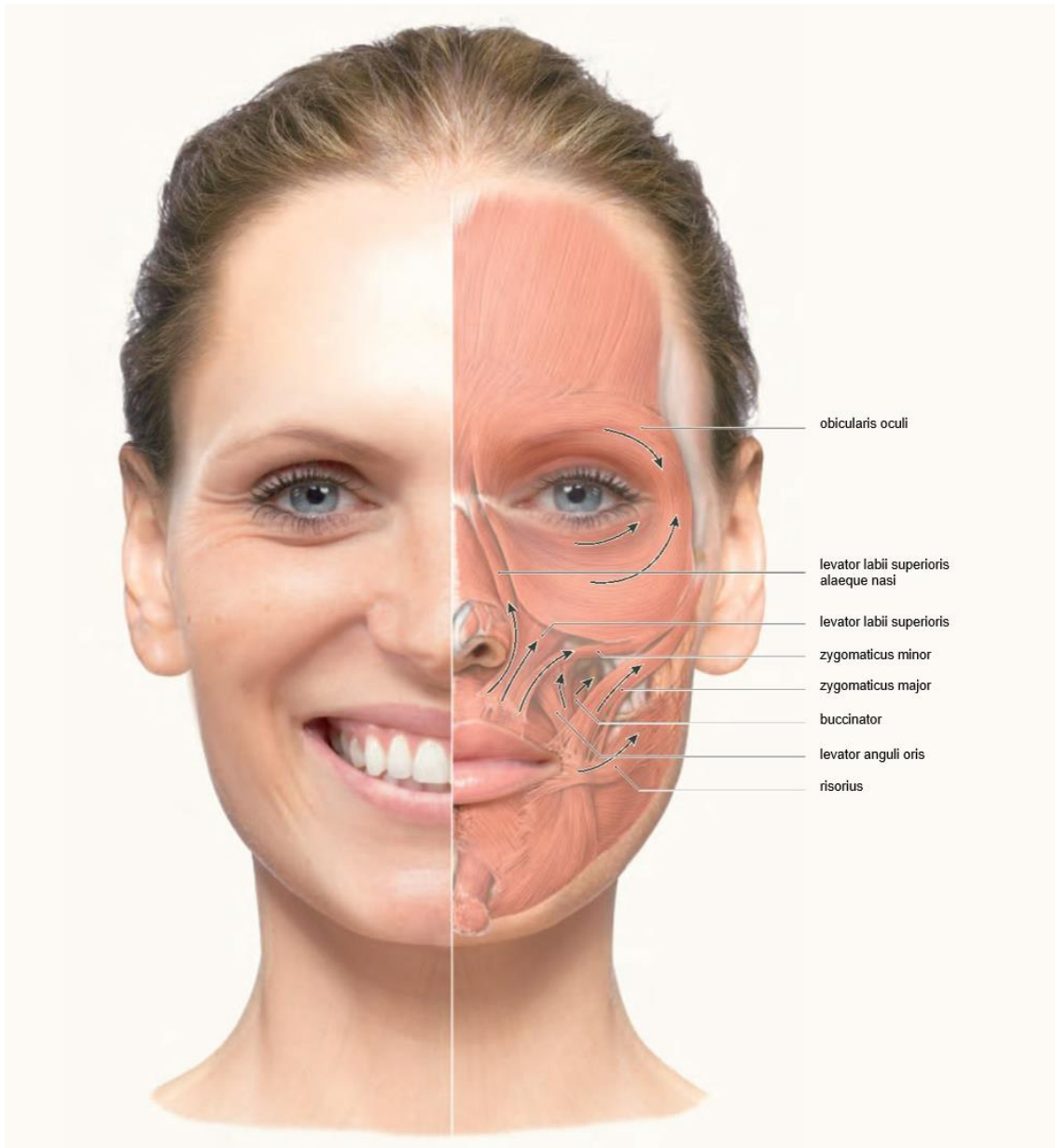


Figure 21. A “true” smile (the Duchenne smile). (Modified from Radlanski & Wesker 2021 with permission of publisher.)

The companion smile muscles to the risorius are the zygomaticus major and zygomaticus minor muscles. Apparent from their names, these muscles both originate at the zygomatic process of the maxillary bone. The zygomaticus major is the larger of these two muscles. Its origin, considerably lateral to its smaller neighbor, is on the side of the face. It inserts into the corner of the mouth. Thus, the zygomaticus major draws the upper lip outward and superiorly forming a smile. This muscle is one of the largest facial muscles and can become fatigued from overuse. This is why people returning from a joyous event, such as

a wedding, report that their face hurts. The zygomaticus major receives its innervation from the zygomatic and buccal branches of the facial nerve.

Originating medial to the zygomaticus major is the zygomaticus minor. It inserts into the lateral part of the upper lip. Notably, its insertion is medial to the zygomaticus major. The action of the zygomaticus minor is to draw the upper lip predominantly superiorly and only slightly outward. It receives its innervation from the buccal and zygomatic branches of the facial nerve (Cobo et al. 2017). Although the zygomaticus minor is categorized as a “smile” muscle, it does not consistently express a smile. Only when the zygomaticus minor contracts in tandem with the zygomaticus major, does it participate in the expression of smiling. Without the contribution of the zygomaticus major and when opposed by the depressor muscles inferiorly, the zygomaticus minor conveys sadness or pain. This is represented by an elevated upper lip with a bulge of the nasolabial fold. The opposing depressor muscles accounts for the subtle downturn of the corners of the mouth (**figure 22**).

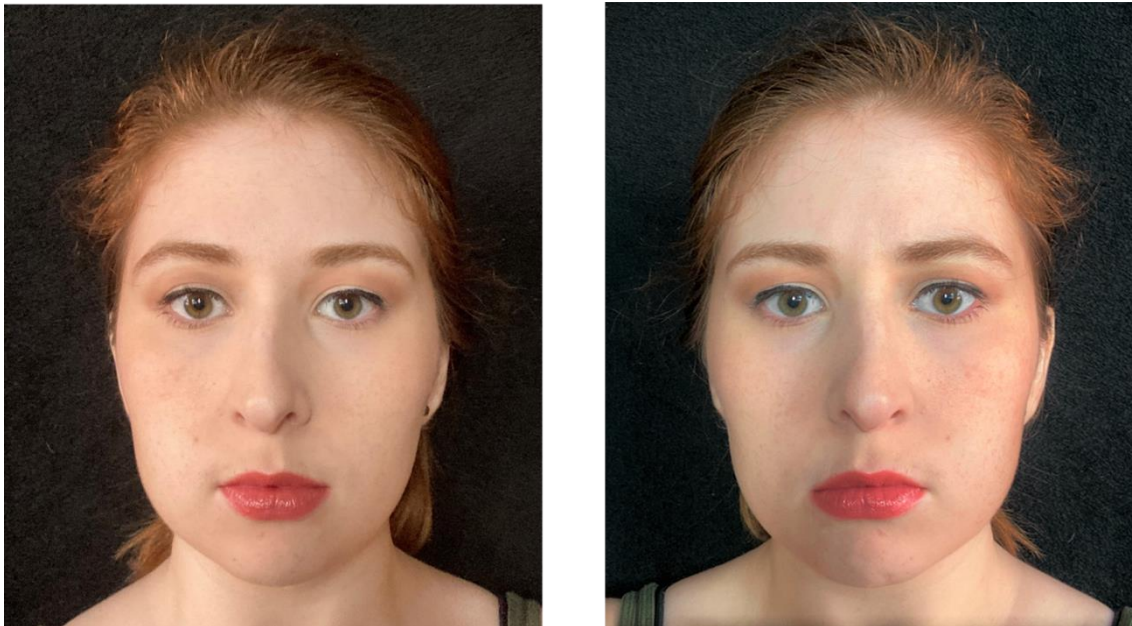


Figure 22. The zygomaticus minor expressing sadness or pain (right illustration).

The third and final group of perioral muscles radiate from the orbicularis oris inferiorly. They are known collectively as the depressor muscles. They are the depressor anguli oris, the depressor labii inferioris and the mentalis. These muscles are easily

remembered by their Latin names: “the muscle that depresses the angle of the mouth”, “the muscle that depresses the lower lip”, and “the muscle of the chin”, respectively.

The depressor anguli oris is a triangular muscle with a broad base. It originates at the inferior border of the mandible and extends superior-laterally to insert into the skin at the corner of the mouth. Its fibers run in diverse directions, but its principal function is to draw the angle of the mouth downward and laterally during opening, forming the expression of sadness (Hur, Kim, and Lee 2014; Kim et al. 2016). The depressor anguli oris receives its innervation from the marginal mandibular branch of the facial nerve.

Deep to the depressor anguli oris is a small quadrilateral muscle, the depressor labii inferioris. This muscle originates at the inferior border of the mandible (the oblique line), and extends superiorly and medially to insert into the skin and mucosa of the lower lip and into fibers of the obicularis oris (Prendergast, Facial Anatomy. In Advanced Surgical Facial Rejuvenation). It is supplied by the marginal mandibular branch of the facial nerve. The depressor labii inferioris depresses, draws laterally, and everts the lower lip. It contributes to the expressions of sorrow, doubt and irony (Standring 2016).

The mentalis muscle is the third and final muscle of the depressor group. The fibers arise from the incisive fossa of the mandible and descend to insert to the skin of the chin. The mentalis acts on the lower lip, wrinkling the skin of the chin. It helps to protrude and evert the lower lip in drinking and also in expressing doubt or disdain. The mentalis is innervated by the mandibular branch of the facial nerve (Standring 2016).

**e. The Orphan/Other Group**

The fifth and concluding group of muscles of facial expression fall within the “Orphan” category. These are the three mimetic muscles that bear no association to a localized anatomic region. They are the platysma, the occipital-frontalis and the buccinator muscles (**figure 23**).

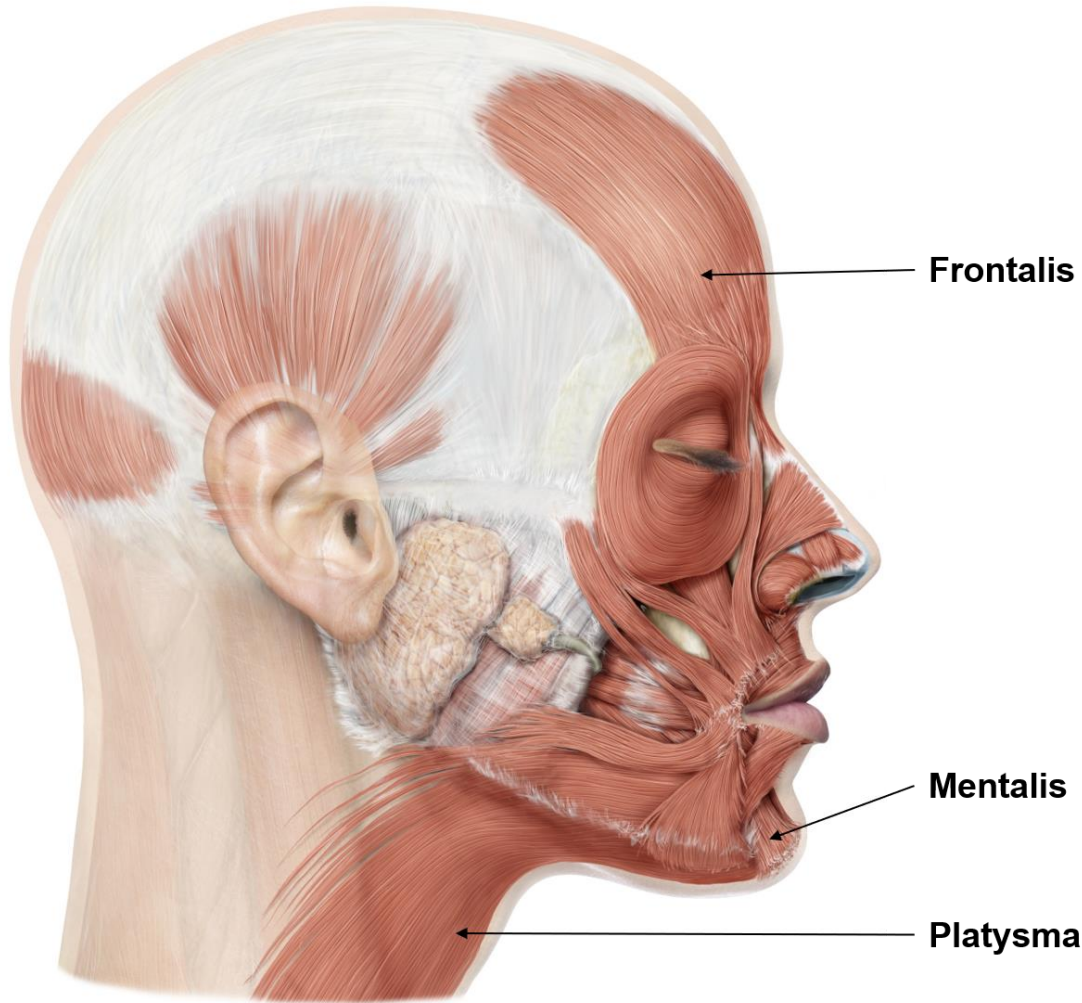


Figure 23. The three muscles not classified by region. (Modified from Radlanski & Wesker 2012 with permission of publisher.)

The platysma muscle is described by its Latin derivation, meaning broad and flat as in “plateau”. It originates in the fascia of the superior chest and inserts into the mandible and fascia of the lower face. The platysma is supplied by the cervical branches of the facial nerve. The platysma draws the lower lip laterally and wrinkles the skin of the neck. It creates the facial expression of horror, surprise or disgust.

The second muscle in the “Other” category is the occipitofrontalis. It has a paired anterior and a paired posterior component. The anterior and posterior parts are connected by an aponeurosis. The anterior belly of the occipitofrontalis muscle is called the frontalis and is the main elevator of the brows. It arises from the epicranial aponeurosis and passes forward over the forehead to insert into fibers of the orbicularis oculi, corrugators, and dermis over the brows. Contraction raises the eyebrows and causes horizontal furrows over the forehead. The

frontalis receives innervation from the temporal branch of the facial nerve. The posterior bellies are termed the occipital portions. Each occipital part (occipitalis) arises by tendinous fibers from the lateral two-thirds of the highest nuchal line<sup>24</sup> of the occipital bone and the adjacent region of the mastoid part of the temporal bone. It extends forwards to join the aponeurosis. The occipital part of occipitofrontalis is supplied by the posterior auricular branch of the facial nerve. The overall action of this muscle complex is to raise the eyebrows and the skin over the root of the nose creating the expressions of surprise or horror. Additionally, the frontal parts draw the scalp forward causing the forehead to wrinkle as in the expressions of worry or concentration (Standring 2016).

The last mimetic muscle in this category is the buccinator. The buccinator is a quadrilateral muscle that forms the lateral wall of the oral cavity. This muscle originates from three locations: the alveolar process of the maxilla superiorly, the alveolar process of the mandible inferiorly, plus a fibrous structure called the pterygomandibular raphe which resides in the middle. The superior-most fibers from the maxilla and pterygomandibular raphe traverse obliquely downward to insert into the lower lip while the inferior-most fibers originating in the mandible and pterygomandibular raphe travel obliquely upward to insert into the upper lip, thus creating an intersecting pattern at the oral commissures. The muscle pulls each commissure laterally and compresses the cheek. This muscle assists in mastication and nursing in infants. It also forcibly expels air if you are a glass blower or trumpeter. Its facial expressions are limited to the display of exasperation or “blowing raspberries” (**figure 24**). The buccinator receives innervation from the buccal branch of the facial nerve but there may be anastomoses with the neighboring zygomatic or mandibular branches.

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<sup>24</sup> The nuchal line is a bony prominence on the skull.



Figure 24. Jazz trumpeter Dizzy Gillespie noted for bilaterally stretched buccinator muscles. The central cheek indentation is a taut risorius muscle. Photo public domain creative commons license <http://it.wikipedia.org/wiki/Immagine:Dizzygillespie88.jpg> { {PD-user-w|it|wikipedia|Pino alpino} }

## 2.5. Innervation of the Muscles of Facial Expression

### i. Anatomy of the Facial Nerve

The muscles of facial expression contract in response to stimulation via selective fibers of the facial nerve (CN VII). The facial nerve is among the most complex of the cranial nerves (Standring 2016; Radlanski and Wesker 2015). This intricate nerve contains four types of fibers (innervation)—each type with a different task and unique route as they traverse the skull. Facial communication involves only one of these fiber types: the “special visceral efferent” (SVE) type. Thus, the SVE component of the facial nerve is the focus of this manuscript. (The other three component fibers of the facial nerve are: 1) the “general visceral efferent component (GVE)”, 2) the “special visceral afferent (SVA)” component, and 3) the

“general somatic afferent (GSA)” fibers). **Figure 25** illustrates the special visceral efferent system.

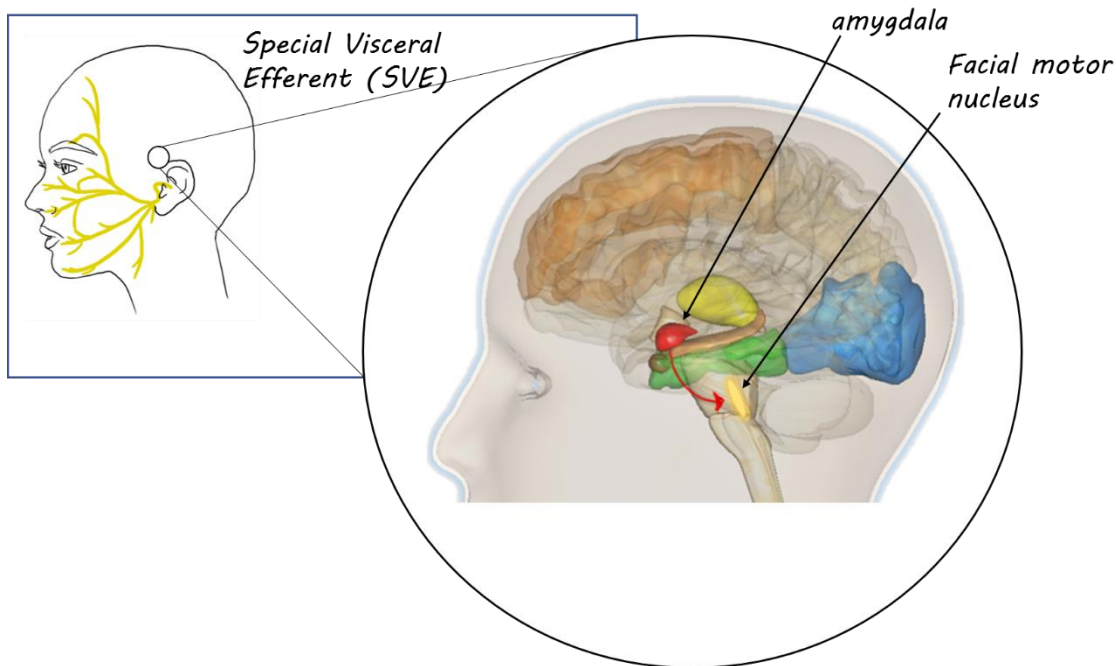


Figure 8 Special visceral efferent innervation. Source: author original.

The cell bodies of each of the four types of innervation are located in the brainstem (Dulak and Naqvi 2019). But each individual type is clustered in distinct regions known as nuclei (or ganglia). The cell bodies of the SVE (the nerve fibers that innervate the muscles of facial expression) are located in the brainstem within the motor nucleus of the facial nerve. (To underscore the fundamental importance of facial communication in humans, the facial motor nucleus is the largest of the cranial nerve motor nuclei (Cattaneo and Pavesi 2014).)

The cell bodies of the other types of CN VII fibers also are located in the brainstem—the general visceral efferent, in the region known as the superior salivatory nucleus. The cell bodies of the general somatic afferent and the special visceral afferent neurons are found in the geniculate ganglion located deep within the petrous portion of the temporal bone.

From the brainstem, all four components enter the skull together through the acoustic meatus. Their fibers remain anatomically separate and distinct. Although traveling the same course, the large special visceral efferent component, special visceral afferent, is separate from the other components that group together. The three grouped components are named the

nervous intermedius. The solitary special visceral afferent component is designated the facial nerve proper. After entering the acoustic meatus, all four components continue to course together within a bony tunnel called the facial canal. Within the facial canal, the components take a sharp turn, or genu. (The aforementioned geniculate ganglion resides in this portion of the facial canal, deriving its name from “genu”). Distal to the geniculate ganglion, the components of the facial nerve begin to diverge taking various courses passing through the temporal bone.

I address here only the course of the special visceral efferent component of the facial nerve because it is most relevant to facial expression because these fibers innervate the muscles of facial expression. Before leaving the temporal bone, the large special visceral afferent component gives a branch to the stapedius muscle (muscle that stabilizes the stapes bone in the inner ear). The remaining fibers then exit the skull through the stylomastoid foramen. Before traversing the parotid gland, the nerve distributes branches to two muscles not involved in facial expression—namely the posterior belly of the digastric muscle and the stylohyoid muscle. Within the parotid gland the facial nerve branches like a tree into five terminal branches innervating the muscles of facial expression (**Figure 26**). These branches are readily remembered through an assortment of popular acronyms. They are from superior to inferior: temporal branch, zygomatic branch, buccal branch, marginal mandibular branch and the cervical (a.k.a., superficial cervical) branch.

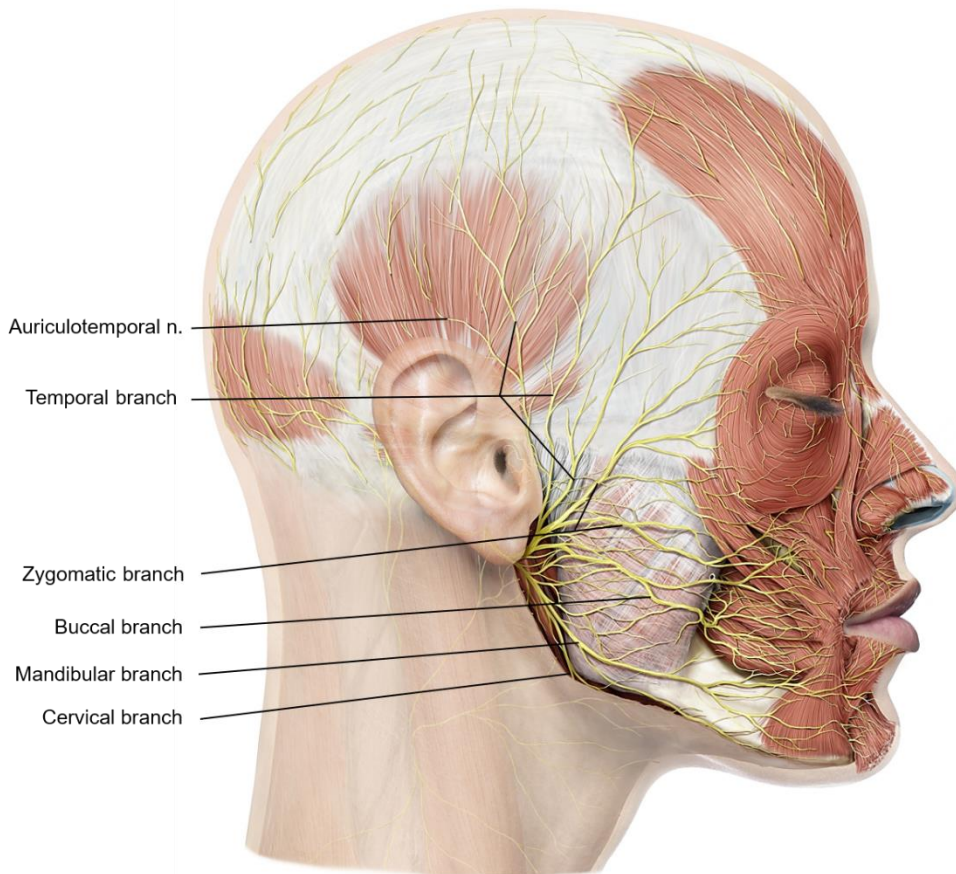


Figure 26. The terminal branches of the facial nerve. (Modified from Radlanski & Wesker 2012 with permission of publisher.)

The five branches arborize within the parotid gland before distributing to the muscles of facial expression. In most cases, the motor branches of the facial nerve innervate the muscles of facial expression from their deep surfaces (Freilinger et al. 1987). Approximately 70% of the time, the three branches in the midcheek are collateralized. That is, arcades interconnect adjacent branches (Davis et al. 1956). This connection provides an element of reserve capacity in the event of injury. In contrast, both the temporal branch of the upper division and the marginal mandibular branch of the lower division are more likely to be terminal and uncollateralized. Therefore, they are less forgiving of injury (Baker and Conley 1979).

In short, the mimetic muscles are actuated by impulses that travel through the terminal branches of the facial nerve. These muscles contract in highly refined and coordinated patterns to reflect thoughts, wants, desires, and emotions that originate within highly specialized regions of the brain. These expressions are signaled in the face because the

muscles of facial expression mold the attached overlying skin into recognizable mounds and furrows.

## **2.6. Summary/Conclusions for Muscles of Facial Expression**

The anatomy of the face has been long studied. However, this thesis provides a new perspective. With advancements in medical imaging within the past decade, we have seen the emergence of a new role for the face. The human face is a major part of a person's identity, social and cultural interactions, psychological status, and provides the unique means to communicate on an emotional level. Thus, socialization and communication are the principal and essential roles of the face. These facial functions are critical to the survival of individuals and humans as a species. This chapter addressed the distinctive anatomic features of the muscles of facial expression and the structure of the human face that allows it to serve its principal roles of communication and socialization.

Specifically, a critical review of the literature showed that the face is anatomically-configured to fulfill its principal role. The muscles of facial expression have unique features that make them suitable for this specialized purpose. These features are both gross and microscopic. In short, their anatomic form supports their functional role. Additionally, I described the descriptive anatomy of the muscles of facial expression. The muscles of facial expression, taken as an integrated system, fulfill the role of communication and socialization that is integral to human survival.

This chapter described the innervation of the muscles of facial expression. The muscles of facial expression have an intricate mode of innervation. This complexity and expansiveness of innervation underscores the critical importance of the muscles of facial expression to humans. Furthermore, the mechanisms by which humans create more than seven thousand facial expressions are complex. Our understanding is still evolving.

## **2.7. The Neuroanatomy of the Face**

### **2.7.0. Introduction to Neuroanatomy of the Face**

Humans have developed sophisticated systems for both expressing an emotion or intention and interpreting the facial display of another. The control of the mimetic muscles, face recognition, and the interpretation of facial expression takes place within the brain. (Puce et al. 1995) were among the first to report clusters of face-specific neurons in the temporal regions of the brain. Since then, our understanding has expanded to encompass at least seventeen interconnected anatomic regions that are part of an extended network for facial communication. The neurophysiology is a subsequent chapter. However, this chapter will introduce the essential neuroanatomy underlying the physiology of the face and illustrate the diversity and intricacy of the neural components of the facial communication system.

The essential central nervous system structures that participate in facial communication can be categorized in five groups: structures pertaining to:

- 1) The visual apparatus,
- 2) Face-specific neurons—i.e., “face patches”,
- 3) The limbic system,
- 4) Frontal lobe structures and
- 5) Other, unclassified.

### **2.7.1 The Visual Apparatus**

The visual apparatus provides the sensory input for face recognition, facial expression and facial interpretation (**figure 27**).

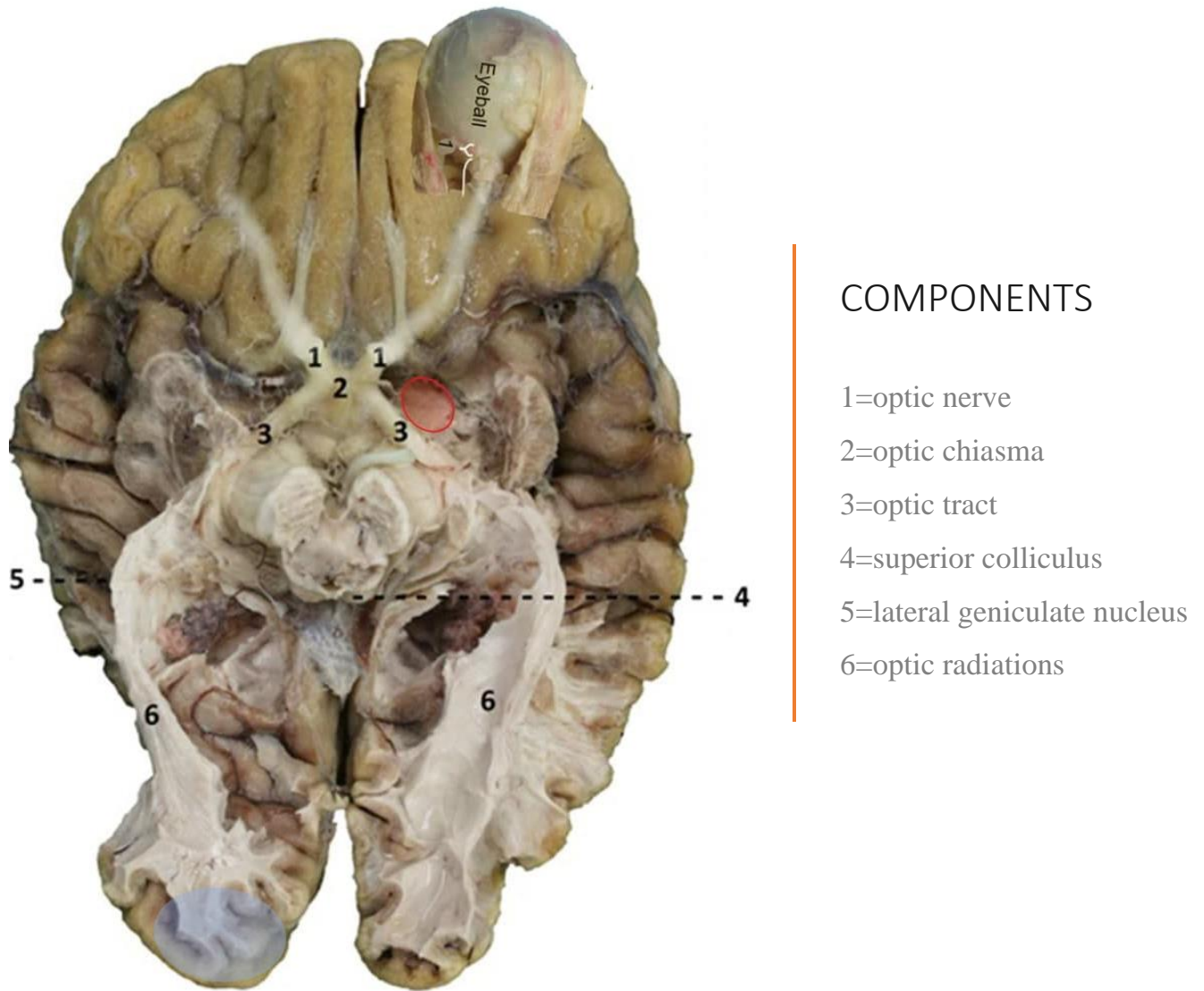


Figure 27. The brain (when viewed from below) showing the component of the visual apparatus involved in facial communication. (Adapted from Nooij RP, Hoving EW, van Hulzen ALJ, Cornelissen FW & Renken RJ (2015). Preservation of the optic radiations based on comparative analysis of diffusion tensor imaging tractography and anatomical dissection. Nooij et al. 2015. CC by 4.0

The visual apparatus is comprised of the retina (the layer of cells lining the posterior surface of the eye) and the optic nerve (nerve fibers conveying visual signals) that branch to form the optic tract (Remington 2012). In turn, the optic tract sends most fibers to a junctional point (synapse) known as the lateral geniculate nucleus, and directs a small number of fibers (10%) to a region within the midbrain known as the superior colliculus. The superior colliculus is the initial point of a subcortical visual pathway termed the retino-colliculo-thalamo-amygdala (RCTA) pathway. This pathway constitutes the high-speed neural pathway that gives emotional content to visual stimuli. It runs through the superior colliculus and

thalamic relay stations (e.g., the pulvinar) to arrive at the amygdala (within the limbic system) where signals launch the mechanism for the brain to release emotion-modulating chemicals (Soares et al. 2017; Diederich et al. 2014). The RCTA pathway is unconscious. This subcortical visual pathway is referred to as “blindsight” because patients with damage to the predominant visual pathway (discussed subsequently) still respond to visual stimuli. In the alternate, predominant pathway known as the geniculo-striate pathway, the visual signals travel from the lateral geniculate nucleus via the optic radiations to the primary visual cortex in the occipital lobe of the brain.

### 2.7.2 The Face Patches

The next group of central nervous system structures involved in processing faces are the “face patches”. Early research focused on these face-specific clusters of neurons within the temporal lobes (Haxby and Gobbini 2011; Kanwisher and Yovel 2006). These face-specialized areas are: the fusiform face area (FFA), the occipital face area (OFA), and the superior temporal sulcus (STS) (a.k.a., inferior occipital gyrus). The location of the face patches are illustrated in (figure 28).

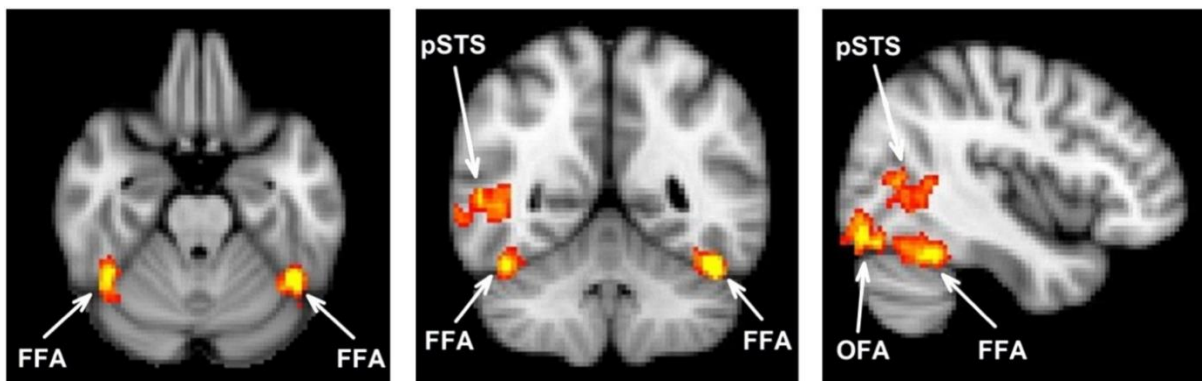


Figure 28. Multiplanar MRI illustrating the face patches. Axial, coronal and right sagittal MRI images of the brain. From Harris, R. J., Young, A. W., & Andrews, T. J. (2014). Brain regions involved in processing facial identity and expression are differentially selective for surface and edge information. *NeuroImage*, 97, 217–223. <https://doi.org/10.1016/j.neuroimage.2014.04.032>. CC by 3.0.

The occipital face area (OFA) is located on the lateral surface of the occipital lobe, either in, or in the vicinity of the inferior occipital gyrus (IOG). TMS (transcranial magnetic stimulation) and fMRI (functional MRI) studies suggest that the OFA preferentially

represents the *parts* of a face (including the eyes, nose, and mouth). Because of the OFA's direct and proximal connection to the primary visual cortex (PVC), the OFA is believed to be the gateway to the recognition and processing of faces (Pitcher, Duchaine, and Walsh 2014). That is, the OFA tops the hierarchy involving several face-processing regions of the brain.

A substantial body of research has centered on the fusiform face area,<sup>25</sup> located in the lateral middle fusiform gyrus of the temporal lobe. In contrast to the OFA's focus on face *parts*, the FFA is believed to be involved in the *holistic processing* of faces, and it responds to the *shape* of facial features as well as the *spacing* between them (Yovel and Kanwisher 2004; Liu, Harris, and Kanwisher 2010). The fMRI studies of Bernstein et al. (2018) showed that the FFA is implicated in gender and identity face-processing.

The third face patch, the superior temporal sulcus (STS), also makes a specialized contribution to face perception and recognition. The superior temporal sulcus is thought to be responsive to *movement-specific* facial expression (Iidaka 2014; Pitcher, Duchaine, and Walsh 2014; Srinivasan, Golomb, and Martinez 2016). Facial movements such as eye-gaze or mouth movements are critical to the facial communication process. Thus, it is not surprising that there is a specific anatomic region devoted to this function.

### 2.7.3 The Limbic System

The face patches are considered the core of facial communication, but they interconnect with other regions of the brain, most intimately with the limbic system. Thus, the limbic system constitutes a third group of central nervous system (CNS) structures important to facial communication. The limbic system is comprised of several functionally and anatomically interconnected nuclei and cortical structures. In 1878, Paul Broca was the first to name this general region of the brain "*le grand lobe limbique*", the French term for the region's large oval shape (Torricco and Abdijadid 2022). **figure 29** illustrates the location of

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<sup>25</sup> The fusiform face area is situated within the posterior-lateral aspect of the fusiform gyrus of the temporal lobe. The early literature refers to this small cluster of neurons in the singular, "area". Subsequent research determined that the FFA was, in fact, two small adjacent (but distinct) clusters of neurons: the mid fusiform face area and the posterior fusiform face area. The correct terminology should be in the plural, "areas", but neuroscientists still use the singular.

limbic structures. The limbic system lies superior to the brainstem, inferior to the cerebral cortex and generally surrounding the thalamus.

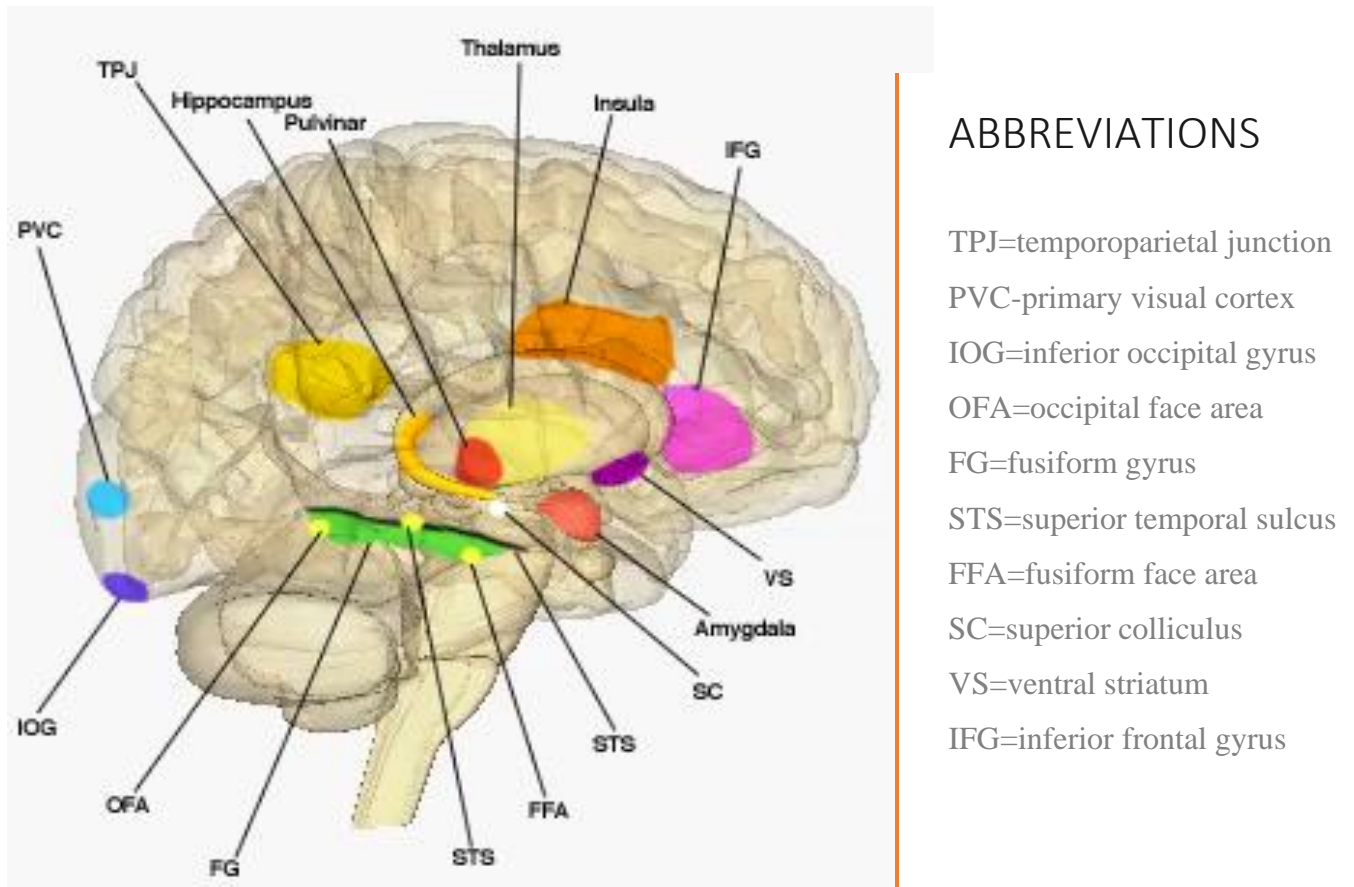


Figure 29. The cortical and the subcortical components of the face-processing system.  
Source: author original.

The five components of the limbic system that have been implicated in face-perception/processing are the:

- 1) Amygdala
- 2) Hippocampus
- 3) Thalamus/hypothalamus (thalamic tract)
- 4) Pulvinar (region of thalamus)
- 5) Insula (anterior portion is considered part of limbic system)

**Figure 30** shows the location of the aforementioned components and their anatomic relationship to other intracranial face-processing structures.

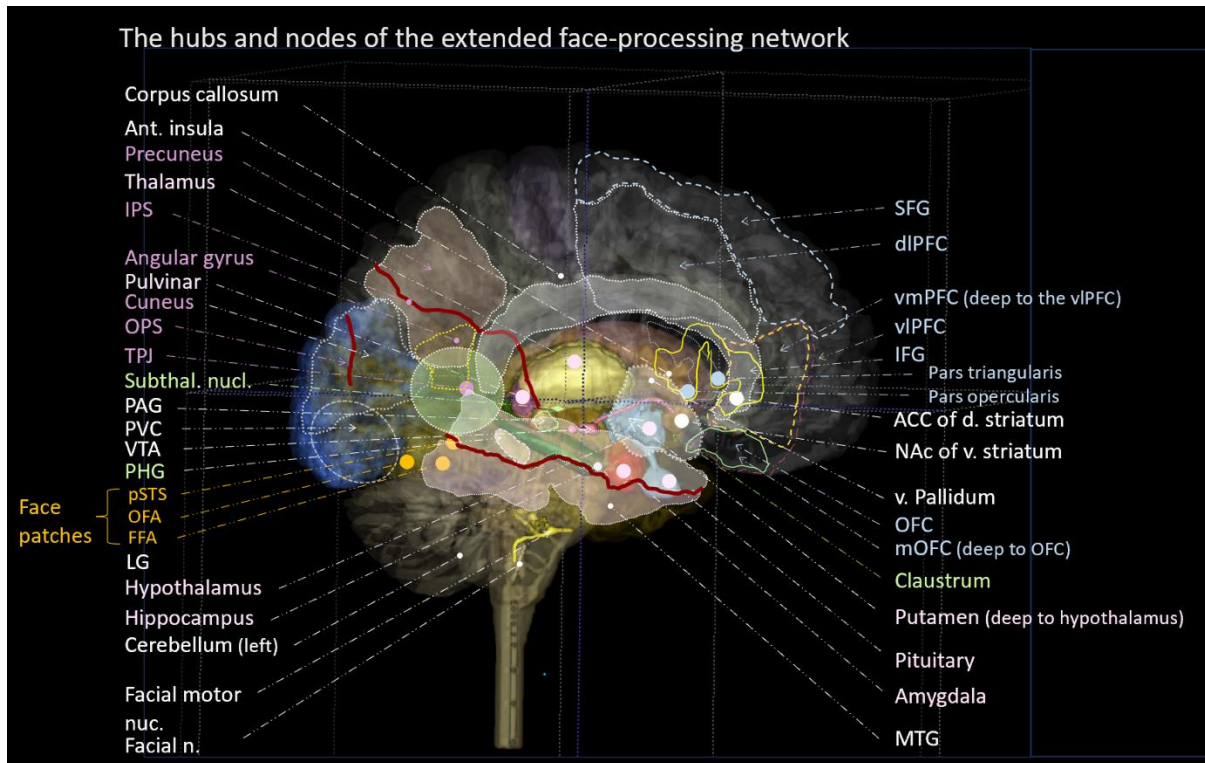


Figure 9. The extended face-processing network. This figure illustrates the anatomic relationships of key limbic structures with the extended face-processing system. Abbreviations are explained in the list of abbreviations. Source: Author's original.

The amygdalae are deep, paired structures, located in the medial aspect of the temporal lobe. The Latin term, amygdala, aptly describes the shape of these structures—almond-shaped. This anatomic region is more appropriately referred to as the “amygdaloid complex” because it is comprised of approximately thirteen individual clusters of neurons or nuclei. Selected nuclei (the central and basolateral nuclei) have been implicated in face-perception/processing (Calder and Nummenmaa 2007).

A large body of research has emerged to delineate the role of the amygdala in face-processing tasks. Face-processing tasks that have been localized to the amygdalae are:

1) Émotionnel expression perception (Zald 2003; Hariri et al. 2002; Whalen et al. 2013; Wang et al. 2004),

2) Dynamic expression perception (Harris, Young, and Andrews 2014) and reflexive orienting to expressions (Gamer et al. 2013; Gamer and Büchel 2009).

Additionally, the amygdala has been shown to be involved in:

- 1) Understanding a face as threatening or not (Morris et al. 1998), or
- 2) Monitoring the direction of gaze of a face (Kawashima et al. 1999), and
- 3) Establishing the reward value of stimuli in general (Baxter et al. 2000).

Moreover, studies show that the amygdala plays a central role in:

- 1) The recognition of faces and facial emotion,
- 2) Mediating eye gaze (Fried, MacDonald, and Wilson 1997), and
- 3) Maintaining eye contact (Spezio et al. 2007).

Additionally, as previously mentioned, the amygdala is the terminus of the RCTA pathway that gives emotional content to visual stimuli. Thus, the amygdalae, within the limbic system, are part of the extended network of facial communication. There, within a cluster of specific nuclei, highly refined and intricate tasks critical to human facial communication take place. These tasks will be further addressed in Chapter III.

Like the amygdala, the hippocampus is within the limbic system and forms part of the extended network of face perception/processing. Although often cited as singular, there are two hippocampi—one in each cerebral hemisphere. The term hippocampus comes from the Greek word for seahorse because the hippocampus resembles a seahorse (**figure 31**).



Figure 31. Hippocampus removed from the brain (left) compared to a seahorse. credit Lazlo Seress. CC by 4.0.

In general, the hippocampus is thought to be a crucial structure in memory consolidation. However, the hippocampi play an intriguing role in facial recognition. Quiroga et al. (2005) reported that single neurons within the hippocampi coded for specific faces. Quiroga's single-neuron discovery acquired the appellation, "the Jennifer Aniston neuron" named after the celebrity actress whose identity was embedded in the left hippocampus of an experimental subject's brain. (The full study and its implications in face identity recognition will be addressed subsequently in Chapter III.)

At the most medial aspect of the limbic system are situated the thalamus/hypothalamus (sometimes referred to collectively as the thalamic tract). The thalamic tract lies immediately superior to the brain stem. The thalamus derives its name from the Greek  $\theta\acute{\alpha}\lambda\alpha\mu\omicron\varsigma$  or "chamber". The hypothalamus, as the Greek term implies, is situated below the thalamus. Anatomically, it is a midline structure comprised of right and left halves. The thalamus is comprised of many nuclei (**figure 32**).

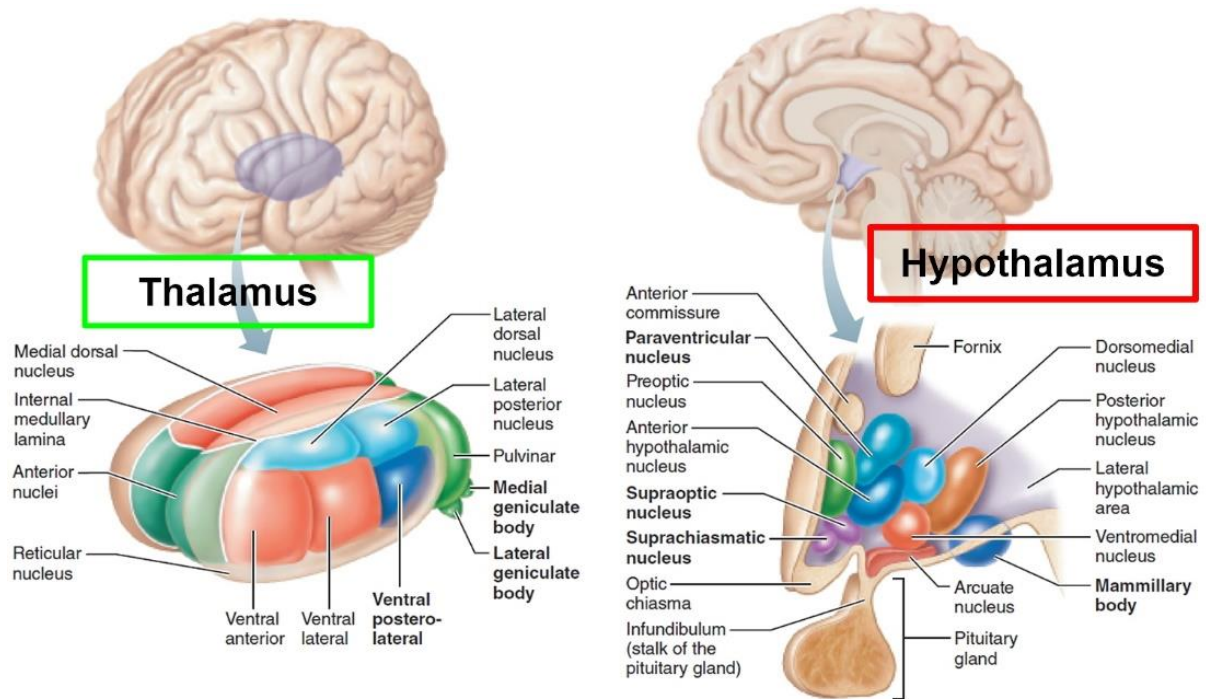


Figure 32. The location and composition of the thalamic tract. Modified from Pearson Education 2016.

The thalamus is multifunctional, but traditionally believed to act as a relay station, relaying information between different subcortical areas and the cerebral cortex (Gazzaniga, Ivry, and Mangun 1998). The hypothalamus is classically thought to control normal body functions, i.e., maintain homeostasis (Gazzaniga, Ivry, and Mangun 1998). The hypothalamic nuclei are illustrated in the above **figure 32**.

Interestingly, the thalamus/hypothalamus assume a novel function from the perspective of facial expression/interpretation. That is, the thalamic/hypothalamic tract is both a repository for, and a manufacturing site of neurohormones in the brain (Palkovits 1982). At least six of these neuropeptides have been shown to be integral to facial communication: serotonin, endorphin, acetylcholine, oxytocin/vasopressin, noradrenalin and dopamine. These are the neurohormones that generate feelings that actuate the muscles of facial expression and reciprocally the neurohormones that react to facial expressions that make us empathetic to other peoples' feelings. These chemical signals can be transmitted via neuronal synapses or via the circulatory system. Remarkably, from the anatomic perspective, the thalamus/hypothalamic region is both the most connected region of the brain and also proximal to a profuse vascular system. In this instance, form clearly follows function.

A publication by Wolfe, Deruelle, and Chaminade (2017) illustrated the highly-refined role of neurochemicals in face-processing. In an fMRI study, the investigators probed the hypothalami of twenty adult subjects. They recorded activity within two highly localized oxytocin-synthesizing nuclei, the supraoptic nucleus (SON) and paraventricular nucleus (PVN), in response to implicit processing of four categories of faces: sibling, best friend, celebrity and unknown. They found increased response of PVN specifically toward sibling and friend faces. In contrast, the SON responded to all visually familiar faces, suggesting that it has a more general function. Remarkably, from an anatomic perspective, the SON responded to all familiar faces *but* lateralized on the left for friend and right for sibling. Thus, the neurochemical processing of faces is both physiologically and anatomically intricate, and highly specific.

The nuclei pulvinare (or the pulvinar as it is known) is the posterior-most nucleus of the thalamus. The term, pulvinar, comes from classical Latin *pulvinus* or "cushion". Anatomically, it is indeed the posterior cushion upon which the body of the thalamus sits. The pulvinar resides in a privileged location within the brain. It is adjacent to the primary visual cortex, yet connects anteriorly with the retina and has proximal connections to the amygdala. From the face-processing perspective, the pulvinar is a novel nexus linking the visual and emotional systems in facial communication.

It has been long known that the pulvinar influences communication between cortical areas. It is known also that this region of the thalamus is a junction for a variety of sensory stimuli, notably visual signals. Only recently have we discerned via high resolution fMRI that there are clusters of neurons selective for faces within the posterior ventral pulvinar (Arcaro et al. 2018). Moreover, Koizumi et al. (2019) suggested that the posterior pulvinar primes the nearby PVC to anticipate a fearful face but not a happy face. When presented with a threatening face, or expectant threatening face, the pulvinar informs the amygdala to respond with the feeling of fear.

As described previously, the pulvinar is a nucleus along the retino-colliculo-thalamo-amygdala (RCTA) pathway. The RCTA is a rapid pathway for reacting to urgent or threatening visual stimuli. Using fMRI with global and local tractography methods, (McFadyen, Mattingley, and Garrido 2019) recently reported that this subcortical route to the amygdala in the human brain is recruited for face-processing. The data indicated that the

pulvinar was selectively activated with faces, as opposed to nonfaces. The pulvinar relayed the signal to the amygdala for emotional input (**figure 33**). Thus, the pulvinar nuclei are another limbic structure implicated in emotional face-processing.

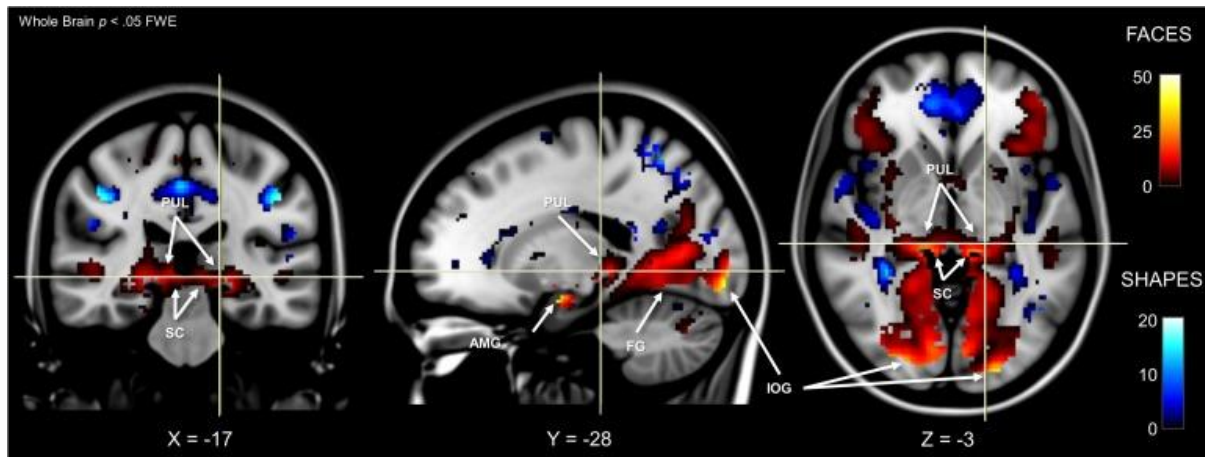


Figure 33. The role of the pulvinar in face-processing. Selective activation in the pulvinar (PUL) for faces (red). Shapes (blue) activate other brain regions. From McFadyen 2019. McFadyen, J., Mattingley, J. B., & Garrido, M. I. (2019). An afferent white matter pathway from the pulvinar to the amygdala facilitates fear recognition. *eLife*, 8, e40766. <https://doi.org/10.7554/eLife.40766>. CC by 4.0.

The insula<sup>26</sup> at the junction of the frontal, parietal, and temporal lobes of each hemisphere of the brain. The insulae are divided into two parts: the larger anterior portion and the smaller posterior part. Because of functional connections, the insulae are considered part of the limbic system (Sun, Wang, and Cui 2015). Studies (see Shura, Hurley, and Taber (2014) for a review) have shown that the insulae are richly interconnected to other regions of the brain.

There is a volume of work implicating the insula with both the production and interpretation of facial expressions (van der Gaag, Minderaa, and Keysers 2007; Pohl et al. 2013; Jenkins et al. 2017; Jabbi and Keysers 2008; Showers and Lauer 1961).

The insula appears to be a site for fine discrimination of facial expressions. In one study, Chen et al. (2009) demonstrated that the right insula differentiates disgust from happy facial expressions. Moreover, the right insula responded stronger to disgust and happy

<sup>26</sup> Latin for “island”, an “island” of cerebral cortex deep within the lateral sulcus (aka Sylvian fissure)

expressions than to neutral facial expressions. In another fMRI investigation, Quarto et al. (2016) reported that the left insula was activated for fearful faces, but showed lower activity during social judgment of angry faces. A recent clinical report substantiated that the insula is involved in motor activation of the muscles of facial expression. Cantone et al. (2019) reported a patient with a rare right anterior insular infarct (loss of oxygen to neurons resulting in cell death) triggered an abnormal facial expression of disgust and fear. Tippett's recent report (Tippett et al. 2018) demonstrated that right anterior insular stroke impaired the recognition of happy, angry, and disgust faces. Curiously, this corroborates earlier observations that it is the *right* insula with dominant activity concerning facial expressions (Abbott et al. 2014; Blonder, Bowers, and Heilman 1991; Bowers et al. 1985).

In short, the insular cortex, deep within the brain and profusely connected to the amygdalae and hippocampi, has been implicated in a diversity of tasks related to facial communication. Similar to the case of the hippocampi, facial recognition appears to be lateralized in the insula. The precise role of the insula in face-processing is yet to be delineated.

#### **2.7.4 Frontal Lobe Structures**

The prefrontal cortices occupy the anterior regions of the frontal lobe. Components of the prefrontal cortex are part of the extended face-processing network and they play a variety of roles in facial communication.

Anatomically, the prefrontal cortex is divided into five main regions: the superior prefrontal (SPFC), the middle (medial) prefrontal cortices (MPFC), the lateral frontal cortices (LFC) the orbital frontal cortices (OFC) and the inferior frontal cortices (IFC). These main regions are further subdivided anatomically. For example, there are ventrolateral, dorsolateral, and ventromedial prefrontal cortices (**figure 34**).

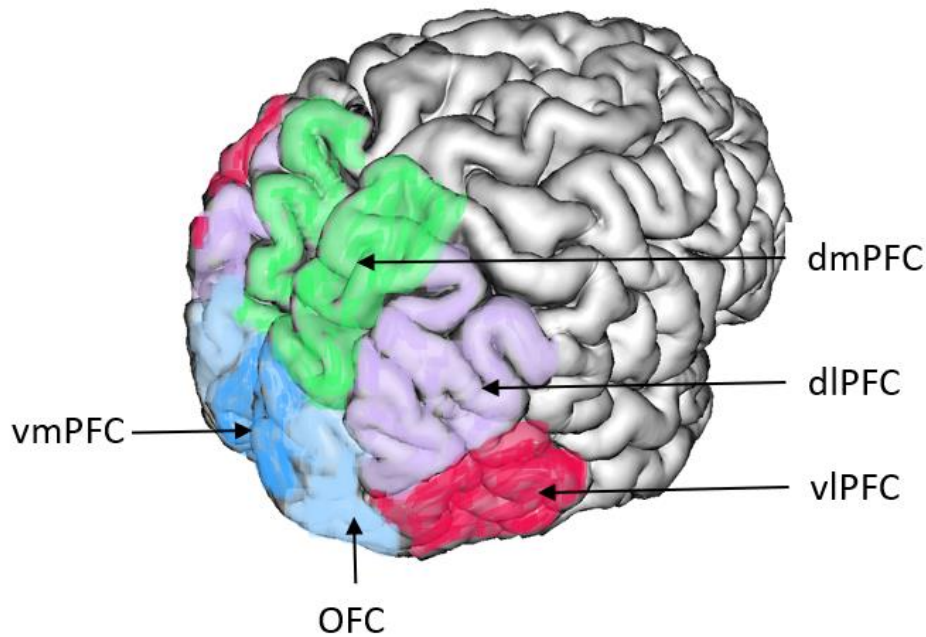


Figure 34. Components of the prefrontal cortex. Source: author's original contribution.

The precise roles of these regions of the frontal lobes are an ongoing source of investigation. Four distinct regions have received considerable attention concerning faces: the orbitofrontal cortex, the ventromedial frontal cortex, ventrolateral frontal cortex and the inferior frontal cortex. These frontal lobe neurons participate in face-processing via their strong reciprocal connections with the face patches and limbic system.

Current theory is that the frontal cortical structures are modulators for the core face-processing areas. That is, distinct regions of the prefrontal cortex provide judgement and/or valence to faces in a well-defined, delimited manner. For example, neurons in the posterior medial orbitofrontal cortex specifically respond to facial beauty and sexual relevance (Aharon et al. 2001; Ishai 2007). Moreover, Kranz and Ishai (2006) further demonstrated in a fMRI study that the medial occipital frontal cortex could respond in a gender- and sexual-orientation specific way, with more activation for the gender relevant to an individual's sexual preference. Intriguingly, if one shifts one's anatomic orientation a few millimeters anteriorly to the anterior medial orbitofrontal cortex, then one finds judgement/valence specific neurons that respond to food similar to the way the proximal neurons in the pmOFC

(prefrontal medial orbitofrontal cortex) respond to sex (Troiani et al. 2016). Thus, such important facial communication parameters as mate selection and desire or rejection of specific foods, are allocated to a small select cluster of neurons within a specific, constrained region of the prefrontal cortex.

Other studies also point to the specificity of precisely delimited regions of the prefrontal cortex in facial communication. For example, (Guntupalli, Wheeler, and Gobbini 2017) showed a progressive pathway by which humans decipher the identity of a face regardless of direction from which the face is viewed. The investigators identified via fMRI that the view-invariant representation of identities in the human face perception system is accomplished in the right inferior frontal face area (rIFFA) of the frontal cortex.

Similarly, discrete sites within the ventromedial prefrontal cortex have been shown to activate for specific face-related functions. Heberlein et al. (2008) examined a cohort of eight patients with damage to the ventromedial prefrontal cortex (vmPFC). This vmPFC-lesioned group appeared to have particular difficulty judging fearful, surprised, sad, and disgusted faces. A control group of eight subjects with damage to the neighboring dorsal and/or lateral prefrontal regions was not impaired. Thus, there is evidence for discrete recognition of specific emotional facial expressions restricted to the ventromedial prefrontal cortex of the frontal lobe. Moreover, it is not unexpected that the ventromedial prefrontal cortex is implicated in emotional recognition. Strong connections between the ventromedial prefrontal cortex and amygdala (the brain's emotional center) have been reported in the rat brain (McDonald, Mascagni, and Guo 1996) and in humans (Banks et al. 2007).

The inferior frontal cortex (IFC) is subdivided into three parts or “pars”: the pars opercularis, the pars triangularis, and the pars orbitalis. This particular region of the brain is readily identified from its characteristic surface features. The gyri comprising this region resemble the letter “M”. Each leg of this “M” is a pars. The two most caudal <sup>27</sup>“legs” are the pars opercularis and the pars triangularis, respectively. The pars opercularis and triangularis have been shown to play a role in face-processing. These roles will be discussed in Chapter III, The Physiology of the Face.

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<sup>27</sup> The term, caudal in neuroanatomy describes a direction toward the back of the brain.

In summary, frontal lobe structures play a variety of essential roles in facial communication. Prefrontal cortex neurons participate in face-processing via their strong reciprocal connections with the face patches and limbic system. The contemporary literature suggest that discrete clusters of frontal neurons modulate the core face-processing areas of the brain by providing judgement and/or valance to the representation of facial expressions.

### 2.7.5 Other Intracranial Structures

Earlier, I cited the superior colliculus as a component of the retino-colliculo-thalamo-amygdala (RCTA) visual pathway. This pathway constitutes the unconscious, high-speed neural pathway that gives emotional content to visual stimuli *in general*. Recent research suggests that regions within the superior colliculus of macaque monkeys are involved *directly* with the detection of faces (Le et al. 2020).

Whereas this electrophysiological study was in nonhuman primates, there is support that the human superior colliculus behaves similarly (Johnson, et al. 1991). Moreover, Solcà et al. (2015) reported a blindsight patient showed residual visual functions; in particular the ability to unconsciously distinguish between normal faces and faces with arbitrarily-placed facial features.

The corpus striatum is a part of the basal ganglia. Anatomically, it lies lateral to the thalamus and proximal to other limbic structures. It has two parts: dorsal striatum and ventral striatum. The dorsal striatum is further divided by an internal capsule into two parts: the caudate nucleus and the putamen. The ventral striatum contains the nucleus accumbens. The striatum interconnects with the visual system, regions of the neighboring limbic system, and motor regions of the brain. Components of the corpus striatum have been shown to respond to social valence of faces. For example, in an fMRI study, Bartels and Zeki (2000);(2004) reported subjects observing pictures of a loving partner elicited higher blood oxygenated level-dependent (BOLD) activity in caudate/putamen and VTA (ventral thalamic area) compared to viewing pictures of friends matched for age, gender, and length-of-friendship as their partners. Moreover, distinct regions of the caudate, putamen, striatum are activated depending upon whether the face is that of a romantic lover or the face of a child to its loving mother (Zeki 2007). It is noteworthy that the caudate nucleus and the putamen of the striatum

show corresponding activity with the hippocampus (memory function) and the insula (region of limbic system involving discrimination of emotional facial expression) (**figure 35**).

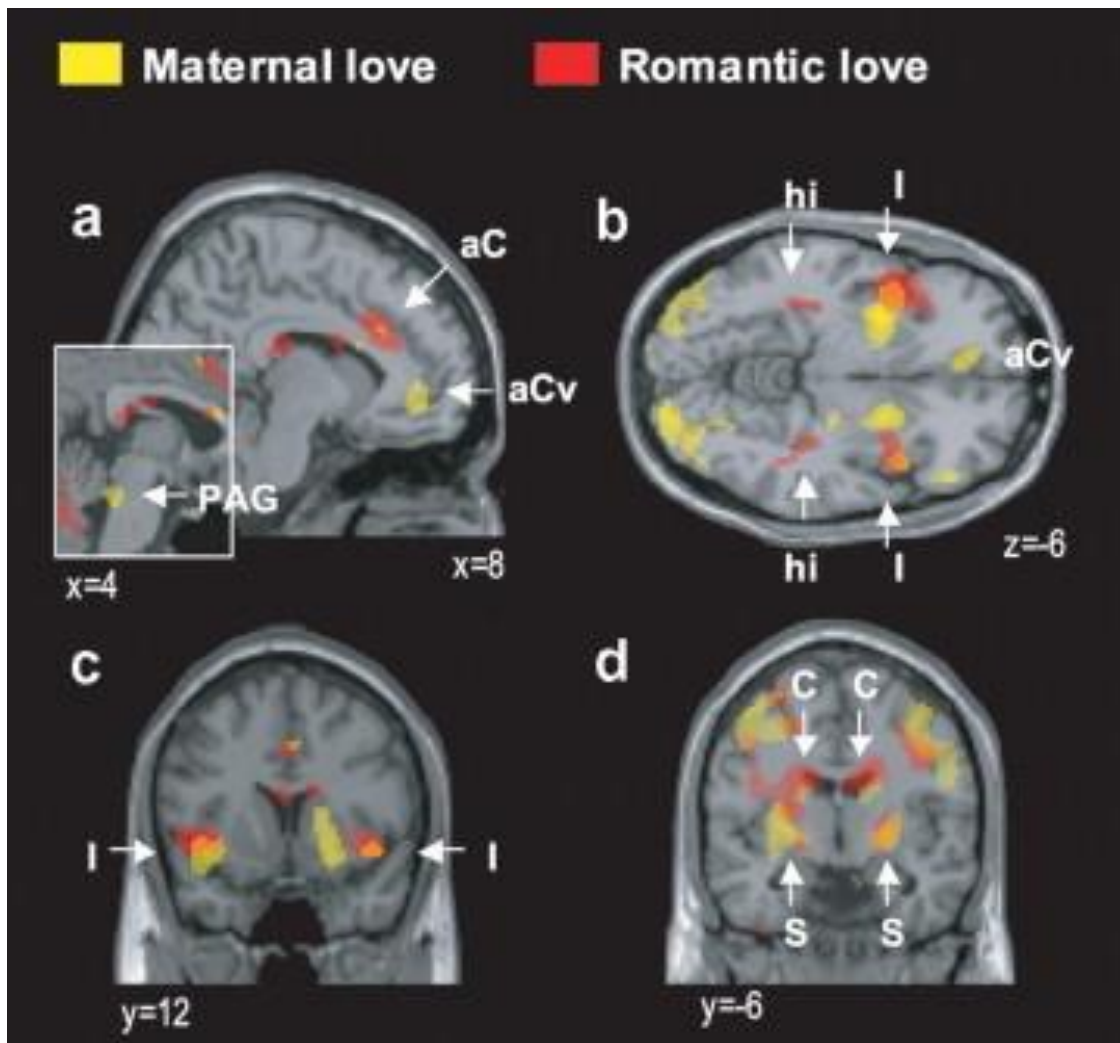


Figure 35. The corpus striatum and love. Brain activity produced by maternal love and romantic love (in both males and females) (shown in red and yellow). Abbreviations: aC, anterior cingulate cortex; aCv, ventral aC; C, caudate nucleus; I, insula; S, striatum (consisting of putamen, caudate nucleus, globus pallidus); PAG, periaqueductal (central) gray; hi, hippocampus. From Zeki 2007. Zeki, S. (2007). The neurobiology of love. *FEBS Letters*, 581(14), 2575-2579. doi:10.1016/j.febslet.2007.03.094. (By permission of publisher)

The temporoparietal junction (TPJ), as the name suggests, is situated at the confluence of the temporal and parietal lobes of the brain. There is little consensus concerning the anatomic boundaries that define this rather large region of the brain (Schurz et al. 2017). Schurz et al. performed a meta-analysis of publications that defined the macro, micro, and functional anatomy of the TPJ. They found that the TPJ likely included the angular gyrus of the parietal lobe, much of the superior and middle frontal gyrus, the superior temporal sulcus, and even portions of the occipital lobe.

It is revealing to note a significant anatomic relationship that is remarkably absent from the face-processing literature. That is, from an anatomical perspective, the TPJ is a component of a contiguous series of cortical gyri extending posterior-anteriorly from the angular gyrus in the parietal lobe, crossing the parietal temporal sulcus to the TPJ. From the TPJ, the contiguous gyral cortex becomes the superior temporal gyrus (proximate to the STS). Then the gyrus continues through the middle temporal gyrus, a.k.a., Brodmann Area 21 (BA21), turns medially, branching into the anterior insular cortex. Then turns rostrally, to enter the frontal lobe, continuing into the inferior frontal gyrus (IFG), before turning in a superior direction to be contiguous with middle and superior frontal gyri (that contain the dorsal and ventral prefrontal cortices (refer to **figure 36**).

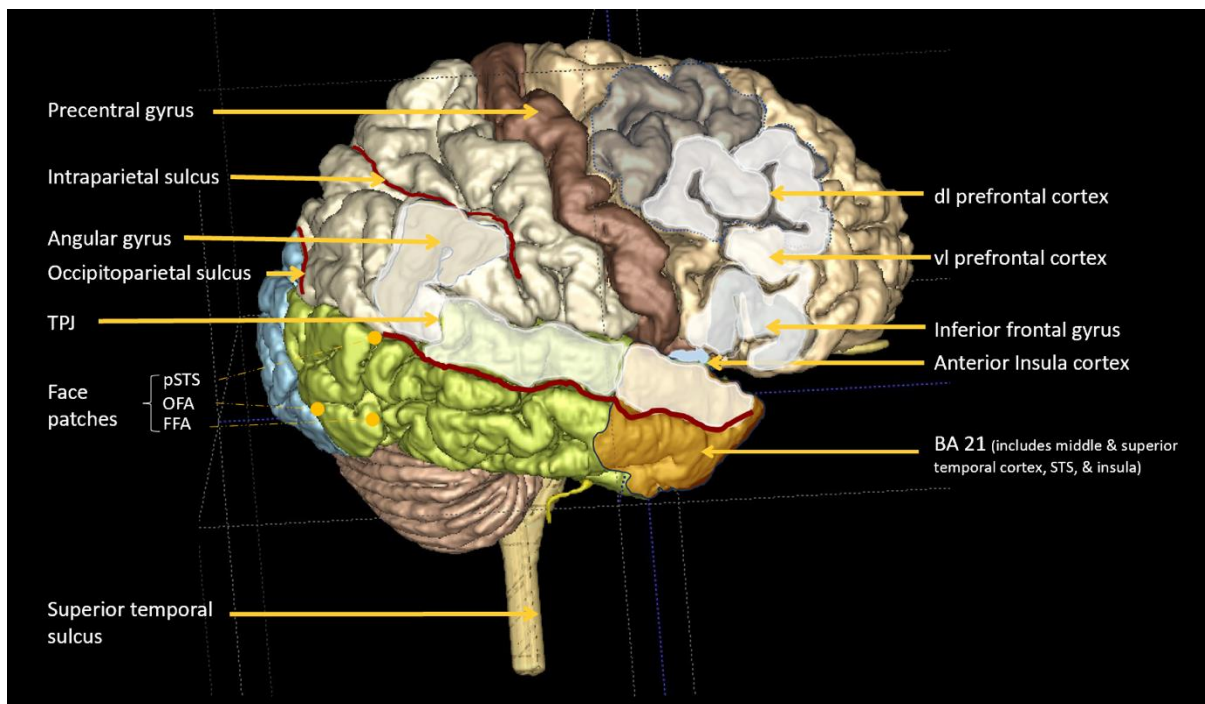


Figure 36. The contiguous gyri constituting a novel face-processing pathway. Source: author original.

The observations reported in this thesis point out that each of the aforementioned anatomic sites, appear to be nodes on a distributed neural network (DNN) by which I postulate that humans identify the faces of conspecifics, or identify their own faces in the mirror, or visual images of themselves. This anatomic-physiologic relationship will be amplified in Chapters III and IV.

In brief, the temporoparietal junction is a bilateral expanse of neurons with a variety of functions—most of which relate to attention and self-awareness. (There also seems to be a distinction between functions of the right and left TPJs). Haxby and Gobbini (2011) were among the first to report the TPJ was sensitive to human faces. The work of Apps et al. (2012) underscored the complexity and keen specificity of selected neurons in face-processing. In an fMRI experiment, Apps addressed the specific questions; what regions of the brain are activated when we look at our own faces in a mirror, and what regions are activated when we view photographs of our past self? In other words, how do we distinguish ourselves from others? The results of this study suggested that recognizing one's past and current facial appearances relies on processing carried out in distinct neural circuits involving multiple regions of the brain including the temporoparietal junctions. Noteworthy was the observation that *different* regions of the temporoparietal junctions were recruited to recognize one's current face from one's past self.

The angular gyrus (AG) is a horse-shoe-shaped gyrus in the parietal lobe contiguous with the superior temporal gyrus in the temporal lobe. The AG is situated immediately caudal to the superior temporal sulcus (STS). Liu et al. (2021) showed decreased activation of the right angular concomitant with impaired ability to recognize happy faces in patients with major depressive disorder.

Immediately superior and rostral<sup>28</sup> to the AG is the intraparietal sulcus (IPS). The left IPS has been shown to activate during self-recognition of one's own face (Kircher et al. 2000).

## **2.8. Summary/Conclusions for Chapter II**

This section of Chapter II, addressed the anatomy of the nervous system that allows the human face to serve its principal roles of communication and socialization. It also addressed the neural pathways that regulate facial function.

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<sup>28</sup> The term, rostral in neuroanatomy describes a direction toward the front of the brain.

The neuroanatomy underlying the physiology of the face is diverse and intricate. This chapter described how the various components of the facial communication system work together to enable humans to fulfill complex and essential psychological and sociological tasks such as recognizing one's self, conceiving of one's identity, choosing a desirable mate, feeling positive about the faces of friends and aversive to the faces of strangers, recognizing kin, feeling parental love for one's offspring, feeling romantic love toward one's mate, attributing beauty to faces, and even moderating one's sexual orientation.

Facial emotional expression is an interplay between the muscles of facial expression and a collection of intracranial neurons. This system enables humans to both express emotions in their faces and perceive emotions in faces of others. The distinctive neuroanatomy is central to human survival both as individuals and as a species.

## CHAPTER III – The Physiology of the Face

### 3.0. Introduction

As discussed in Chapter II, the muscles of facial expression are distinctive. The unique anatomic features of the muscles of facial expression permit fine, subtle, rapid, and smooth movements needed to constitute the vast vocabulary of facial expression. There are two anatomic components of facial communication: the muscles of facial expression, and anatomical structures within the brain that play essential roles in both the interpretation and production of facial expressions. These elements work together to constitute the functional physiology of the human face.

Facial physiology entails complex systems both to express emotions or intentions, and to interpret facial expressions of others. Thus, facial communication is a two-component system: making faces, and reading others' faces.<sup>29</sup> Facial expression requires both components for viable communication and socialization.

Recent advances in neuroimaging such as functional MRI (fMRI), positron emission tomography (PET), near infrared spectroscopy (NIRS), magnetoencephalography (MEG), and diffusion tensor magnetic resonance imaging with fiber tractography (DTI-FT) have led to a fundamental understanding of the structure, anatomy, and neural pathways involved in facial expression. The physiology of the face is not yet well delineated, but our understanding of the processes is expanding and evolving. Chapter III, “The Physiology of the Face”, presents an up-to-date understanding of how the face functions to affect communication and socialization. The chapter begins with a discussion about the physiology of the skeletal muscle comprising the muscles of facial expression. Next, the text speaks to the underlying neurochemistry of emotions. Then, the text overviews the physiological steps involved in identifying faces, interpreting facial expressions, and generating facial expressions.

Subsequently, I address some of the more recent and intriguing findings about more subtle

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<sup>29</sup> In medical terminology, facial communication has an efferent and an afferent component. The *efferent* component is comprised of nerves leading away from the brain. This corresponds to making facial expressions. The *afferent* component consists of nerves carrying impulses toward the brain. This corresponds to recognizing/interpreting the facial displays of conspecifics.

workings of facial communication. This chapter will not be a classical presentation of medical physiology, but rather I shall present the topic from a dual perspective that integrates both medical and social aspects.

### **3.1. The Physiology of the Muscles of Facial Expression**

As stated previously, facial communication is a two-component system. Not only can humans recognize and interpret facial expressions, but also, they can move facial muscles with precision in order to generate facial displays. Communicating via facial display requires the facial muscles to contract to generate the more than seven thousand known facial expressions. Chapter II set forth the physiology of muscle contraction. But, in brief, as a preface to the *neurophysiology* in this chapter, the physiology of muscle contraction will be reviewed here.

Muscles are embedded with the “ends” (the neuromuscular junctions) of nerve cells that originate within the brain. Uniquely, facial muscle fibers have multiple endplates (motor endplates) within each muscle compared to other skeletal muscles. This permits the refined movements of facial muscles needed for speech and/or subtle expression of emotion or intent. In response to a thought or feeling, chemicals are released within the central nervous system. These neurochemicals (see following section) travel along nerve pathways leading to one or more facial muscles. At the terminus of their path (the neuromuscular junctions), they initiate a sequence of chemical events that cause the muscle to contract<sup>30</sup>.

### **3.2. The Neurochemistry of Facial Communication**

The neurochemistry of facial communication merits an introduction because neurochemical signaling is the mechanism by which the central nervous system communicates with itself and the rest of the body. Therefore, although facial expression is a localized activity of the face, it impacts on dispersed organ systems, mediates general health, and is associated with affective behaviors. Facial expression achieves its far-reaching influences via neurohormonal emotional modulating systems (neuropeptides) centered in the brain (Prokai

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<sup>30</sup> See <https://basicmedicalkey.com/physiology-of-the-muscular-system> for details.

2008). Neuropeptides may be either neurotransmitters that direct chemical signals locally between proximal nerve cells, or they may be hormones that are disseminated via the circulatory system to distant sites within the body. Neuropeptides are the fundamental mechanism by which the nervous system observes and responds to stimuli. These chemical messengers, made up of small chains of amino acids, are synthesized and released by neurons. Humans have a diverse collection of neuropeptides that can influence a multitude of activities. There are over 100 known neuropeptides<sup>31</sup>.

Neuropeptides are stored and released from vesicles (subcellular “containers”) within neurons. (Ludwig and Leng 2006) calculated that there are ~10,000 vesicles in a single hypothalamic neuron. Each of these neurons releases ~10 million molecules per second. It has been estimated that the contents of hundreds of vesicles will be released from a neuron over a time scale of seconds. So, millions of neuropeptides are likely released in a short burst from just a single cell. The impact of the release of these small protein-like molecules is massive. Neuropeptides have been implicated in various aspects of face-processing<sup>32</sup>. Because a key site for the production and storage of neuropeptides is within the brain’s limbic system (Palkovits 1982), it is not surprising that neuropeptides are tied to the expression of emotion.

A previous review of the literature implicated six neuropeptides associated with the production and/or interpretation of facial expressions: serotonin, oxytocin, dopamine, endorphin, acetylcholine, and noradrenalin (Zeichner, Radlanski, and Zeichner 2021b). Each of these neuropeptides selectively modulates different aspects of facial communication.

#### **i. Serotonin**

Serotonin, (aka 5-HT), is a monoamine neuropeptide. In general, serotonin has been associated with happiness, focus, and calmness. Specifically, pertaining to facial emotion processing, Del-Ben et al. (2008), showed that serotonin modulated brain regions concerned with facial emotion. Also, several studies showed that serotonin facilitated the recognition of positive facial expressions (Harmer et al. 2003; Murphy et al. 2006).

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<sup>31</sup> A resource of data on all known neuropeptides expressed in the human brain has been compiled by the Human Genome Organization Gene Nomenclature Committee (<http://www.neuropeptides.nl/tabel%20neuropeptides%20linked.htm>) (“Gene (Gene Symbol)” n.d.).

<sup>32</sup> Face processing is the neurophysiological process by which humans distinguish, recognize, interpret, and react to faces.

## **ii. Oxytocin**

Oxytocin, the social bonding, nurturing, empathy-inducing neuropeptide, plays a substantial role in facial expressions that sustain social bonding, particularly, smiles among kin, friends, and/or community members (Rychlowska, Wood, and Niedenthal 2017). The mechanism by which oxytocin is thought to relate to facial expression is multifold. For example, reciprocal smiling between parent and infant involves oxytocin (Riem et al. 2012). Secondly, oxytocin enhances functional brain connectivity<sup>33</sup> and stimulates the reward centers of the brain thus enabling a parent to experience joy and involvement with their infant (Peltola, Strathearn, and Puura 2018). The resultant positive facial expression communicates to the infant. Additionally, oxytocin has been shown to enhance one's ability to appreciate the facial expressions of others by "the theory of mind" (ToM) (Lee et al. 2014). Finally, oxytocin increases a person's attention to the eyes of faces—an important aspect of interpreting facial displays (Le et al. 2020).

## **iii. Dopamine**

Dopamine (a contraction of 3,4-dihydroxyphenethylamine) is nicknamed the "feel good" neuropeptide. It is released when one experiences reward-related pleasure. Dopamine participates in several aspects of facial expression—most particularly to the large vocabulary of pleasurable facial displays such as smiles of satiation, reward, reinforcement, pleasure, and sexual gratification. Also, dopamine has been shown to play a role in motor control of facial muscles (Lotharius and Brundin 2002; Zhang and Burock 2020). Furthermore, dopamine interplays with other neuropeptides that manifest as a facial expression. For example,  $\beta$ -endorphins suppress the release of gamma-aminobutyric acid (GABA), which, in turn, results in the accumulation of dopamine in the nucleus accumbens and ventral tegmentum of the brain (Turton and Lingford-Hughes 2020), thus leading to a facial display signaling positive affect.

## **iv. Endorphin**

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<sup>33</sup> Functional connectivity is a measurement used in fMRI imaging studies to quantify the extent of the connection between linked regions of the brain.

$\beta$ -Endorphins are neuropeptides that exert effects both within the brain and in other regions of the body. They are best known for their pain-relief and mood-elevating effects.  $\beta$ -Endorphins are produced primarily in the anterior lobe of the pituitary gland, and in pro-opiomelanocortin (POMC) cells located in the paraventricular nucleus of the hypothalamus (Pilozi, Carro, and Huang 2020). This peptide readily distributes via neural tracts to other areas of the brain (Dalayeun, Norès, and Bergal 1993).

$\beta$ -Endorphins have been shown to modulate facial expression. For example, a study by (Hicks et al. 2019) examined the mechanisms of “runner’s high”. They described the link between  $\beta$ -endorphin and the feeling of euphoria experienced by athletes engaged in endurance running. In this instance, a physiologic activity such as exercise triggers a limbic response via several neuropeptide intermediaries to generate a feeling. The neuropeptide, in turn, signals the facial muscles to generate a euphoric facial display characteristic of “runner’s high”.

#### **v. Noradrenaline**

Noradrenaline and adrenaline<sup>34</sup> have been associated with feeling fear or ill-at-ease and they are linked also to the stress response. Modulating the levels of these neuropeptides has been shown to mediate mood, and thereby influence both the production of facial displays and the perception of facial displays. For example, Berk et al. (2001) reported that laughter reduced adrenalin (a derivative of noradrenalin) levels in experimental subjects, thus diminishing the feeling of stress. Consequently, the faces of the subjects reflected happiness. Moreover, data from Harmer et al. (2001) suggested that noradrenergic processes are not only involved in stress responses, but also in the perception of facial expression. Harmer administered propranolol, a drug that blocks adrenergic receptors<sup>35</sup> in the brain, or a placebo to experimental subjects. The subjects viewed photos of the six universal facial expressions of emotion plus a neutral face. Harmer found that the experimental subjects exhibited

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<sup>34</sup> The name "noradrenaline" (from Latin *ad*, "near", and *ren*, "kidney") is more common in the United Kingdom, whereas "norepinephrine" (from Ancient Greek *ἐπί* (*epí*), "upon", and *νεφρός* (*nephros*), "kidney") is usually preferred in the United States.

<sup>35</sup> Adrenergic receptors are sites on neurons that bind to the neurotransmitters adrenaline and noradrenaline, which induce a fight-or-flight response in the body and play a role in attention, focus, panic, and excitement.

selectively impaired recognition of sad faces compared to controls. Thus, noradrenaline may not only produce happy facial expressions, but also may impair the perception of sad faces.

#### **vi. Acetylcholine**

Acetylcholine, another neurotransmitter within the brain, has been implicated in memory, motivation, arousal, and attention (Sam and Bordoni 2022). These neural states are the prerequisite for facial communication. Acetylcholine is the chemical primer for face-processing. Not only is acetylcholine needed for interpreting facial displays, but also acetylcholine is required for proper contraction of the muscles of facial expression. Thus, acetylcholine plays a vital role in facial communication.

### **3.3. The Afferent Pathways of Facial Communication<sup>36</sup>**

#### **i. An Overview of the “Classic Model”<sup>37</sup> of Neural Mechanisms by Which Humans Recognize Conspecifics and Interpret Facial Expression**

The development of the classic face-processing model emerged from the work of (Kanwisher, McDermott, and Chun 1997). Kanwisher and coworkers identified a cluster of neurons within the right fusiform gyrus that preferentially responded to faces. Kanwisher termed this face-responsive region, the fusiform face area (FFA). Additionally, the investigators observed increased activation associated with the inferior bank of the right superior temporal sulcus<sup>38</sup> (STS). Subsequent investigations determined that face-processing went beyond the mere perception of faces attributed to the FFA. Humans have the ability to perceive and identify faces, as well as to recognize facial expressions. (Haxby, Hoffman, and Gobbini 2000) proposed an extended network of areas distributed throughout the brain that could coordinate the complex tasks of processing faces. Their model integrated regions of the

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<sup>36</sup> In this thesis, afferent and efferent pathways are presented separately. Afferent appears first in the text because it is more complex than the efferent system.

<sup>37</sup> The “classic model” of face-processing was put forth more than twenty years ago by (James V. Haxby, Hoffman, and Gobbini 2000) and subsequently extended by (James V. Haxby and Gobbini 2011).

<sup>38</sup> A sulcus is the depression between adjacent gyri. The “bank” refers to the neuroanatomical term for the progressive rise on either side of this depression.

limbic system (to account for emotional expressions) and prefrontal cortical regions (to account for judgement, valence, and to moderate affect). Summarized in **figure 37** is an overview of human face-processing according to the extended face-processing “classical model”. The classical model conceives four processing hubs with neural connections both with themselves and with connections to each other. Thus, each specialized brain region is a node that acts in concert with other nodes on a distributed neural network.

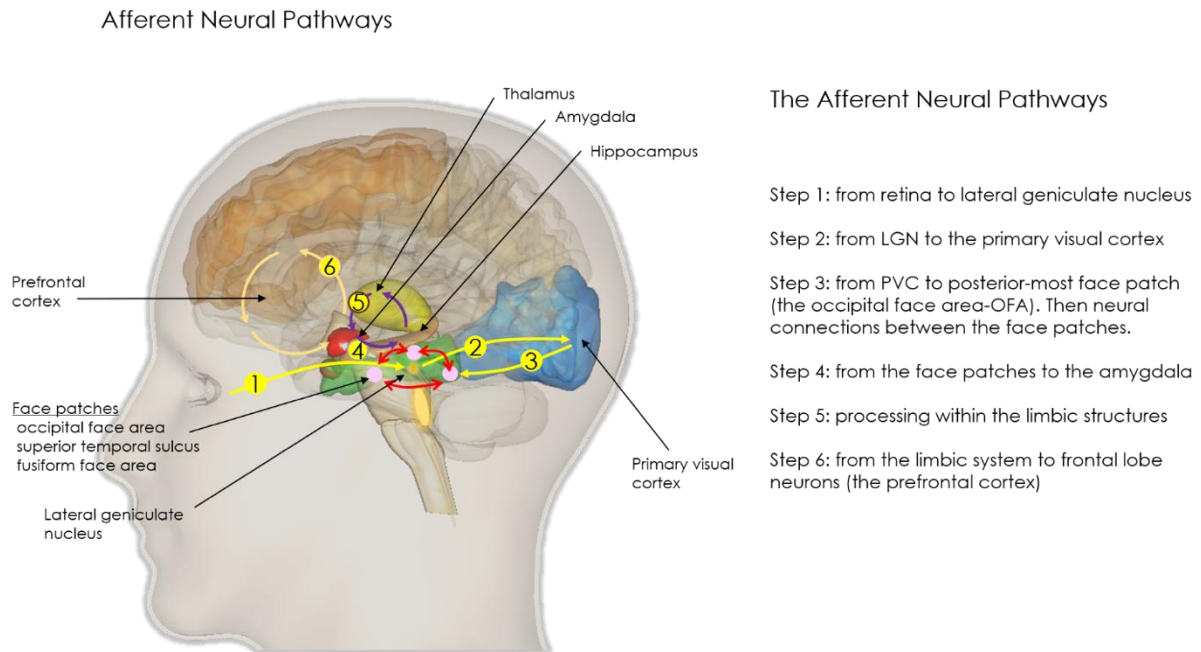


Figure 37. The afferent neural pathways. Source: Author’s original.

The dominant afferent neural pathway for face recognition and interpretation originates via the geniculo-striate (GS) pathway. In the GS pathway, visual stimuli from the retina travel along the optic nerve to the lateral geniculate nucleus (Step 1). Then via the optic radiations to the primary visual cortex in the occipital lobe of the brain (Step 2), where signals are binarily decoded for further processing. The decoded visual stimuli are conveyed next to the face patches for further discrimination (Step 3). From the face patches, the signal is distributed to the limbic system (Step 4), wherein lies the amygdala, (responsible for emotional regulation and supplying emotional content); the hippocampus, (the memory center adding memory content); the thalamus and hypothalamus, (home of neuropeptide production) and the anterior insula<sup>39</sup> that further process the signal (Step 5). The elements of

<sup>39</sup> Some anatomists consider the anterior insula to be a functional part of the limbic system.

the limbic system loop the signal between the frontal lobe structures, moderators of face-processing, (Step 6).

## **ii. The Need for an In-Depth Model of Face-Processing**

It has been long-established that the processing of face information involves a distributed neural network. Each node and/or hub on the neural network makes a unique contribution to the recognition, interpretation, production, or response to faces (Zeichner, Radlanski, and Zeichner 2021). Yet, new knowledge from diverse fields of study has accumulated in the past decade: additional nodes in the extended network, new internodal connections, more information about pathomechanisms involving facial communication disorders. Recent work from our laboratory has determined that there are no fewer than fifty interconnected anatomical sites that participate in processing faces<sup>40</sup>. Because the field lacked a comprehensive, up-to-date model to describe the physiology of facial communication, this thesis collated the various pieces of published research, fit the segments of knowledge together, and using a meta-synthetic methodology, extended the classical model beyond its previous iterations. Thus, the subsequent subsections of this chapter report a proposed contemporary face-processing model and postulate a network map for a specialized processing task to exemplify the future direction of this thesis project.

## **iii. A Contemporary Model of Face-Processing**

In this contemporary, expanded model of face-processing, the interpretation of a facial expression begins with the visual apparatus—specifically the receptors of the retina. Next, the fibers of the optic nerve convey the visual signals via the optic tract. In turn, the optic tract sends most fibers through a junctional point known as the lateral geniculate nucleus. Then, via the optic radiations, the signal reaches the primary visual cortex (PVC) in the occipital lobe of the brain. The visual stimulus transmits via axonal<sup>41</sup> conduction to the most posterior layer of the PVC. This region is designated V1. The signal is propagated

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<sup>40</sup> Work in progress—unpublished.

<sup>41</sup> An axon is a projection of a neuron that carries impulses away from the body of a nerve cell.

anterior-ventrally through the extra-striate<sup>42</sup> layers of the PVC (i.e., V2, V3, hV4<sup>43</sup>) before it is relayed to face-specific clusters of neurons within the temporal lobes, the aforementioned face patches. There is a high level of neuroactivity in the PVC within the initial microseconds of stimulation. Almost instantaneously, the visual signal is binarily decoded as face vs. object. It is believed that selected neurons in V1 extract edges, thus crudely sorting objects with straight edges from rounded faces (Blumberg and Kreiman 2010). There is an auxiliary, primal neural pathway called the reticulo-colliculo-thalamo-amygdala pathway (RCTA) that assists in discriminating faces from nonfaces. The RCTA pathway was described in detail in Chapter II. It's role in facial recognition is further elucidated later in this chapter (Section 3.5.i)

The work of (Petro et al. 2013) uncovered another critical step in face-processing that occurs in V1. In an fMRI experiment, they reported early gender and threat decoding of faces in V1. Whereas this was not discussed in the early literature, it is biologically advantageous to rapidly discern gender (for mating purposes) and friendly vs. threatening faces for survival of society. Thus, the early decoding of these facial features is critical. The findings of Axelrod et al. (2019) underscored that critical facial features, such as gender and age of a face, are discerned also in V1 within 250 milliseconds after stimulus.

Because faces are of high relevance to humans and other social animals, face-related signals are preferentially routed via what is known as the ventral visual stream, or pathway (Grill-Spector et al. 2018). The ventral stream travels antero-ventrally from V1 through V2, V3 and hV4 toward the temporal lobes (See **figure 38**).

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<sup>42</sup> V1, when viewed microscopically, has stripes, so it is called “striate”. The other layers of the PVC do not have microscopic stripes so they are designated “extra-striate” layers.

<sup>43</sup> hV4 is the designation for the region of the visual cortex in humans that involves complex coding of color and form—critical for coding faces. In the published literature, the “h” preceding V4 makes clear this region refers to humans, whereas simply “V4” refers only to monkeys.

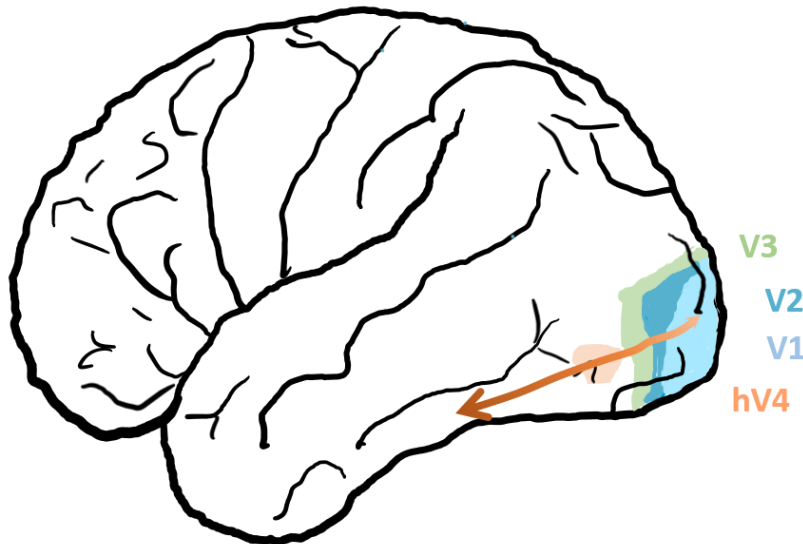


Figure 38. The ventral stream through four regions of the primary visual cortex, as visual signal is propagated to the face patches. Source: author’s original.

From V1, the visual stream feeds forward to V2. In primates, V2 has been shown to differentiate color, spatial frequency and object orientation (Anzai, Peng, and Van Essen 2007). The third visual cortex, V3, is situated anteriorly to V2. Its role in face-processing is believed to be to discern motion (Tootell et al. 1997). The finding that the pSTS (the most dorsal face patch) also processes facial motion correlates with its direct connection with the dorsal aspect of V3. Anterior to V3 is hV4. Notably, the face-selective regions of hV4 abut the OFA (the most posterior face patch). hV4, like V2, differentiates color, but at a much more refined level. Additionally, hV4 resolves high spatial frequency features (Winawer and Witthoft 2015).

Upon leaving the PVC, the visual signals are relayed, via the aforementioned ventral pathway, to face-specific clusters of neurons within the temporal lobes, the “face patches”. The face patches form the core of the face-processing system (according to the classical model). Researchers have identified three types of face patches in humans—the occipital face area (OFA), the fusiform face areas (FFA)<sup>44</sup> and the posterior superior temporal sulcus (pSTS). These clusters of neurons are symmetrically situated bilaterally. Thus, there are eight

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<sup>44</sup> The fusiform face area (FFA) generally is described in the literature as a single “face patch”. However, the FFA has been demonstrated to consist of two separate clusters of neurons within the fusiform gyrus. The first cluster is located on the posterior lateral aspect of the fusiform gyrus and is designated the pFus-faces. The second cluster is located on the lateral fusiform gyrus, about 1–1.5 cm anterior to pFus-faces, and tends to overlap the anterior tip of the mid-fusiform sulcus (MFS). This patch is referred to as mFus-faces (Grill-Spector et al. 2018).

face patches (four in each hemisphere) that are dedicated to processing faces (see **figure 39**).

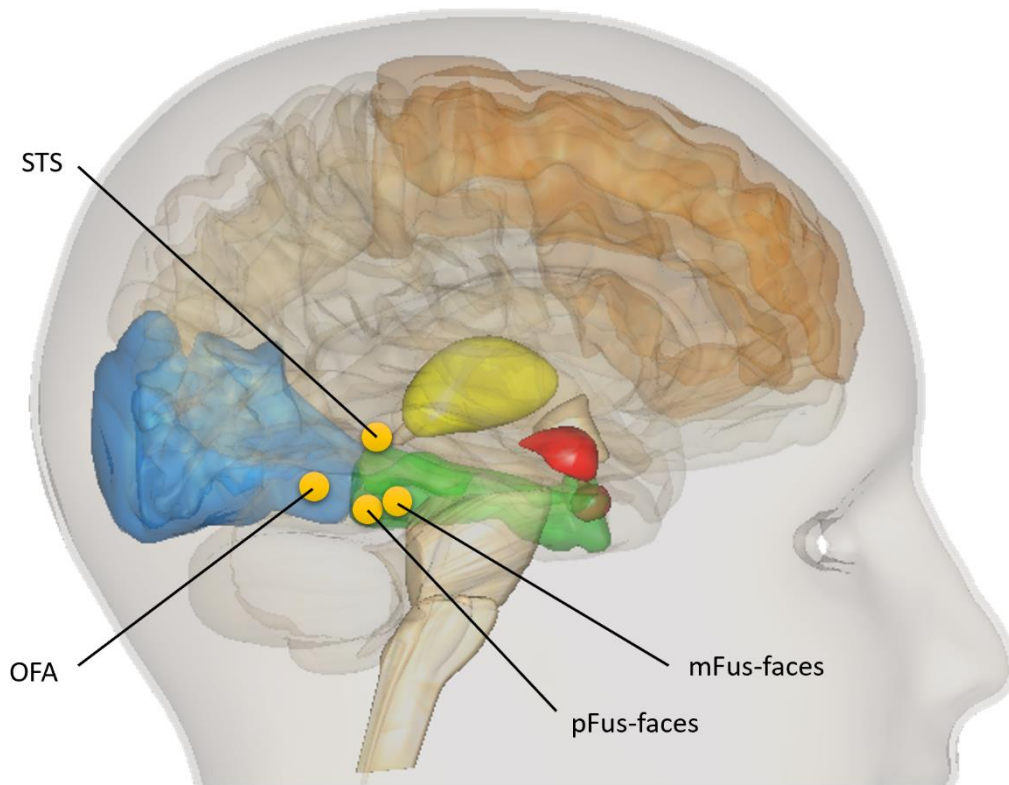


Figure 10 The face patches are the neuronal clusters associated with face-processing. pSTS = (posterior Superior Temporal Sulcus), OFA = (Occipital Face Area). The mFus-faces (Mid-Fusiform Face Area) and the pFus-faces (Posterior Fusiform Face Area) are known collectively as the FFA (Fusiform Face Area). The pSTS is a cluster of neurons situated within the superior temporal sulcus near the junction with the parietal lobe. The OFA is located near the junction of the occipital and temporal lobes. The FFA is two distinct clusters of neurons within the fusiform gyrus (colored in green). Structures of the limbic system are shown for orientation (yellow = thalamus, red = amygdala). Source: author's original contribution.

The face patches are functionally interconnected, and each face patch has a specific function. These neurons work together to integrate the various aspects of facial recognition. For example, the OFA preferentially represents the *components* of a face (including the eyes, nose, and mouth). The OFA is located closest to the primary visual cortex from where it receives its stimuli. Thus, the OFA is considered the gateway to the other face patches (Pitcher, Walsh, and Duchaine 2011). Another face patch, the FFA, contributes to a different aspect of face-processing. In contrast to the OFA's focus on face *parts*, the FFA is believed to be involved in the *holistic processing* of faces, and it responds to the *shape* of facial features as well as the *spacing* between them (Liu, Harris, and Kanwisher 2010; Yovel and Kanwisher 2004). Additionally, the studies of Bernstein et al. (2018) showed that the FFA is implicated in gender and identity face-processing.

The third face patch, the pSTS, also makes a specialized contribution to face perception and recognition. The pSTS is thought to be responsive to *movement-specific* facial expression (Iidaka 2014; Pitcher, Duchaine, and Walsh 2014; Srinivasan, Golomb, and Martinez 2016). Facial movements such as eye-gaze or lip movements are critical to the facial communication process. More recently, Elbich, Molenaar, and Scherf (2019) reported connections from the right pSTS to the right OFA and to the right FFA. Together, the face patches process the visual signals that enable humans to recognize faces and interpret facial expressions. These small collections of specialized cells are the core of communication and socialization. The right pSTS has an atypical connection to the left cerebellum. This unexpected connectivity is discussed in a footnote later in this chapter.

The face patches are also interconnected with the limbic system (which constitutes another hub in the extended face-processing network) via a “feed forward” mechanism, i.e., a unidirectional connection from the FFA to the amygdala. Within the limbic system are a group of central nervous system structures, important to emotional facial expression. Components of the limbic system contribute to the emotional and memory content of facial expressions and interpretations. The nodes within the limbic system are listed in **Table 8** along with their anatomic relationships and their roles in facial communication. The face-processing nodes of the limbic system are depicted with pink-colored labels in **figure 40**,

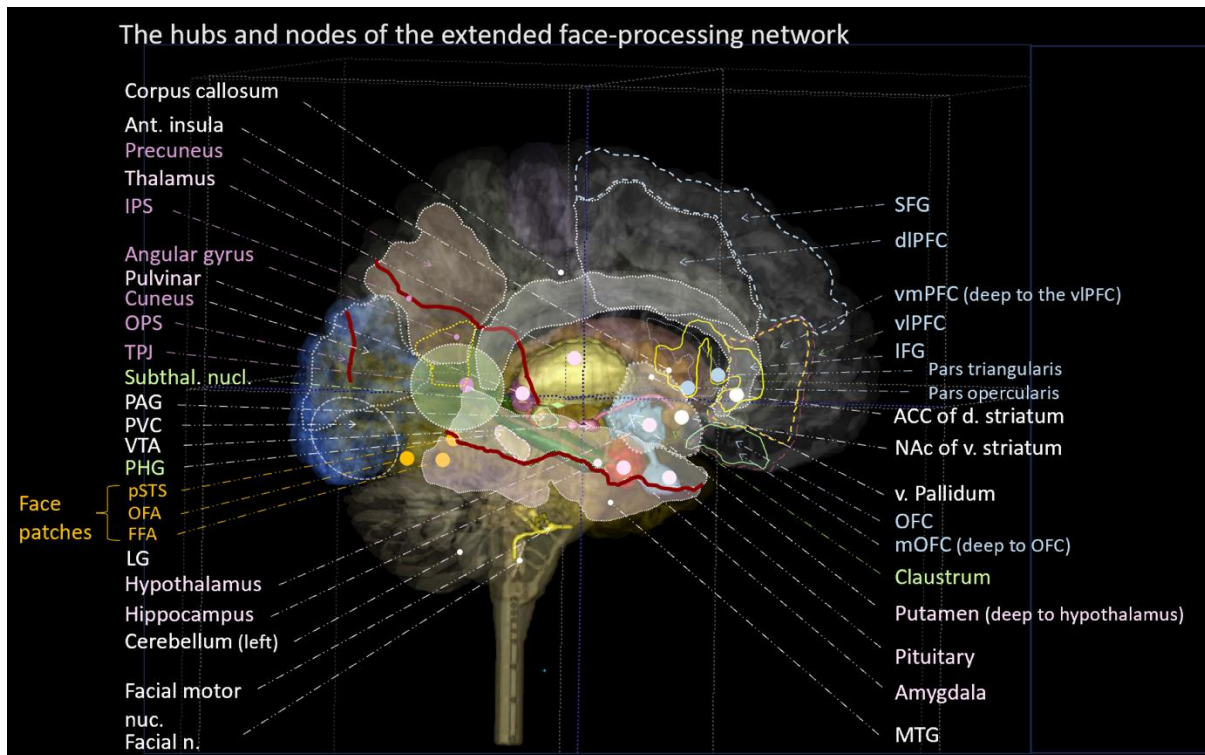


Figure 40. Hubs and nodes of the extended face-processing network. A systematic trimodal, multidisciplinary literature analysis revealed fifty-seven distinct nodes (forty-four without counting bilaterally active nodes) implicated in face-processing. The nodes are

interconnected. Nodes labeled in pink color are the **limbic hub**. Nodes labeled in pale blue color are part of the **prefrontal cortical network**. Nodes labeled in orange color constitute the **face patch network**. Nodes labeled in mint green form a **paralimbic complex** of nodes. Nodes associated with the **parietal/occipital hub** are labeled in lavender color. Uncategorized (“orphaned”) nodes are labeled in white. Source: author’s original.

There are secondary connections between the amygdala and hippocampus (Cao et al. 2020), the amygdala and various regions of the prefrontal cortices (Gangopadhyay et al. n.d.) There are further connections to other core limbic structures, and connections to caudal occipital and parietal locations in the network (Rus et al. 2016). Additionally, Lahnakoski et al. (2012) reported the interconnection of the amygdala to the pSTS which they characterized as a secondary hub richly interconnected with the amygdala and nodes in the fronto-temporal, frontal parietal, and fronto-insular networks. More details about the roles of the limbic system are addressed in section 3.5, wherein specialized aspects of facial physiology are used to illustrate the complex arrangements of nodes and neural networks.

There are nodes on the expanded face-processing model proximal to the limbic system. I term these sites “paralimbic nodes”. Most act as relay junctions between limbic elements and peripheral nodes in the extended network. The paralimbic nodes are described in **Table 9**. These areas are depicted with lime green-colored labels in the above **figure 40**.

The limbic structures also connect with higher levels of the brain, i.e., cortical structures. For example, the prefrontal cortex interconnects with the limbic system and moderates the emotional responses to the perception of facial displays (Aharon et al. 2001; Ishai 2007; Kranz and Ishai 2006; Troiani et al. 2016; Heberlein et al. 2008; Banks et al. 2007). The nodes within the prefrontal cortical complex are listed in **Table 10** along with their anatomic relationships and their roles in facial communication. The face-processing nodes of the prefrontal cortical complex are depicted with pale blue-colored labels in the above **figure 40**.

In other regions, such as the corpus striatum, the brain interprets subtle variations in facial expressions, such as distinguishing the difference between a mother’s smile and a lover’s smile or distinguishing between the face of a lover or a friend (Zeki 2007; Bartels and Zeki 2000). Such interconnections with higher levels of the cortex are termed top-down

regulation. Top-down regulation dominates the specialized communication pathways illustrated in section 3.5.

**iv. A Specific Contemporary Model of Face-Processing Constructed from Meta Syntheses**

**Figure 41** is an exemplar synthesized from data compiled in this project. The model demonstrates the elements of a processing network derived from a supplemental investigation I conducted into the pathophysiology of smiling. This figure is a compendium of multidisciplinary research on the pathophysiology of the human smile.

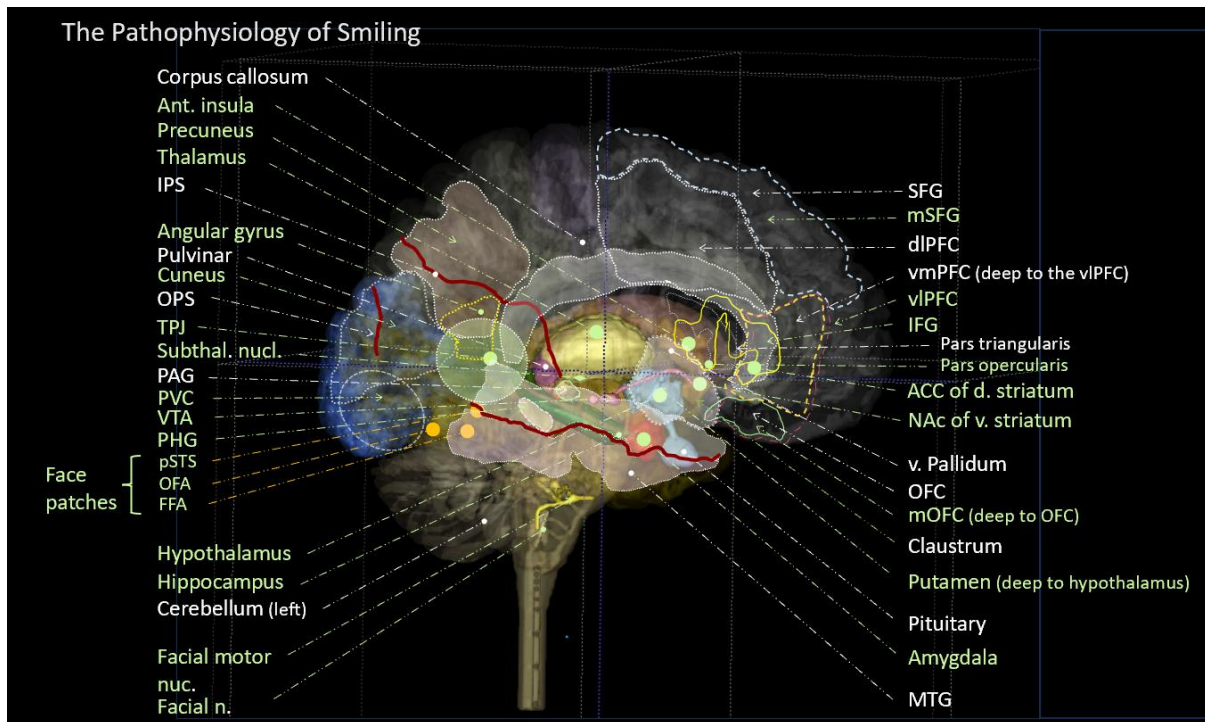


Figure 41. The pathophysiology of smiling and a network map. This analysis revealed fifty-seven distinct nodes (forty-four without counting bilateral active nodes). Twenty-six nodes were implicated in the facial expression of happiness as revealed by smiling or dysfunctional smiling. The nodes labeled in green are part of the “smiling” network.

**3.4. The Efferent Pathways of Facial Communication**

Generating a facial expression is less complex than interpreting another’s facial expression. Making faces elicits the elements of the efferent pathways. It is a two-step process. In this aspect of facial communication, the desire to express an emotion originates

within the limbic system. The amygdala signals to the facial motor nucleus in the brainstem (Step 1) directing humans to make a facial display in accordance with the neuropeptides secreted within the hypothalamic tract, as discussed in the previous chapter. In most instances, the neurochemical processes are rapid and the face immediately communicates the emotion that the person feels. **Figure 42** illustrates the mechanism by which humans produce a facial display.

The Efferent Neural Process of Facial Expression Production

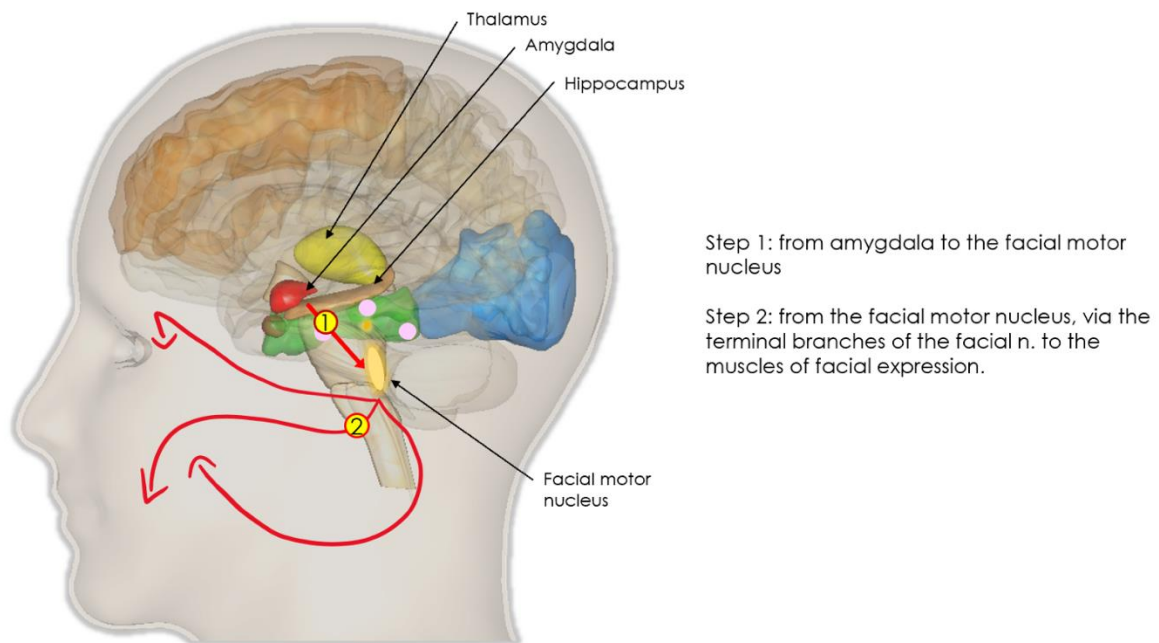


Figure 42. The efferent process of facial communication. Source: author's original contribution.

### 3.5. The Physiology of Specialized Aspects of Facial Communication

Certain aspects of facial physiology are central to human communication. It is instructive to understand the physiological basis of these core processes.

#### i. **Pareidolia: The Neural Mechanism for Finding Faces Everywhere**

People often report seeing a face in a tree, Jesus in toast, or the Virgin Mary in a tortilla. Such illusions are known as face pareidolia. This section begins with a discussion of face pareidolia because this intriguing condition can inform about the neural mechanisms associated with facial recognition.

Whereas collections of objects that look like faces abound on social media, face pareidolia is not a product of human culture<sup>45</sup>. A recent discovery that rhesus monkeys experience face pareidolia when viewing pareidolia objects and when viewing the faces of their conspecifics, points to the fact that face pareidolia is driven by features of the nervous system that are shared across primate species (Taubert et al. 2017; 2018). The human brain has evolved to detect faces rapidly because it is socially advantageous.

Pareidolia, a preferential bias toward false positive identification of faces, can be understood as a conspicuous false positive in a neural system finely tuned to detect and extract sensory cues from human faces. Face pareidolia suggests that the human visual system is highly tuned to perceive faces, likely due to the social importance of faces and our keen ability to process them (Liu et al. 2014). The social consequence of failing to detect a true face is high, thus the system has adapted toward a preferential bias for false positives.

Cumulative research on pareidolia has shown that similar brain loci and neural pathways activate for illusory faces as activate for human faces. In an fMRI experiment, Liu et al. (2014) reported activation of the FFA in subjects viewing pareidolia objects. They also showed activity in regions of the prefrontal cortex and the primary visual cortex like that observed when subjects viewed human faces. Their findings suggested that human face-processing has a strong component whereby sensory input, with even the slightest suggestion of a face, can result in the perception of a face, albeit a misperception. These fMRI findings were consistent with electrical and magnetic-evoked responses in subjects viewing pareidolia objects and human faces (Hadjikhani et al. 2006; Proverbio and Galli 2016). In addition, pareidolia seems to reflect the activation of sensory mechanisms that extract social information from human faces, such as gaze, head, and body direction. That is, evidence that pareidolia objects with eye-like features contribute reflexive shifts in the spatial direction of an observer's attention (Takahashi and Watanabe 2013) producing the same response as to real faces. That is, a human will engage the “eyes” of a pareidolia object in the same way that they would look into the eyes of a real person.

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<sup>45</sup> Examples of objects that look like faces can be found at <https://www.flickr.com/groups/facesinplaces/pool/>.

Studies of pareidolia point to a core set of facial features that trigger orientation to faces. The features consist of two eye-like dots and a central circle within an oval (a “protoface”). The literature reflects that a protoface triggers a rapid subcortical neural pathway, the RCTA pathway (previously described in Chapter II) that accounts for rapid identification of faces. For example, an electrophysiological study by (Van Le et al. 2020) in trained macaque monkeys, suggested that line drawings of protofaces preferentially activated the superior colliculus (part of the RCTA pathway). Specifically, regions within the superior colliculus responded stronger and faster to protofaces than to nonface patterns. Correspondingly, Johnson et al. (1991) reported that nine-month-old human infants oriented to protofaces, but not to patterns of inverted or improperly-placed protoface features. Thus, there appears to be a primitive subcortical pathway in both human and nonhuman primates that selectively orients to faces with great rapidity. Furthermore, Shah et al. (2013) showed that even in adults with autism spectrum disorder, a condition characterized by deficits in facial recognition, subjects were able to track protofaces comparable to neurotypical controls. The literature, when viewed collectively, suggested that there is a core, facial recognition neural pathway that exists in nonhuman primates, human infants, and persists into human adulthood.

## **ii. How Humans Recognize the Faces of Other Humans**

The notion that facial identity-processing is accomplished via a network of nodes spread across various regions of the brain<sup>46</sup> was proposed more than twenty years ago by Haxby, Hoffman, and Gobbini (2000), based on earlier work of Bruce and Young (1986). Since then, other models have contributed to understanding how humans recognize conspecifics by their faces. The classic view is that face identity is processed along a pathway (a DNN) consisting of a “core” processing area and an “extended” network mainly involving elements of the limbic system. Later research implicated regions of the prefrontal cortex in processing facial identity. This thesis analyzed existing published models of face identity processing, then integrated the classic models with data from contemporary research to propose an updated view about how humans recognize other humans. The background is

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<sup>46</sup> Haxby et. al.’s original concept of dispersed nodes along an extended neural pathway is popularly known today as a distributed neural network (DNN).

presented in the ensuing paragraphs. This section culminates with the meta synthesis of all the diverse studies and proposes a new and extended model for facial identity processing.

The classic view is that face identity is processed along a ventral temporal pathway, including the occipital face area (OFA) (Gauthier et al. 2000) and the fusiform face area (FFA) (Kanwisher, McDermott, and Chun 1997). Several fMRI studies have shown that identity information is decoded in the OFA and the FFA (Nestor, Plaut, and Behrmann 2011; Natu et al. 2010; Anzellotti, Fairhall, and Caramazza 2014; Anzellotti and Caramazza 2016; Dobs, Bühlhoff, and Schultz 2016). There is fMRI evidence that facial identity is processed also in the posterior superior temporal sulcus (pSTS) (Dobs, Bühlhoff, and Schultz 2016; Anzellotti and Caramazza 2016).

Subsequent to processing in the aforementioned face patches, the signal is routed to the limbic system. Elements of the limbic system interact to facilitate the recognition and identification of faces. For example, the amygdala contributes to the facial recognition process (Cao et al. 2020; Rutishauser et al. 2011; Mormann et al. 2015; Herrington et al. 2011). Also, within the limbic system, connections to the hippocampi (thought to be crucial structures in memory consolidation) play an intriguing role in facial recognition. In 2005, Quiroga et.al. reported that single neurons within the hippocampi coded for specific faces. This study highlighted the import of a single brain cell in face recognition. That is, a single neuron in the left posterior hippocampus of one experimental subject responded to all pictures of actress Jennifer Aniston, and also to Lisa Kudrow, her co-star on the TV series "Friends", but not to pictures of Jennifer Aniston together with actor Brad Pitt, and not, or only very weakly, to other celebrity and non-celebrity faces, landmarks, animals or objects. In another experimental subject, pictures of actress Halle Berry activated a single neuron in the right anterior hippocampus, as did a caricature of the actress, images of her in the lead role of the film "Catwoman," and a letter sequence spelling her name. It seems where faces are concerned, a single neuron may code a memory for an individual identity.

The amygdalae and hippocampi play another interesting role in facial recognition. The work of Cao et al. (2020) provides insight into these roles. In this study, the investigators recorded neural activity from the amygdala and hippocampal neurons in neurosurgical patients using implanted depth electrodes while the subjects viewed static images of famous faces. Cao observed that there were feature-selective neurons within the amygdala and

hippocampus. One category of neuron responded only to eyes. The other category, only to mouths. Whereas both eye-sensitive and mouth-sensitive classes of neuron were found in both amygdala and hippocampal regions, the percentage of eye-sensitive neurons was higher in the amygdala than in the hippocampus (This will have bearing in the next chapter where I discuss neuropsychiatric conditions, such as autism spectrum disorder and major depressive disorder). Furthermore, the authors determined that these feature-selective neurons coded for judgment of social traits, thus providing insight into the neural mechanism for how humans judge other humans from their facial features within milliseconds. Cao reported that the firing rate for fixations on the eyes significantly correlated with the perceived social traits of *warm*, *practical*, and *charismatic*. Mouth-selective neurons were associated with the social traits of *competent*, *feminine*, and *youthful*. The authors reported that the above results were primarily driven by amygdala neurons. (The stronger correlations between neuronal responses and social trait judgments in the amygdala was consistent with human lesion studies). Thus, in addition to participating in facial recognition, it appears that the unique functional role of feature-selective neurons in the amygdalae and hippocampi is to impart social judgement to the features of faces.

There is evidence that the amygdalae play a role in discriminating between happy faces and fearful faces. In another study of neurosurgical patients with implanted electrodes, Wang et al. (2014) demonstrated that there were distinct neurons within the amygdalae that were responsible for distinguishing between happy and fearful faces. Interestingly, in a fMRI study, van Harmelen et al. (2013) investigated whether adult patients and healthy controls (HC) reporting childhood maltreatment showed enhanced amygdala reactivity to emotional faces compared to patients and HC reporting no abuse. They determined that patients reporting emotional abuse or neglect (even without physical or sexual abuse) showed amygdalar hyperactivity and concurrent enhancement of the amygdala-medial prefrontal cortex for *all* emotional faces. One might predict from the literature that because of the amygdala's prominent association with fear, one would expect hyperactivity to negative emotions only. However, the amygdala showed hyperactivity to happy faces. The authors suggested that adults who suffered childhood maltreatment compensate for their anxious or depressive episodes by being attracted to friendly faces and avoiding angry faces. It is remarkable, and not generally appreciated, that the human face-processing system functions to self-cure two of the most prevalent and debilitating neuropsychiatric disturbances (anxiety and depression). Such examples will be explored in Chapter IV, "The Pathology of the Face".

Frontal lobe structures also have been shown to contribute to facial identity-processing. Guntupalli, Wheeler, and Gobbini (2017) showed a progressive pathway by which humans decipher the identity of a face regardless of direction from which the face is viewed. The investigators identified via fMRI that the view-invariant representation of identities in the human face perception system is accomplished in the right inferior frontal face area (rIFFA) of the frontal cortex. There are other frontal lobe structures involved in top-down modulation<sup>47</sup> of facial recognition. Recently, Nikel et al. (2022) identified a facial identity-specific region within the frontal lobes, specifically the pars opercularis in the right inferior frontal gyrus. In this fMRI experiment, subjects viewed faces and non-faces while the experimenters measured neural responses. Among the face-selective areas, the pars opercularis responded to faces, but preferentially to animate faces. Additionally, Blank, Wieland, and von Kriegstein (2014) reported that the pars triangularis in the inferior frontal gyrus (IFG) was involved in facial identification based on a metaanalysis of patient lesion data.

### **iii. The Special Case: How Humans Recognize and Distinguish Their Own Faces**

It is fascinating to contemplate how humans recognize their own faces and distinguish themselves from others. Several investigations described the neural processes underpinning self-face recognition (Platek et al. 2006; Kircher et al. 2000). The neural networks are expansive. Kirscher et al, attempted to map out the neural systems involved in self-face recognition. They identified activation of the right-sided limbic system, including hippocampus, insula, anterior cingulate, as well as the junction between the right superior/middle temporal lobes (BA21, a.k.a., the STS)<sup>48</sup>, the left inferior parietal gyrus (BA 40-aka the intraparietal sulcus), the left middle frontal gyrus (BA 8/9-aka the IFG), and the superior frontal gyrus (BA 45/46 aka, the mPFC). In addition, the right precuneus, the right

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<sup>47</sup> Top-down modulation in neuroscience is when signals travel from the higher cortical centers of the brain to the subcortical regions.

<sup>48</sup> BA is the abbreviated form for Brodmann Area. Korbinian Brodmann (1868-1918) was a German neurologist who is believed to be the first to map the cerebral cortex.

subthalamic nucleus and the cerebellum<sup>49</sup>, on the left side, were activated. Platek et al. (2006) similarly described bilateral, multi-lobal activation of brain regions recruited in discriminating one's own face. In their experiments, brain response to self-face showed activation in the right superior frontal gyrus, the right inferior parietal lobe, the left middle temporal gyrus and the right medial frontal lobe. Moreover, the authors reported activated regions common to Theory of Mind processes (the anterior temporal lobes).

The work of Apps et al. (2012) called attention to the complexity and keen specificity of selected neurons in face-processing. In an fMRI experiment, Apps addressed the specific questions; what regions of the brain are activated when we look at our own faces in a mirror, and what regions are activated when we view photographs of our past self? The researchers reported that the results of this study suggested that recognizing one's past and current facial appearances relies on processing carried out in distinct neural circuits involving multiple regions of the brain, including the temporoparietal junctions (TPJs). Noteworthy was the observation that *different* regions of the temporoparietal junctions were recruited to recognize one's current face from one's past self.

In an fMRI experiment, Sugiura et al. (2012) tasked subjects with identifying pictures of their own faces in a group of other faces. The subjects showed an enhanced response in the ventral medial prefrontal cortex (vmPFC) and right occipitoparietal sulcus when selecting and identifying themselves amongst a collection of others.

#### **iv. The Physiology of Core Social Facial Functions—Gender, Race, Age, Health, and Affective State**

There are core functions of facial interpretation that are essential to survival. The face is so important that the human brain devotes more neural “real estate” and computing power to faces than any other aspect<sup>50</sup>. These physiological processes are almost instantaneous.

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<sup>49</sup> Conventional neurophysiology associates the cerebellum with the control of motor functions. But, when it comes to face-processing, the cerebellum plays an atypical role in a cognitive process. Specifically, identifying one's own face. The reason likely is an obscure anatomic neural connection between the left cerebellum and the right pSTS.

<sup>50</sup> It is estimated that the brain is comprised of 86 billion neurons and more than a trillion synapses. Much of this is associated with faces. The second most attention in the brain is given to hands, and the third most real estate is

When humans view another human's face, there is an immediate determination of: gender, race, kinship, age, health, and affective state of the other human. These five critical neurophysiological processes are discussed in the paragraphs below.

**a. Gender**

Face gender perception is vital for survival because this function contributes to mate selection. Neuroimaging studies demonstrated that face gender perception involves the occipital face area (OFA), lateral fusiform gyrus (LFG), and fusiform face area (FFA) (Podrebarac et al. 2013; Wiese et al. 2012; Freeman et al. 2010). Additionally, Kaul, Rees, and Ishai (2010) reported activation of the OFA, FG, STS, inferior frontal gyrus (IFG), insula, and orbitofrontal cortex (OFC). Initial perceptual representation regarding face gender is processed in the FFA and LFG (Podrebarac et al. 2013; Freeman et al. 2010). The OFA is involved in the initial processing stage of the face perceptual network and spatial relation of faces (Wiese et al. 2012).

There appears to be two stages of gender determination in human face-processing. There is an initial structural feature-dependent gender determination, followed by a subsequent holistic face-processing mechanism. Using magnetoencephalography (MEG), (Liu, Harris, and Kanwisher 2002) established that face-processing proceeded through two stages: an initial stage of face categorization occurring 100 milliseconds after the visual stimulus, and a later stage at which the identity of the individual face is extracted at 170 milliseconds following the stimulus. Thus, the two stages integrate facial information that results in an ultimate gender determination. Therefore, humans have developed a two-stage neurophysiological process whereby they can determine suitability of a conspecific for mating based on facial features in less than 170 milliseconds.

**b. Race**

Only recently, investigators have probed the neural mechanisms underlying racial bias based on face-processing. The social impact of face-processing in race determination deserves

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related to speech. It is not often appreciated that the prime domain of the human brain is communication (whether it is gesture or verbal).

consideration. Memes<sup>51</sup>, such as the inability of Caucasians to identify individuals with different facial physiognomy (other races) and vice-versa, have become social anathema in many cultures. The descriptor, “they all look alike to me,” while offensive, has been shown to have solid scientific neural foundations. Similarly, fear and loathing of another race is hardwired into the primal (subcortical regions) of the human brain. “In-group/out-group” discrimination has been considered as an evolutionary mechanism selected for the advantages of group survival (Hewstone, Rubin, and Willis 2002). The neurophysiology concerning these impactful social issues is presented below.

It has long been known that adult humans better recognize faces within their own race relative to faces of other races (Malpass and Kravitz 1969). This “race effect” is found in infancy as well (Kelly et al. 2005; Bar-Haim et al. 2006; Markant, Oakes, and Amso 2016; Lee, Quinn, and Pascalis 2017). The race effect appears to broaden through childhood, into adolescence and adulthood. Young et al. (2012) attributed this intensified race effect to greater environmental levels of perceptual experience and social salience.

Nonetheless, the race effect displays plasticity, as evidenced by the “reversed race effect” in face-recognition in adults who were adopted into other-race families at ages three to nine years old (Sangrigoli et al. 2005). In adults, differential representation of own- and other-race faces correlates with behavioral measures of “race effect” in face recognition (Golby et al. 2001).

The neural networks involved in racial face-processing are not limited to the core processing areas (the face patches), but also recruit limbic structures, such as the amygdala and hippocampus, and areas within the prefrontal cortex. As described below, the amygdala shunts facial recognition involving other races to the “cognitive fear circuit”, where other-race faces generate negative implicit associations (Brosch, Bar-David, and Phelps 2013). Curiously, the amygdala also directs processing of other-race faces to the “disgust circuit” (Liu et al. 2015).

Recently, Valdez et al. (2022) described race-selective activation of loci in the human face-processing system. In their report, (Valdez et al. noted that upon viewing a face, neurons

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<sup>51</sup> Here, the meaning of meme is “an element of a culture or system of behavior passed from one individual to another by imitation or other nongenetic means”.

fired in the anterior cingulate gyrus (a.k.a., anterior cingulate cortex—ACC), the hippocampus, and the amygdala. The neural activation was race-selective. That is, preferential firing when viewing “other-race” faces. It is striking that racial discrimination is centered in the limbic system, which is noted for imparting emotional content to stimuli. Similarly, earlier fMRI studies suggested different hemodynamic<sup>52</sup> responses when subjects perceive in-group vs out-group members (Liu et al. 2015; Freeman, Schiller, et al. 2010; Chiao et al. 2008).

The ACC and the amygdala are involved in preferential neural firing with “out-group” stimuli. This is significant because the ACC and amygdala form part of a primitive predator fear circuit known as the “reactive fear circuit” (RFC). The RFC includes the dorsal anterior cingulate (dACC), insula, amygdala, and periaqueductal gray area (PAG) (Qi et al. 2018; Mobbs et al. 2020). The RFC responds rapidly and immediately to predatory threats. Thus, it is significant that the human brain reacts with such rapidity and intensity to faces of another race to produce innate fear behaviors. Moreover, race-selective neural firing in the ACC may signal preconscious race classification (Katsumi and Dolcos 2018; Hughes, Ambady, and Zaki 2017).

In contrast to “reactive fear circuits,” the “cognitive fear circuit” (CFC) engages higher brain regions—principally the ventro-medial prefrontal cortex (vmPFC), the ventro-lateral prefrontal cortex (vlPFC), and the hippocampus. Contrasting the RFC, the CFC is slow and deliberate. It interconnects the memory facets of the hippocampus and the judgement and valence facets of the PFC with the amygdala. Neuroimaging research involving the CFC has implicated the amygdala and the vlPFC in vigilance for threat (Vuilleumier et al. 2001; Nomura et al. 2004; Monk et al. 2006; Whalen 1998). Also, it is within the vmPFC and the hippocampus of the CFC that facial recognition takes place. In these higher centers of the brain, the “race effect” can be mitigated.

The facial display of disgust has been shown to relate closely default mode with prejudice (Jones 2007). Individuals with higher sensitivity to disgust have been found to exhibit enhanced rejection of out-groups and with a more negative attitude toward

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<sup>52</sup> Hemodynamics refers to the movement or flow of blood. More specifically, this term refers to the measurement of the flow of blood in the human body. It encompasses such measures as heart rate, blood pressure, vascular resistance, cardiac output, etc.

homosexuals (Inbar et al. 2009). Recently, neuroimaging studies have pointed out that processing of the disgust signal and prejudice-related information shares neural correlates, such as insula, amygdala, ACC, and orbitofrontal cortex (OFC) (Kubota, Banaji, and Phelps 2012; Jones 2007). The disgust perception of racial faces and its underlying neural circuits are thought to be represented in **figure 43**.

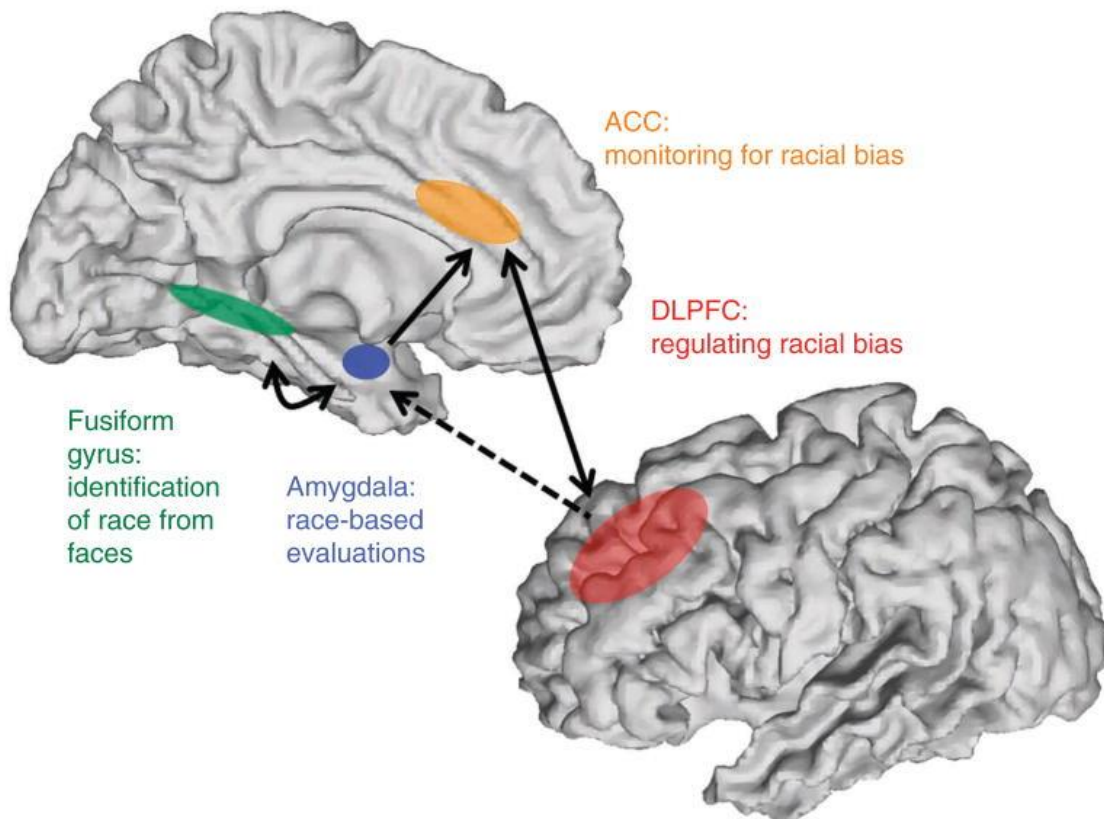


Figure 43. The disgust circuit. Source: Kubota, J., Banaji, M. & Phelps, E. The neuroscience of race. *Nat Neurosci* 15, 940–948 (2012). <https://doi.org/10.1038/nn.3136>. Reprinted with license from the publisher.

Human brains are primitively hardwired to react urgently to the faces of other races with vigilance, withdrawal, or aggression. It is for survival.

It should be noted that humans do have the neural mechanisms to engage higher cortical areas to mitigate instinctive behaviors and be able to engage in prosocial behaviors with out-group conspecifics. For example, Laurence, Schmid, and Hewstone (2018) surveyed a sample of United Kingdom neighborhoods and workplaces for attitudes toward outgroups. The authors found that positively-valenced inter-group contact can drive a positive effect and suppress a negative effect on out-group prejudice. Further support for the plasticity

concept of racial neural prejudice is reflected in the writings of Levy and Hughes (2015). The authors point out that developing children adjust their attitudes towards out-groups according to their stages of development. Before seven years of age, children display preference for ingroup and rejection of the outgroup. With the development of higher cognitive processes, the child is increasingly able to understand the individual rather than the group-based qualities of conspecifics, yet the older child still prefers contact with like individuals. After age seven, with the onset of concrete operational thinking, there is a decline in group-based biases. Thus, prejudice increases with age. Levy and Hughes analyzed seventeen available strategies to counteract the innate prejudice in developing humans. They concluded that only social cognitive methods could mitigate the racial/ethnic social bias.

**c. Kinship**

There is evidence in humans that recognition of kinship from facial features has high social value (DeBruine 2004; 2005; 2002; Platek et al. 2004; Platek, Keenan, and Mohamed 2005). For example, DeBruine (2004) demonstrated that facial resemblance generated positive regard for images of children whose faces had been morphed to resemble the adult subject. Thus, facial resemblance promotes prosocial behavior by investing a parent in a child that is kin and ensuring that the child will be nurtured by adult kin.

DeBruine's earlier work (DeBruine 2002), showed another prosocial feature concerning the ability of humans to recognize conspecifics as kin from their facial features. Facial features communicate trustworthiness. DeBruine found greater levels of trustworthiness in subjects playing a trust game with opponents whose faces had been morphed to resemble the subject than in non-self-resembling faces. The capacity to trust, using self-referent phenotypic matching mechanisms, is a societal benefit according to Hamilton's theory of inclusive fitness (insects and animals exhibit numerous prosocial behaviors toward their kin to increase the survival chance of genes similar to their own) (Hamilton 1964). The theory may apply also to human beings. Furthermore, the limbic system involvement in trustworthiness is a dominant component in human behavior (Rajmohan and Mohandas 2007). Emotions are potent activators in prosocial behavior. Because the feeling of security is a particularly important consideration in trustworthiness assessments, humans' preference for people who resemble themselves may increase their trust in such people and curb aggression toward conspecifics who are kin.

While there may be genetic advantages to prosocial behaviors resulting from self-resembling facial cues, there are concomitant disadvantages. Hamilton's theory of inclusive fitness accounts for the advantages. However, if humans were to be sexually attracted to kin, then there would become a genetic cost of inbreeding. Is there a mechanism within face-processing to override sexual desirability at the genetic cost of inbreeding? In a facial morphing experiment, DeBruine (2005) investigated sexual appeal of self-resembling faces. She found that experimental subjects showed no preference for self-resembling faces. Moreover, the results indicated that self-resembling faces are not desirable for short- or long-term relationships. In contrast to earlier findings of DeBruine, it appears that although the faces of kin promote trustworthiness thus propagating the species, there are concurrent neural mechanisms within the face-processing system to counteract inbreeding (Zhao et al. 2023).

Dal Martello and Maloney (2006) identified the specific facial features that enabled humans to identify kinship. They concluded that observers judged kinship better when viewing the upper half a child's face than the lower half. Platek and Kemp (2009) used fMRI to investigate the neural substrates associated with viewing faces of kin. They found that kin faces activated the posterior cingulate and cuneus (posterior regions of the brain). On the other hand, discrimination of self-resembling faces from familiar morphs activated anterior medial regions of the brain (anterior cingulate cortex, ACC, medial prefrontal cortex (mPFC)).

#### **d. Age**

The determination of a conspecific's age is an important core social function of the human face-processing system. When determining the age of a face, humans are sensitive to the subtle features and their age-associated changes such as the quantity and color of hair, skin elasticity, texture of skin (size of pores, prevalence of wrinkles, and the presence of capillary varicosities), distribution of adipose tissue, length of the nose and ears, thickness and texture of eyebrows, size of the eyes, and the shape of the lips (Burt and Perrett 1995). The literature points to social significance associated with mankind's ability to determine facial age and derive rapid social judgements. (Secord, Dukes, and Bevan 1954) showed that faces perceived as distinguished, intelligent, and determined were older, had thin lips, and had wrinkles at the eye corners. Recently, in a trust game experiment, Li et al. (2021) showed that people trusted the faces of older people more than they did younger people. These social

judgements imparted from an elderly face, immediately apprise an unaffiliated human that the person with the aged face is not a volatile threat, but rather the facial features communicate that the aged individual is distinguished, approachable and capable of sharing wisdom or guidance to the social group.

The perception of facial age plays an important role in both mating and child-rearing. Preferential facial features differ between men and women. Studies have shown that men were most attracted to the facial features of young women (Muñoz-Reyes et al. 2015; Buss 2004; Mathes et al. 1985; Bovet et al. 2018). On the other hand, women preferred the facial features of older men, but women's preferences varied by hormonal levels. Little et al. (2010) reported preferences for masculinity in male faces were highest in women who were at a reproductively active age: preferences for masculine features were lower when females were peri-pubescent or post-menopausal. These observations correlated with biological and evolutionary concepts. That is, from a reproductive perspective, it is better for a man to bond with a young woman than with a woman with waning reproductive capacity. Thus, men are receptive to facial cues of fertile females. On the other hand, male fertility is not confined to a narrow age span. Women are receptive to the facial features of older males. The older face signals greater stability, stature, and perhaps greater resources than a young male. From an evolutionary standpoint, the female preference for bonding with an older male may be driven by the likelihood of survival of the offspring that is enhanced by the stature and resources of the father (Kościński 2007). In short, humans communicate age via their faces, and there are innate neural mechanisms that generate social judgements related to mating. In short, facial age communicates suitability to mate.

Age-related facial features are believed to signal parent-offspring interaction. Many mammalian infants have distinct facial features to communicate their age. These features trigger caring instincts in their parents and inhibit aggressive behavior in all adults.

In mammals, one indicator of young age is a large cranium compared to face and large eyes. These age-signaling facial features and its social/behavioral effects also have been found in humans. Kościński (2007) noted that there was a correlation between facial attractiveness and perceived age in infant faces. The authors pointed out that cute human infants are characterized by large eyes and pupils, and a large forehead. Hückstedt (1965) found that women prefer babyish proportions to such a degree that they consider children

with pathologically enlarged crania to be attractive because this is an exaggerated baby-like trait. Such distinctive, “cute” childlike facial features have become known as “baby schema.” Glocker et al. (2009) experimentally tested the effects of infant facial features on the perception of cuteness and the motivation for caretaking. In this study, college-age subjects viewed photos of infant faces having high or low correlation to the anthropometric facial characteristics of “cuteness” (“baby schema”). They found that high baby schema infants were rated as cuter and elicited stronger motivation for caretaking than the low baby schema infants. Lobmaier et al. (2010) found that women showed greater sensitivity to infant cuteness than men. The findings supported the prior work of Sprengelmeyer et al. (2009) showing that the difference was enhanced in women taking hormonal contraception and diminished in postmenopausal women. McCabe (1984) reported that children whose faces looked older than their young chronological age (i.e., had lost the baby schema) got less care from their parents and were maltreated more frequently.

Thus, being able to detect and react to a cute face, is a prosocial behavior built into the physiology of face-processing. An interesting consequence of emotional response to cute faces is “cute aggression.” Faces of animals and human infants demonstrating a high baby schema have been shown to elicit cute aggression in human adults (Safaraiard 2022; Stavropoulos and Alba 2018). Cute aggression is a playful-aggressive response such as squeezing, pinching cheeks, or biting in response to overwhelming positive emotion from something cute. There is some evidence from neuroimaging studies to suggest the neurocorrelates of cute aggression directed at infant faces. Glocker et al (2009) showed that more distinctive baby schema elicited increased activation in brain regions associated with reward-processing (i.e., the nucleus accumbens, which they showed to be interconnected with several face-processing areas) in college-aged men and women. Another study conducted in both fathers and non-fathers compared neural processing of infant versus adult faces (Mascaro, Hackett, and Rilling 2014). This study demonstrated that in fathers, infant faces elicited greater activation in the orbitofrontal cortex (OFC), temporal parietal junction (TPJ), medial frontal gyrus (MFG), superior frontal gyrus, ventromedial prefrontal cortex (vmPFC), and precuneus. These neural regions also represent part of the face-processing system. In another fMRI study by Endendijk et al. (2020), the authors found that infant faces elicited widespread activation in bilateral visual cortices, in the hippocampus, sensory-motor areas, parietal and frontal cortices, and in the insula. Many of these regions are face-processing areas. The authors linked the activation in the insula in response to infant faces to its roles in

social-emotional processing, empathy for others, and salience processing. A collection of prior research with parents also reported similarly increased insular activity to infant faces, particularly to faces of their own children (Mascaro, Hackett, and Rilling 2014; Leibenluft et al. 2004; Atzil, Hendler, and Feldman 2011; Abraham et al. 2014; Strathearn et al. 2008). In other studies, Cunningham and Brosch (2012); Feldman (2017) reported increased activity in the amygdala and putamen, especially in nurturant mothers. They postulated that this could be an indication of reward or motivational salience-processing of the infant faces.

Furthermore, additional studies found increased amygdala and striatal responses to visual cues of parents' own infants (Stoekel et al. 2014; Wonch et al. 2016; Abraham et al. 2014; Strathearn et al. 2008). Corresponding animal studies of mothering in rodents, ungulates (sheep or other hoofed animals) and nonhuman primates also demonstrated the importance of the amygdala for the expression of voluntary non-aggressive maternal responses such as pup licking and retrieval, and the importance of dopamine release in the striatum for normal mothering (Lonstein, Lévy, and Fleming 2015). In brief, cuteness aggression appears to be a neural mechanism for regulating extreme positive emotion in response to viewing faces of infants. It recruits the salience and reward pathways commonly tied to face-processing.

It is only recently that investigators have been able to describe the neural correlates of caregivers' responses to infant faces. Using fMRI, Zhang et al. (2022) measured the functional connectivity<sup>53</sup> in men and nulliparous women who viewed infant faces. They found that compared with men, the neural activation in nulliparous women increased in several brain regions during the processing of infant emotional faces, such as visual areas (fusiform gyrus, inferior and middle occipital gyri, and lingual gyrus), limbic areas (limbic cortical, and posterior cingulate cortex), temporoparietal areas (parietal lobule, and middle temporal gyrus), temporal areas (middle temporal gyrus), and the cerebellum. Similarly, they observed increased functional connectivity in the default mode network (DMN)<sup>54</sup> (e.g., inferior parietal lobule, postcentral gyrus, precuneus, and middle temporal gyrus). Thus, the

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<sup>53</sup> Functional connectivity is a measure of how regions of the brain interact with each other. Using fMRI methods, one can map the neural pathways that interconnect regions of the brain while the brain is performing specific functions.

<sup>54</sup>The DMN is a network of neurons that is active when the brain is in a resting state. That is, when the brain is not focused on external stimuli but instead when one is contemplating oneself or others. There is recent evidence of activation of the DMN in connection with faces.

processing of infant faces involves a large array of neural structures. Moreover, the literature suggested that the connectivity between these brain regions may be gender-biased.

In summary, the capacity of the human brain to discriminate the age of a face accounts for prosocial behaviors with regard to young and old conspecifics. There appears to be gender-specific determinants that may be genetic, hormonal, and/or neurodevelopmental. The complex neural pathways enable humans instantaneously to communicate socially-critical information such as mate availability, childcare needs, and threat perception.

#### **e. Health**

Humans can extract health status from a conspecific's face. Among the first authors to demonstrate that facial symmetry has a positive influence on health were Grammer and Thornhill (1994). They presented images of faces of differing symmetry to participants who rated attractiveness, dominance, sexiness, and health of the faces. The investigators found that facial symmetry is perceived as a signal of health. Shackelford and Larson (1997) also investigated the relationship between facial symmetry and health, with similar results to Grammer and Thornhill. Specifically, Shackelford and Larson compared the participants' facial photographs to their health records. The data showed that facial asymmetry signaled psychological, emotional, and physiological distress. In 2016, Švegar conducted a meta-analysis evaluating the findings of 19 previous studies, with regard to the relationship between facial symmetry and health. Švegar showed that individuals with high facial symmetry are perceived as healthier than less-symmetrical people. The value of this capability enables humans to assess who may be ill with contagious disease and should not be approached. Also, faces reflect mental illness. The mentally ill person also poses a threat and the face initiates avoidance behaviors.

There are facial features that code for health and vitality. For example, early in the face-processing network, humans assess facial symmetry. This has biological value because humans can rapidly determine the health of a conspecific or the desirability to mate. Symmetrical people of both sexes are reported to have greater emotional and psychological health, and symmetrical men were also found to have greater physiological health, than their asymmetrical counterparts (Fink et al. 2006). Moreover, facial symmetry has been shown to correspond to the perception of health (Shackelford and Larsen 1997) in male and female

ratars. Subsequently, Shackelford and Larsen (1999) monitored the health of experimental subjects for four weeks. The authors categorized the subjects for facial attractiveness. They concluded that subjects, having an attractive (i.e., symmetrical) face showed fewer symptoms. Moreover, they demonstrated greater cardiovascular health in subjects with attractive faces. Thus, the human face-processing system appears to have the capability of determining the health status of conspecifics.

**f. Affective State**

The ability to accurately interpret emotional facial expressions is crucial to successfully navigating social interactions. Human face-processing has an inherent mechanism by which we communicate our mood and recognize the mood of conspecifics. Mood state is not static but fluctuates, and different affective (mood) states significantly impact facial recognition: That is, affective states can generate biases that impair or enhance recognition of specific emotional facial expressions. For example, (Schmid and Schmid Mast 2010) found that inducing a negative mood in experimental subjects hampered the participants' ability to recognize happy, but not sad facial expressions. Moreover, Lee et al. (2008) demonstrated that inducing a negative mood state biases neurotypical adults to perceive ambiguous facial expressions as negative expressions.

Not only does affective state impact on facial recognition, but affective disorders have been shown also to impair the production of emotional facial displays. For example, (Rehman et al. 2010) showed that depressed individuals have impaired ability to generate a smile. Arnold & Winkielman (2021) recently reported that depressed patients displayed reduced spontaneous smile mimicry. The clinical implication of these and other findings will be discussed in the next chapter, the Pathology of the Face.

**v. The Physiology of the Face in Sex and Love**

As stated earlier, humans acquire important information about the affective states of others via facial communication. This communication takes place in such core human functions as bonding and sexual relations. Primates use facial gestures both to attract mates and to communicate within sexual relations. Hughes and Nicholson (2008) proffered that the ability to detect sexual enjoyment of a partner by way of facial expression, may communicate

the likelihood of a partner's willingness to engage in future copulations. The authors suggested that humans may need the ability to detect, and then ensure a partner's sexual enjoyment, to promote future copulations through positive reinforcement and/or emotional attachment. Thus, facial expressions could communicate a partner's level of sexual satisfaction and/or devotion to their mate.

Facial expressions code for sexual excitement. Based on the classic work of Masters and Johnson (1966), Fernández-Dols, Carrera, and Crivelli (2011) used the facial action coding system<sup>55</sup> to decode facial expressions during sexual excitement. The investigators identified the most prevalent facial movements associated with the plateau/orgasm phase of sexual excitement to be: brow lower (AU4), brow lower and cheek raise (AU4 + AU6), with closed eyes (AU43), jaw drop (AU26), and lips parted (AU25)—with closed eyes more prominent in women subjects. Subsequently, Chen et al. (2018) described a distinct collection of facial action units that corresponded to the facial expressions accompanying orgasm. They identified many AUs corresponding to Fernández-Dols' experiment. Additionally, Chen et al. found that the facial movements of orgasm were culturally-specific—Westerners commonly included wide-open eyes and a vertically stretched mouth, whereas East Asians included smiling—these movements were combined with cross-cultural face movements such as brow raising and closed eyes. In general, orgasm was represented by face movements that expand the face outward (e.g., brow raising in both cultures; mouth opening and eyelid raising among Westerners). Such facial displays can communicate affective states to others and influence their behaviors—for example, indicating completion of a sexual act in orgasm or acknowledging satisfaction toward a partner. They identified many AUs corresponding to Fernández-Dols' experiment. Additionally, Chen et al. found that the facial movements of orgasm were culturally-specific—Westerners commonly included wide-open eyes and a vertically stretched mouth, whereas East Asians included smiling—these movements were combined with cross-cultural face movements such as brow raising and closed eyes. In general, orgasm was represented by face movements that expand the face outward (e.g., brow raising in both cultures; mouth opening and eyelid raising among Westerners). Such facial displays can communicate affective states to others and influence their behaviors—for

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<sup>55</sup> For an explanation of the facial action coding system, refer to Chapter 1.

example, indicating completion of a sexual act in orgasm or acknowledging satisfaction toward a partner.

There is evidence to support a possible neurophysiological mechanism for the distinct facial expressions associated with sexual excitement. Sexual excitement and orgasm are both linked to the reward and pleasure areas of the basal ganglia (Redouté et al. 2000; Rauch et al. 1999; Karama et al. 2002; Holstege et al. 2003; Arnow et al. 2002). In other words, sexual excitement involves the recruitment of dopaminergic pathways, predominantly the mesolimbic (ML) pathway. Interestingly, elements of the ML pathway, such as the nucleus accumbens, the ventral pallidum, the anterior cingulate cortex, the ventromedial prefrontal cortex, and the dorsomedial prefrontal cortex are imbedded in the brain's face-processing network. That is, to express pleasure, gratification and/or satiation via the muscles of facial expression, neural signals pass through parts of the ML pathway.

Not only do facial expressions provide a means for communication during copulation, but also facial displays have been shown to signal the willingness to mate. Recently, (Haj-Mohamadi, Gillath, and Rosenberg 2021) described a distinct facial expression in women with the head turned to one side, head tilted down slightly, a slight smile, and eyes turned forward that signaled a desire to mate that activated sex-related association networks in men experimental subjects. Other studies reported unique facial displays associated with lust. For example, Eibl-Eibesfeldt (2017) has described flirtatious tongue flicking in Yanomami women as a sign of lust, and observed similar behavior in central European women. Gonzaga et al. (2001) described four expressions of lust: licking, puckering, and touching the lips as well as protruding the tongue. A study by Kendon (1975) concluded that females regulate human courtship interaction by managing male arousal and approach partly through their facial expressions. Additionally, Petersen and Higham (2020) noted facial expressions in men associated with sexual desire that parallel non-human primate displays performed surrounding sexual solicitation and mating. For example, smiling, head nodding, and leaning toward a speaker are thought to display affection or love, and manipulations of the mouth, including lip biting, lip licking, lip touching, and tongue protrusion, are associated specifically with sexual desire (Givens 2016; Gonzaga et al. 2001). These behaviors parallel the 'pucker' and 'tongue in-and-out' displays expressed by certain non-human primates. While the neural pathways have not been studied in humans, the neurophysiology of facial sexual displays are believed to be similar in humans as in anthropoid primates.

**vi. The Mechanism of Facial Mimicry**

Facial mimicry is commonly defined as the tendency to imitate facial expressions of other individuals (Seibt et al. 2015). We are all familiar with the contagion of smiling, frowning, or yawning. Facial mimicry is involuntary, and can be observed widely in mammal and bird communication (Rizzolatti et al. 1996; Carrillo et al. 2019; Prather and Mooney 2015). Dimberg, Thunberg, and Elmehed (2000) documented that humans mimic emotional facial expressions of others within 1,000 milliseconds. Human infants rapidly develop the ability to mimic faces (Jones 2009).

There is evidence for the biological advantages to mimicry. That is, facial mimicry is a form of communication that has been considered a “social glue” (Chartrand and Bargh 1999) because it can generate a feeling of “connection” which in turn favors prosocial behavior and positive relationships (Chartrand 2013; Lakin 2003; van Baaren 2004).

For psychologists, physicians, social scientists, and communication scientists, it is constructive to understand the neural correlates of facial mimicry. It is believed that mirror neurons underlie facial mimicry. Mirror neurons are clusters of nerve cells found in specific regions of the brain. These specialized cells are known as sensory-motor neurons<sup>56</sup>. The mirror neuron system is believed to account for extraordinary levels of communication, because it permits an individual to be able to experience the emotional state of another as if it were their own feelings. It has been demonstrated that via the mirror neuron system (MNS), one can feel another’s pain or experience another’s joy or grief (Carrillo et al. 2019; Bastiaansen, Thioux, and Keysers 2009). The nodes of the MNS are shown in **figure 44**.

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<sup>56</sup> Sensory-motor neurons are duplicitous nerve cells. They can accept sensory stimuli plus they are able to initiate a motor (muscle) response.

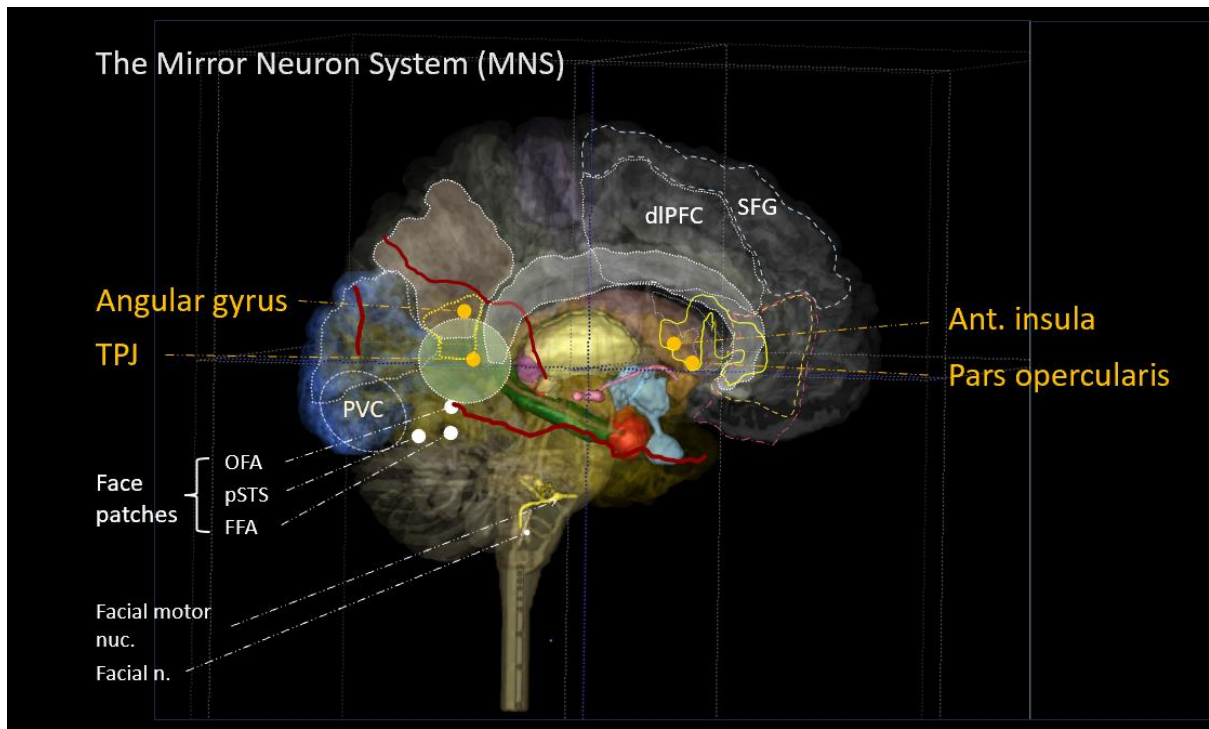


Figure 44. The elements of the mirror neuron system. Four loci have been found to participate in the mirror neuron system. They are labeled in orange. Source: author's original contribution.

Mirror neurons play a critical role in the recognition of facial emotional expression, in empathy, and in “theory of mind” (ToM). A recent finding in our laboratory (Zeichner et. al, 2023) that six neuropsychiatric conditions with facial expression dysfunction share deficits of the MNS.

#### **vii. The Physiology of the Theory of Mind (ToM)**

The concept of “Theory of Mind” plays a prominent role in human communication. ToM is a socio-cognitive concept wherein humans can gain access to a conspecific's inner state of emotions. Discernment of other persons' emotional states by evaluating their facial expressions is a key aspect of social interaction (Ekman 1972). As stated earlier, shared emotional feelings might be traced back to mirror neuron mechanisms (Bastiaansen, Thioux, and Keysers 2009).

There is increasing evidence from neuroimaging studies that core components of a human mirror neuron system (hMNS) are involved in face-processing. Carr et al. (2003)

demonstrated that elements of the hMNS (including the inferior frontal cortex, i.e., IFC) are involved in the imitation and observation of facial expressions of emotions. For the expressions of pain and disgust, functional neuroimaging studies showed evidence that the processing of one's own emotional experience and the observation of another person having a similar emotional experience may engage overlapping brain networks (Singer et al., 2004; Wicker et al. 2003). Using event-related fMRI, Schulte-Rüther et al. (2007) reported that common networks involving the MNS moderated the face-processing networks in test subjects while measuring for empathy. Furthermore, empathy-related processing of emotional facial expressions recruited brain areas involved in mirror neuron and theory-of-mind (ToM) mechanisms.

#### **viii. The Special Role of the Smile in Human Health Status and Communication**

The smile is a prominent and vital facial expression that is central to human communication and socialization. The physiology of smiling merits special discussion because this particular type of facial communication is central to human survival; that is, smiles are central to mating and proliferation of the human species (Haj-Mohamadi et al., 2021). Smiles are critical to nurturing infants (Strathearn et al. 2008), are essential to communicating kinship or affiliation, and signaling or abating aggression (Martin et al., 2017). Smiles also telegraph the presence of pathogens or toxins (Chapman et al. 2009; Whitton et al. 2014; Cannon, Schnall, and White 2011).

Facial communications provide an efficient way to initiate a relationship or select a mate (Keltner 2003). Moore (2010) reviewed ways that nonverbal communication is involved in human courtship. She found that flirting behaviors involving the face, such as sustained eye contact, smiling, coy gazing, and self-touching played a dominant role in the initiation or courtship processes (Henningsen 2004; Muehlenhard et al. 1986; Renninger, Wade, and Grammer 2004; Tisdale and Sheldon 2018). Recently, Haj-Mohamadi et. Al (2021), described a facial expression with a slight smile signaling desire to mate that activated sex-related association networks in male experimental subjects. Also, smiles are critical to nurturing infants. For example, reciprocal smiling between parent and infant (Riem et al., 2012) is a key component of the nurturing process.

Not much has been written about the mechanisms of initiation of and reaction to smiling. Yet, it has been shown that smiling activates multiple prosocial neural pathways. For example, Zeki (2007) demonstrated distinct regions of the caudate, putamen, and the striatum activated when subjects viewed the smiling face of a loved one. It is thought that smiling can be triggered via dopamine pleasure pathways. Dopamine pathways are neuronal connections in which the neuropeptide, dopamine, travels to areas of the brain and body to convey important information such as executive thinking, cognition, feelings of reward and pleasure, and voluntary motor movements. During a rewarding or pleasurable experience (such as food, sex, drugs, etc.), the mesolimbic pathway is activated. Dopamine is released and sends signals from the ventral tegmental area (VTA) in the midbrain to the nucleus accumbens (NAc), located in the ventral striatum of the basal ganglia. This creates positive feelings that reinforce the prosocial behavior. The expression of a smile communicates the feelings of well-being.

Not only is smiling involved in human behaviors, but also the act of smiling is linked broadly to general human health status and physiological processes (e.g., immunity, cardiovascular function, metabolic disease, and several neuropsychiatric disorders). For example, smiling mediates the immune response. (Takahashi et al. 2001) reported that laughter increased Natural Killer (NK) cell activity in experimental subjects, thus boosting immunity. Berk et al. (2001) similarly reported that exposure to humorous stimuli also significantly increased NK cell activity. Only recently, however, could we explain how movement of specific muscles of the mouth and eyes can act to mediate the immune response. As mentioned in Chapter II, the limbic system and the facial muscles are linked via neural connections with the face patches and regions of the prefrontal cortex. Additionally, within the limbic system, the neurohormone, dopamine, is produced and stored within the hypothalamic tract. Because the thalamus/hypothalamic region is both the most connected region of the brain and proximal to a profuse vascular system, dopamine is readily distributed locally and systemically (Zeichner, Radlanski, and Zeichner 2021). The dopamine produced within the CNS circulates within the vascular system until it reaches target cells whose cell membranes have dopamine receptors. Such receptors are found on immune cells such as B-lymphocytes and NK cells. When stimulated by dopamine, B-lymphocytes produce antigen. Activated NK cells are cytotoxic cells. That is, they destroy any cell that they do not recognize as “self”. Thus, activated NK cells neutralize both virally-infected cells and tumor cells (Broome et al. 2020). In short, the zygomaticus major and obicularis oculi muscles

contract during smiling or laughing, which in turn triggers several nuclei within the hypothalamic region of the brain to release the neurohormone dopamine. Dopamine is distributed systemically to activate receptors on the cell membranes of immune cells thereby boosting immunity. In addition to the dopamine-activated immune mechanism, Berk et al. (2001) reported increased immunoglobulins (IgA, IgG, and IgM) in experimental subjects lasting at least twelve hours after viewing a comedic video. These findings support immunological enhancement via smiling.

Also, there have been several studies implicating the cardiovascular effects of smiling and/or laughter on general health. For example, Miller et al. (2006) reported that laughter, after watching a comic movie segment, caused the dilatation of the inner lining of blood vessels (i.e., the endothelium), and increased blood flow. Vlachopoulos et al. (2009) reported that "laughter decreased pulse wave velocity, augmentation index, and cortisol levels, and increased total oxidative status" in experimental subjects watching comedic films. In another study of cardiovascular dynamics, Sugawara, Tarumi, and Tanaka (2010) reported that heart rate and blood pressure, ischemia-induced brachial artery flow-mediated vasodilation, and carotid arterial compliance increased significantly in experimental subjects who watched a comic movie. Thus, several beneficial cardiovascular effects have been attributed to laughter of which smiling is a component. Miller and Fry (2009) postulated a mechanism by which laughter produces beneficial cardiovascular health. That is, laughter/smiling may induce the release of  $\beta$ -endorphins, which in turn activates receptors on the endothelial surface to release nitric oxide, which in turn induces smooth muscle relaxation, vessel dilation, and also may reduce vascular inflammation.

Smiling bears a noteworthy relationship to glucose metabolism. Studies have demonstrated a beneficial effect of laughter on postprandial<sup>57</sup> glucose levels (Hayashi et al. 2003; Cokolic et al. 2013). The mechanism by which smiling/laughter affects glucose metabolism was not delineated in these studies, but postulated to be attributed to muscle activity and/or to arise from neuroendocrine suppression of blood glucose. Another study found a decrease in plasma prorenin concentrations in type two diabetic patients after exposure to humor (Nasir et al. 2005).

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<sup>57</sup> Postprandial refers to after eating.

The literature reviewed suggested that smiling and/or laughter moderated pain perception and tolerance. An experiment by Zweyer, Velker, and Ruch (2004) demonstrated a correlation between an increased pain tolerance and genuine (Duchenne) smiles. Dunbar et al. (2012) further hypothesized that laughter stimulated endogenous opioid release (e.g.,  $\beta$ -endorphins), thus elevating pain tolerance.

### **3.6. Summary/Conclusions Chapter III**

Chapter III addressed several little-known findings about the extraordinary physiology by which humans leverage faces for communication and socialization. Some of the more interesting aspects included: 1) That humans are incredibly sensitive to faces, to the point at which they see faces within inanimate objects. 2) That there are intrinsic neural mechanisms linked to faces that rapidly segregate “in-social group” from “out-social group”. These complex neural circuits activate the “emotional brain” triggering negatively-valenced emotions toward out-group faces and prosocial behaviors toward in-group individuals. Several investigations suggested that face-processing is at the core of racial or ethnic prejudice. 3) Facial age discrimination is central to human social structure. Via rapid neural mechanisms for age assessment, society limits aggression toward members with older faces and very young faces, nurtures and protects members with child-like facial features, and permits copulatory behaviors with females whose facial features signal they are of reproductive age or males with mature facial features that represent sufficient stature to support offspring. 4) There is evidence that humans communicate with facial displays while copulating. Furthermore, investigators have codified these facial gestures. 5) The neural mechanism by which primates, and especially human primates, innately and involuntarily mimic facial expressions, plays a vital role in communication. This chapter explained the physiology of the mirror neuron system, the core of facial mimicry. The mirror neuron system also is fundamental to the critical social / communication conceptualization of Theory of Mind (ToM). One cannot communicate effectively if one has no conception or understanding of the state of mind of the person with whom you are communicating. The physiology of the human face allows for this essential insight. Lastly, this chapter illuminated the far-reaching effects of the human smile. Not only is interpreting or generating a smile important part of human communication and socialization, but also smiling is related to

human health status and physiological processes such as immunity, cardiovascular function, metabolic disease, and several neuropsychiatric disorders.

The data derived from this thesis permitted newly illuminated neurophysiological mechanisms for a specialized face-processing task. The example in this chapter illustrated the pathophysiology of smiling.

In conclusion, the key findings of Chapter III included: a contemporary discussion of the neurophysiology for facial identity determination, age/gender/race/health discrimination, mating-related facial mechanisms, and responses thereto. Additionally, this chapter elucidated that there may be distinct neural networks for processing specific facial expressions of emotion.

## CHAPTER IV–The Pathology of the Face: Dysfunctional Facial Communication

### 4.0. Introduction

When all components of the facial communication system remain intact, then the face successfully fulfills its important role: that is, socialization, communication, and identity. However, when there are lesions within the previously-mentioned anatomic components, when the neural connections between loci show diminished function, or when the neurochemical modulating pathways fail, then pathoses emerge.

In brief overview, salient diseases that affect facial communication are:

- i. Prosopagnosia
- ii. Epileptogenic Disease
- iii. Traumatic Brain Injury or Stroke
- iv. Bilateral Amygdala Damage (Urbach-Wiethe disease, herpetic encephalitis)
- v. Impairments of Facial Muscle Movement (Bell’s palsy, Ramsey-Hunt syndrome)
- vi. Disfigurement
- vii. Congenital Abnormalities (William, Turner, Angelman, and Down syndromes)
- viii. Neurodegenerative Disorders (Parkinson’s, Huntington, and Alzheimer diseases)
- ix. Impactful Pathoses of the Face (Autism Spectrum Disorders, Parkinson’s Disease, and Major Depressive Disorder)
- x. Psychiatric Disorders (schizophrenia, obsessive compulsive, and borderline personality disorders)

A key aim of Chapter IV is to highlight functional abnormalities of the human face in diseases that conventionally are not considered “diseases of the face”. Moreover, this chapter aims to inform non-specialists about the pathophysiology of these categories of disease. And, another objective of this chapter is to show the social and economic significance of facial disorders.

## 4.1. Prominent Facial Pathology in Communication Disorders

### i. Prosopagnosia

While not the most prominent pathoses of facial communication, prosopagnosia is likely the most widely-popularized example of a facial communication disorder. Therefore, I shall address prosopagnosia, also known as "face blindness", first. Prosopagnosia, one of the more interesting deficits in face-processing, is the inability to recognize faces, both that of others and, in some cases, oneself. The prevalence of prosopagnosia is relatively low. DeGutis et al. (2023) estimated the prevalence in the United States population ranged between 0.13% and 2.5%. Despite its rarity, this condition receives media attention because prominent celebrities have disclosed or publicized their afflictions (e.g., the actor, Brad Pitt, neurologist Oliver Sacks, primatologist, Jane Goodall, Apple founder, Steve Wozniak, and others).

There are two recognized forms of prosopagnosia: 1) congenital/developmental prosopagnosia (present at birth or developing soon after birth) and 2) acquired prosopagnosia. In congenital/developmental prosopagnosia (CDP), there is yet no clear understanding of the etiology. In a review article, Corrow, Dalrymple, and Barton (2016) pointed to familial and twin studies suggesting that CDP is heritable. Further studies identified gene abnormalities. For example, Cattaneo et al. (2016) found an alteration in the oxytocin receptor gene (OXTR) in a family with CDP. Recently, Sun et al. (2021) reported a mutation in the MCTP2 gene associated with CDP. Our understanding of congenital/developmental prosopagnosia is still evolving.

Acquired prosopagnosia (AP) is thought to result from damage to the brain in areas involved in face-processing. Grüter et al, (2008) suggested that AP resulted from stroke, trauma, or other lesions in the core face-processing areas or in the extended face-processing areas of the brain.

To date, the exact pathophysiology of prosopagnosia is unclear. With advances in our understanding of distributed neural networks (DNN), the evidence suggests that face recognition closely depends on a DNN. That is, multiple interconnected brain regions coordinate in facial recognition. As discussed in prior chapters, in addition to the core face-

processing areas (OFA, FFA, and pSTS), there is an extended set of regions including the amygdala, inferior frontal gyrus, intraparietal sulcus, precuneus, and superior colliculus that are part of the face-processing system. Cohen et al. (2019) used an emerging technique known as lesion-mapping to test whether lesion locations causing prosopagnosia fall within a common brain network, and to identify the critical nodes of this network. Their analysis revealed the right FFA and four left frontal regions (APFC—anterior prefrontal/frontopolar cortex, ACC—anterior cingulate cortex, MFG—middle frontal gyrus, and SFG—superior frontal gyrus) as both sensitive and specific for acquired prosopagnosia. To sum up, the current understanding of the pathophysiology of prosopagnosia is that it results from damage to the right FFA or disruption of the neural pathways connecting the right FFA to the left frontal regions of the brain.

## ii. Epileptogenic Disease

Epileptogenic disorders<sup>58</sup> have provided considerable insight into face-processing deficits. Deep brain stimulation (DBS) is a common intervention for treating epileptic patients resistant to antiseizure medications. DBS is a surgical procedure wherein micro electrodes are placed within specific sites of suspected aberrant electrical activity. Some of the more interesting insight about the role of the fusiform face areas came from the work of Josef Parvizi at Stanford Medical Center. Parvizi et al. (2012)., observed an epileptic patient with micro electrodes placed in the right temporal region (the site previously identified as the epileptic source). The intended purpose of the observation was not face-related, but rather to measure the patient's ability to retrieve the names of objects. When Parvizi activated the electrodes, his patient told him

*“You just turned into somebody else. Your face metamorphized. Your nose got saggy. It went to the left. You almost looked like somebody I'd seen before, but somebody different. That was a trip!”*

Parvizi's observation was fortuitous. The site of these electrodes was determined to be adjacent to the pfus-faces and the mfus-faces. This early clinical observation established that the fusiform face areas were implicated in shape of facial features as described in Chapters II and III.

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<sup>58</sup> Epilepsy is a disruption in the normally organized electrical rhythms of the brain that produces seizures.

It long has been known, that temporal lobe epilepsy (TLE) was associated with deficits in social cognition (Schacher et al. 2006; Ives-Deliperi and Jokeit 2019; Broicher et al. 2012). Seminal to social cognition is the ability to discriminate a face and perceive emotional expression (Steiger and Jokeit 2017). Disruptions in the face networks could explain the social cognitive deficits observed in TLE. There is evidence connecting such deficits in the literature. Bora and Meletti (2016) analyzed facial expression recognition in adult patients with TLE. They found the recognition of facial expressions was diminished for all six basic emotions (anger, disgust, fear, happiness, sadness, and surprise).

In a recent EEG study, Kim et al. (2022) reported that patients with mesial temporal lobe epilepsy were less responsive to faces, particularly involving the amygdala, fusiform gyrus, hippocampus, and parahippocampal regions. As discussed in Chapter III, the amygdala, hippocampus and parahippocampal areas are components forming both the reactive and cognitive fear circuits—critical face pathways for human social activities. In short, research in the field of epileptogenic disorders has demonstrated impairment in elements of the human face-processing system believed to interfere with facial communication.

### **iii. Traumatic Brain Injury**

By studying lesions, such as those acquired through traumatic brain injury, tumor, stroke, or surgical ablation<sup>59</sup>, physicians have gained insight into the pathology of facial communication disorders. Traumatic brain injuries (TBI) typically arise from traumatic brain insults such as motor vehicle accidents, falls, sports injuries, or assaults. When the injury involves regions of the brain concerned with face-processing, then the injury may manifest as a deficit in face recognition, facial expression interpretation, or facial expression production. For example, Rigon et al. (2018), studied forty-six adult patients with moderate to severe TBI six months post-injury (authors did not specify location of the TBI). When compared to healthy controls, the authors found diminished ability to recognize facial expressions of emotion. They found, also, that TBI individuals reported communication problems in general.

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<sup>59</sup> Ablation is the removal of tissue by surgical, morbid process, or the application of a noxious substance.

A stroke occurs either due to disturbed blood flow and oxygen deficiency (ischemic stroke) or bleeding (hemorrhagic stroke) in the brain causing cell death. Cell death can result in paresis (muscle weakness) or paralysis (complete loss of muscle function) when the stroke is in a motor region of the brain. Thus, involvement of the facial motor areas will impair the generation of facial expressions. When the stroke involves the face-processing regions, then deficits in facial expression recognition and/or facial identification may occur. In either case, communication is impaired in stroke patients.

Deficits in facial expression recognition frequently are found in stroke patients (Yuvaraj et al. 2013; Nijssse et al. 2019). In a recent study, of 110 stroke patients, (van den Berg et al. 2021) attempted to define the regions of the brain, and their interconnections, that were undermined during ischemic stroke, and consequently resulted in the impairment of facial expression recognition. They found that stroke patients exhibited diminished recognition of facial expressions overall when compared to healthy controls. More specifically, the authors were able to correlate diminished perception of disgust to damage in the caudate nucleus, while poorer sadness perception was related to damage in the opercular part of the prefrontal cortex. The inferior frontal-orbital cortex, anterior cingulate cortex, and dorsolateral prefrontal cortex (dlPFC) and the superior corona radiata white matter tract (sCRWMT) were related to a poorer recognition of happiness.

This bears an interesting relationship to the fMRI findings of Habel et al. (2005). That is, the perception of happy faces is positively-correlated to the mood of the observer, and the dlPFC appears to be a node in the happy-face network. Habel et al. induced happy or sad moods in experimental subjects. They found that happiness produced strong activations in the dlPFC. Thus, the dlPFC activates when a subject both experiences happiness and observes happiness in the faces of conspecifics. During sadness, more activation was observed in the ventrolateral prefrontal cortex (vlPFC), the anterior cingulate cortex (ACC), the transverse temporal gyrus, and the superior temporal gyrus (STG). Diminished perception of anger centered in the superior temporal sulcus. Overlapping regions included the insula (overlapped anger and sadness), Rolandic operculum (overlapped anger, happiness, and sadness) and putamen (overlapped disgust and sadness).

A recent study of stroke patients with facial paralysis/paresis aligns with a curious aspect of face-processing that has not yet been discussed in the literature (Kuttenreich, von Piekartz, and Heim 2022). Kuttenreich et al. found that stroke patients with paresis (patients unable to use their muscles of facial expression) showed impaired ability to recognize the facial expressions in others compared to stroke patients without paresis. This suggests that facial mimicry is integral to interpreting facial expressions of emotion, and invites further investigation. This notion is supported by the common experience of cartoonist/animators wherein the artist unconsciously mimics the facial expression of the subject they are drawing. This is commonly reflected in the gray literature (“Weird Question: When Drawing Faces, Do You Subconsciously Mimic the Expression You’re Drawing? : R/ArtistLounge” n.d.).

#### **iv. Bilateral Amygdala Damage**

(Urbach-Wiethe disease and herpetic encephalitis) add insight into the understanding of the amygdala’s role in deficits of face-processing. Urbach-Wiethe disease is a rare congenital disorder characterized by progressive bilateral necrosis and calcification of the amygdalae. Herpetic encephalitis is acquired later in life (with one-third of the cases occurring during childhood or adolescence) (“Herpes Simplex Virus Type 1 Encephalitis - UpToDate” n.d.). Infection by herpes simplex type 1 damages the amygdalae subsequent to viral transmission along an axon from a peripheral site on the face via the olfactory or the trigeminal nerves to the temporal lobes of the brain (Dinn 1980; Whitley 2006). Studies in patients with bilateral amygdala damage reported a deficit in their abilities to recognize faces. In a classic study of a patient with Urbach-Wiethe disease, Adolphs et al. (1994) reported that the patient evidenced impaired recognition of facial expressions of emotion with fear being the most prominent impairment. The patient did not experience difficulty processing other facial attributes (i.e., age, gender or identity). In a subsequent study, Adolphs et al. (1999) investigated nine individuals with bilateral amygdala damage (principally encephalitis). The authors reported that the subjects as a group were significantly impaired in recognizing fear. Most subjects were impaired on several negative emotions in addition to fear, but no subject was impaired in recognizing happy expressions.

Because facial communication is a two-way process—humans not only *recognize* facial displays but also *generate* facial expressions—it would be interesting to know if the amygdalae play a role in producing facial expressions. Anderson and Phelps (2000) tested

this premise in a patient with bilateral amygdala damage. They reported that the subject showed deficits in emotion recognition from pictures of faces, yet had an intact ability to produce the corresponding emotion in their own face. In short, findings from “lesion studies”<sup>60</sup> such as those cited above, suggest damage to the amygdala results solely in impaired recognition of negative emotional expressions.

In contrast, functional imaging studies point to a broader role of the amygdalae in facial communication deficits. Wang et al. (2017) pointed out that, to some extent, the amygdala responds to all facial expressions. The authors reported further that “the human amygdala responds to neutral or happy faces measured using BOLD-fMRI and single-neuron recordings.” Similarly, “Amygdala neurons in non-human primates respond to faces, face identities, facial expressions, gaze directions, and eye contact.” Wang et al. (2017) suggested a resolution to the contrasting data. Their fMRI and single-neuron electrophysiology recordings in bilateral amygdala-damaged patients suggested that the role of the amygdala was not to discriminate *particular* facial expressions, but rather to resolve ambiguous expressions, without reference to whether it was a negative or positive emotional expression, and secondly to assess the *degree* of emotion in the facial expression. In summary, the scientific literature, when taken as a whole, indicated that lesions of the amygdala impaired multiple aspects of facial communication.

#### **v. Impairments of Facial Muscle Movement**

In addition to traumatic brain injury (TBI) impairing motor regions of the brain, there are other neuromotor abnormalities affecting facial expression. The most common condition is Bell’s palsy. Bell’s palsy causes weakness or paralysis of the muscles of the face via the facial nerve. The exact cause of Bell’s palsy is unknown, but most cases are associated with viral or bacterial infections involving the facial nerve. It is believed that the infection leads to inflammation, compression, or swelling of the nerve, causing muscle weakness on the affected side of the face causing the face to droop. The condition impedes both speech and facial expression.

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<sup>60</sup>A lesion study is a research method in cognitive neuroscience wherein a focal region of brain damage is correlated to an observable deficit in cognition or behavior.

Another viral infection of the facial nerve is Ramsay-Hunt syndrome. Ramsey-Hunt syndrome is caused by the same virus that causes shingles or chicken pox. After the initial infection, the virus remains dormant until reactivated by stress factors such as other viral infections, nerve trauma, or compromised local immunity (Traylen et al. 2011). Not only are the terminal branches of the facial nerve affected in Ramsey-Hunt syndrome, causing weakness of the muscles of facial expression, but also ear symptomatology such as tinnitus<sup>61</sup>, vertigo, hearing loss, ear rash (zoster oticus), and ear pain. The ear effects are because branches of the facial nerve innervating the ear and adjacent skin are involved, as well as the geniculate ganglion (the structure within the brain where the facial nerve and auditory nerve converge) (Sweeney and Gildeen 2001).

Another type of motor impairment that impacts facial expression is Parkinson's disease (PD). PD is a neurodegenerative disorder characterized by degeneration of dopaminergic neurons. Dopamine has been shown to moderate skeletal muscle. In particular, when PD damages dopamine-producing nerve cells, the ability of nerves to control muscles is affected, resulting in impaired facial movement (Alexander 2004). Because PD has considerable implications in facial communication, I shall address PD in greater detail in a subsequent section.

## **vi. Disfigurement**

It has been estimated that between 1-10% of people are facially disfigured (Faces 2017; Robinson, Rumsey, and Partridge 1996). Facial disfigurement is a consequence of congenital conditions (birthmarks, cleft lips/palates), accidents (burns, scars), cancer (surgical deformities), disfigurements from facial paralysis (including strokes), and a vast number of disfigurements related to skin conditions (vitiligo, psoriasis). While it is self-evident that a partial or complete absence of functional face muscles subsequent to a disfiguring event would impair facial communication, it is less obvious that the psychological sequelae to a flawed identity would hinder communication and socialization. Considerable work confirms that people with facial disfigurement suffer from social stigmatization (Rasset et al. 2022; Shanmugarajah et al. 2012; Abel 2014; Roberts 2014; Hartung et al. 2019; Faces 2017;

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<sup>61</sup> Tinnitus is the medical term for a ringing, roaring, or buzzing sound that does not have an external source. It is a "phantom" sound heard only by the affected patient.

Jamrozik et al. 2017). This likely is a consequence of the innate discriminatory face-processing mechanisms delineated in Chapter III. Jamrozik et al. (2019) tested the hypothesis that a disfigured face communicates social negativity. In this study, observers judged individuals before and after surgical correction of their facial disfigurements. The observers reported “lower emotional valence (i.e., more negative emotion), higher arousal, and lower dominance when viewing pretreatment (vs. posttreatment) photographs” of faces. Moreover, pictured pretreatment individuals were viewed “significantly more negatively in terms of personality (e.g., emotional stability, conscientiousness), internal attributes (e.g., happiness, intelligence), and social attributes (e.g., trustworthiness, popularity)”.

#### **vii. Congenital Abnormalities**

Prominent congenital abnormalities affecting the face include: Williams, Turner, Downs, and Angelman’s syndromes.

Williams syndrome (WS) is a rare genetic condition characterized by intellectual impairment, short stature, cardiovascular anomalies, distinctive facial appearance, and connective tissue abnormalities. Individuals with WS manifest a gene deletion on chromosome 7. Specifically, a deletion of approximately twenty-five genes in the 7q11.23 chromosome region. However, the deletion spares GTF2I (the gene believed to mediate oxytocin) (Procyshyn et al. 2017). The syndrome also is often associated with a personality characterized as “hyper-social” and highly empathetic (Pober 2010). WS’s primary relevance to facial communication is the hyper-sociability of those affected.

Perturbations of several elements of face-processing have been implicated in this behavioral phenotype. For example, WS individuals selectively direct their attention to faces in general, and most notably to the eyes (Pavlova et al. 2016). In individuals with WS, there are neuroanatomical alterations in brain regions associated with face-processing (the amygdala, orbital and medial prefrontal cortices, cerebellum, anterior cingulate cortex, fusiform gyrus, and superior temporal sulcus) (Meyer-Lindenberg et al. 2005; Golarai et al. 2010; Campbell et al. 2009). Most notably, Golarai et al., in a fMRI study, found that the FFA was approximately two times larger among WS than in neurotypical participants.

As cited in Chapter III, the neuropeptide, oxytocin, plays a prominent role in social behaviors. (Dai et al. 2012) reported that basal oxytocin levels in the WS cohort were three times higher compared to neurotypical controls. Haas and Smith (2015) reported that WS subjects expressed the *oxytocin receptor gene* greater compared to controls. This correlates with Procyshyn’s findings that the gene, *GTF2I*, mediates social behaviors via oxytocin in WS individuals.

There is also disruption of myelin in individuals with WS that may be attributed to *GTF2I*. Diffusion tensor imaging (DTI) provided evidence for alterations in white matter<sup>62</sup> tracts and brain connectivity—particularly in fiber tracts that are part of the “social brain”<sup>63</sup> (Marenco et al. 2007). (Avery et al. 2012) measured myelination abnormalities in individuals with WS. They identified myelin abnormalities in the pathway between the orbitofrontal cortex (OFC) and the amygdala. This prefrontal-limbic tract is known to be the neural pathway by which the OFC inhibits amygdala activity (and, as mentioned earlier, a key pathway in the face-processing network). Thus, Nir and Barak (2020) postulated that the hyper-sociability in WS is a result of disinhibition of the amygdala’s usual fear response as a result of myelin aberrations in this tract.

A curious and pertinent observation recently was reported by Gnanadesikan et al. (2023). They found that the *GTF2I*-gene in dogs was responsible for hyper-sociability associated with the dogs’ affinity to work with humans. The findings genetically-connected the hyper-sociability of specific dog behavioral phenotypes with the hypersocial human behavioral phenotype of Williams syndrome.

Synthesizing the data from diverse studies of WS, pointed to a possible pathomechanism for WS as it relates to facial communication. That is, individuals with WS demonstrate a fascination with the human face. WS individuals are noted for their smiling faces, and are

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<sup>62</sup> White matter is the term used to describe collections of neurons that are coated with a fatty, white insulating material called myelin. Myelin speeds conduction velocity of electrical signals that travel along nerve fibers that interconnect functional regions of the brain.

<sup>63</sup> The “social brain” is a network of brain regions that supports complex social interactions, and includes the ventral and lateral parts of the medial prefrontal cortex (mPFC) and the posterior superior temporal sulcus (pSTS), the fusiform gyrus, the temporoparietal junction (TPJ), the precuneus/posterior cingulate cortex (PCC), and amygdala. The reader will recall that these six regions are key components of the face-processing network.

drawn to the smiling faces of conspecifics. They engage conspecifics without fear or social inhibition. Diverse studies demonstrated that key elements of the human face-processing system are perturbed in WS. The perturbation appears to be attributable to an aberrant gene connected with both oxytocin modulation and myelination of neural tracts interconnecting “the social brain”—tracts closely affiliated with face-processing. This mechanism gains support from genetic and behavioral animal observations.

Another face-related congenital abnormality is Angelman syndrome. Like WS, Angelman syndrome (AS) is a chromosome defect. The defect is on chromosome 3, and it is associated with the gene, UBE3A. Patients with AS display a “happy” disposition accompanied by a positive attitude in social interactions, and show social disinhibition. AS is characterized by pervasive smiling and a jerky gait and overall marionette-like jerky motions. This led to the label of “happy puppet syndrome” before the use of “Angelman syndrome” was encouraged (Pelc, Cheron, and Dan 2008).

The pathomechanisms of AS, vis-à-vis face-processing, has not been well-studied. Yet, reviewing the data sets from an fMRI study by Aghakhanyan et al. (2016) allows one to postulate a plausible theory for the pathogenesis of AS as it relates to facial communication. Aghakhanyan et al. reported diminished volume of key structures in the “social brain” common to face-processing areas such as the OFC, the ACC, the amygdala, anterior insula, and left precuneus. Like in Williams syndrome, Aghakhanyan et al. reported that individuals with AS showed aberrations in the prefrontal-amygdala pathway. That observation supported the comparable social disinhibition and hyper-socialization observed in both WS and AS.

The insula is known for its role in discriminating happy facial expressions and in the process of smiling. (Covered in Chapter II of this thesis). The insular abnormality speaks to the happy facies.

Turner syndrome (TS) is another chromosomal abnormality that impacts on facial communication. TS is associated with a complete or partial deletion of an X chromosome, thus the condition primarily affects women. While the most striking features of TS are physical impairments, several studies have shown that women with TS performed poorly in face identification and facial expression interpretation (specifically fear, sadness and disgust) compared to healthy controls (Anaki et al. 2016; Mazzola et al. 2006; Lawrence et al. 2003).

Down syndrome (DS) occurs when an individual has a full or partial extra copy of chromosome 21. Individuals with DS have been shown to have impediments in recognition of facial expressions of emotion and identification of faces. For example, Wishart and Pitcairn (2000) compared a group of individuals with DS to two control groups: one group was comprised of neurotypical children and the other was composed of individuals with non-specified intellectual disability. They found that children with DS performed significantly worse when compared to the neurotypical group on a facial expression matching task involving six basic emotions (happiness, sadness, surprise, fear, anger, and disgust). The DS children had particular difficulty in distinguishing fear and surprise. Williams et al. (2005) and Wishart et al. (2007) reported that children with DS were more likely to confuse fear with sadness than the controls.

In adults with DS, Carvajal et al. (2012) showed that DS subjects did not present any specific deficits in matching emotional significance to faces compared to people with general intellectual disability. However, they found that adults with DS showed some specific deficits in the processing of facial traits. In short, DS is a congenital condition that impedes facial communication.

#### **viii. Neurodegenerative Diseases (NDD)**

Neurodegenerative diseases (NDD) are characterized by selective dysfunction and loss of neurons, glial cells<sup>64</sup>, and the neural networks in the brain. Perception and interpretation of nonverbal communication are crucial to perceive and understand feelings, needs, and desires of patients with NDDs. Thus, effective facial communication is essential to the treatment and care of patients with NDDs. Some relevant NDDs that affect facial communication are: Huntington, Alzheimer, and Parkinson's diseases.

Huntington's Disease (HD) is a rare, fatal genetic condition whose impact on facial communication is twofold—both for making and perceiving facial expressions. The movement abnormalities of HD are known as “chorea”. Chorea is characterized by involuntary, irregular and, random movements that may involve any part of the body.

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<sup>64</sup> Glial cells are the most abundant cells in the central nervous system. Glial cells support neurons, protect the CNS from foreign particles and participate in the development of neurons.

Choreiform movement of the face generally affects the upper face—the orbital muscles, frontalis muscle, and procerus/corrugator supercilii muscles (Fekete and Jankovic 2014). Although upper facial muscles are more often affected, involvement of the lower facial muscles (mouth and periorbital muscles) has been reported as well (Oh et al. 2011). The choreiform movements interfere with the signaling process of the muscles of facial expression.

The interesting clinical manifestation of facial chorea in Huntington patients is that the patients perceive a prodrome (a premonitory sensation) before the involuntary facial movement. Patients often camouflage the movements by incorporating them into semi purposeful movements (“parakinesia”) during social encounters. The social encounters of HD individuals are historically troubled by miscoded facial signals. For example, a patient sensing a unilateral facial tick about to cause the corner of their right mouth to move, will improvise elevation of the left corner of the mouth to produce a smile. However, in the context of the social encounter, a smile is inappropriate. Or, the patient’s involuntary elevation of their eyebrow would signal “surprise” that was inappropriate to the social context. Although clinically well-documented, the effects of parakinesia of HD in facial communication remain unexplored in the literature.

Also, HD patients show noteworthy deficits recognizing facial expressions. In HD patients tested for facial expression recognition using photographs and dynamic videos, (Rees et al. 2014) reported significant impairment of anger, disgust, and fear recognition compared with healthy controls. Of the emotional expression deficits, disgust has received considerable attention. Disgust was demonstrated to be the most severely impaired facial expression in HD patients (Sprenkelmeyer et al. 1996; Mitchell et al. 2005). The fact that disgust is not perceived in faces by HD individuals, nor is it perceived via smell or taste, suggests a common central neuro mechanism. This may involve the anterior insula because the anterior insula plays a role in both responses to facial expression and to offensive taste (for background information, refer to prior chapters in this thesis).

In a recent report, Rosas et al. (2023) noted that in a sample of early HD patients (genetically positive but prior to motor signs), the HD subjects were less accurate recognizing facial expressions, particularly negative expressions of emotion, compared to healthy controls. Particularly noteworthy were the fMRI findings that pointed to disruption of the

pSTS, a key component of several face-processing networks. And, that this could be discerned early in the course of the disease. Thus, with both difficulty making coherent facial expressions, and accurately decoding the facial expressions of others, individuals with HD face social challenges.

Alzheimer's disease (AD) is another neurodegenerative disorder marked by impairment of facial expression recognition, facial identity determination, and facial expression production. Roudier et al. (1998) found that patients with AD were significantly impaired in discriminating facial identities. The study tested thirty-one subjects with AD, hospitalized in a long-term geriatric service. The authors showed paired photographs of individual faces and asked experimental subjects, "Is it the same or two different persons?" AD patients scored significantly lower than matched controls. Allender and Kaszniak (1989) found evidence for independent deficits in both non-emotional and emotional facial recognition tasks in AD. Subsequently, Hargrave, Maddock, and Stone (2002) demonstrated significant impairment in the ability to recognize facial expressions of emotion in AD patients compared with healthy controls. Furthermore, AD patients scored lower than healthy controls for all six emotions tested with the most significant differences shown for sad, surprised, and disgusted faces. AD patients were most impaired in identifying sad faces. In a more recent review article, Torres et al. (2018) reported that among people with mild Alzheimer's disease, happiness was easier to recognize than the other five basic emotions, with sadness and anger the most difficult to recognize.

In addition to deficits in identifying faces and in recognizing facial expressions, there is evidence that AD individuals are impaired producing selected facial expressions of emotion. For example, patients with AD viewing emotion-eliciting images demonstrated an inverted zygomatic activity pattern (i.e., they did not smile) compared to healthy controls, although emotional experiences were rated similarly. In a small study of severely demented patients, complex patterns of facial emotional expressions were not detectable; merely fragmentary expressions were observed (Asplund et al. 1991).

With respect to facial identity discrimination, the literature points to possible neural correlates. Hargrave, Maddock, and Stone (2002) reported that AD patients presented deficits in their abilities to identify faces, and positron emission tomography studies suggested that the cortical areas activated by facial identification tasks included the right lingual gyrus, right

parahippocampal gyrus, right anterior temporal lobe, and middle lateral cortex of the left temporal lobe, orbitofrontal cortex and fusiform gyrus of both hemispheres. Therefore, the aforementioned loci, (or the connections between them), may correlate with the disruption in face identity-processing in AD.

Parkinson's disease (PD) is a progressive neurodegenerative disorder causing motor and cognitive impairment. It affects more than 8.5 million people worldwide and is growing exponentially (Lewin Group 2019). Its notable social significance will be addressed in a subsequent section of this chapter. PD is best known for the presence of muscle tremor, slow movement, and rigidity. Nonetheless, there are significant impairments of facial communication. That is, PD is characterized by several features that account for the inability to express or interpret facial expressions. Among these are: bradykinesia<sup>65</sup> (Bowers et al. 2006), generalized hypomimia<sup>66</sup>, known clinically as the “masked face” (see **figure 45**) (Maycas-Cepeda et al. 2021), and deficits in face-processing (Assogna et al. 2008; Argaud et al. 2018).



Figure 45. Hypomimia (masked face) of Parkinson's disease. Michael J. Fox, American actor and spokesperson for Parkinson's disease research. Paul Hudson (original) Supernino (derivative work), CC BY 2.0

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<sup>65</sup> Bradykinesia refers to sluggish muscle response.

<sup>66</sup> Hypomimia refers to diminished facial expression.

Other studies suggested that deficits in facial mimicry might contribute to impaired facial expression recognition in PD. Livingstone et al. (2016), in an electromyographic study, demonstrated that PD patients showed profoundly weakened and delayed facial mimicry. In another EMG study, Kang et al. (2019) reported both delayed and diminished facial mimicry in PD subjects compared to controls. Prenger and Macdonald (2018) pointed out problems with facial mimicry that contributed to emotion recognition impairments in PD.

Other investigations identified neuroanatomic differences in PD patients compared to healthy controls—specifically in the amygdala, basal ganglia, and orbitofrontal cortex. Moreover, there was damage to mirror neurons Ricciardi et al., (2017). Also, there was disruption to the neural circuits, possibly due to dopamine depletion (Lotharius and Brundin 2002), that caused Parkinson’s patients to experience slowed or absent emotional perception or restricted expression via the face. In a cogent review of diffusion tensor imaging (DTI) studies, Zhang and Burock (2020) highlighted the changes in nonmotor dopaminergic tracts associated with facial expression in PD.

#### **ix. Impactful Pathoses of the Face**

There are three notable facial communication disorders that merit special attention due to their global health burden. These conditions are: Parkinson’s disease, autism spectrum disorders (ASD), and major depressive disorder (MDD).

The features of PD were outlined in the prior section. The impact of PD is significant. In 2019, the World Health Organization estimated that PD affected more than 8.5 million people worldwide and the prevalence is growing exponentially (“Parkinson Disease” n.d.). In 2017, in the U.S. alone, yearly healthcare expenditures were estimated at \$52 billion (Lewin Group 2019). More recently, Yang et al. (2020) project PD prevalence in the United States will be more than 1.6 million with total economic burden surpassing \$79 billion by 2037. Thus, PD is a disease with significant societal impact that will only become more relevant in the future.

Another unexpected disorder of the face that constitutes a high global health burden is autism spectrum disorder (ASD). ASD, a highly-prevalent neuro-developmental disorder, affects almost 2% of the world’s population (Christensen et al. 2019). In a recent

surveillance summary, the CDC reported that the prevalence of ASD in the United States is trending upward (Maenner et al. 2023).

The hallmarks of ASD are: delayed development, problems with speech, restrictive and repetitive behaviors, and self-stimulating behaviors such as rocking, hand flapping, spinning, etc. (“Signs and Symptoms of Autism Spectrum Disorders | CDC” n.d.). It is not well-known, however, that ASD predominantly is a disorder of the face (Zeichner, Zeichner, and Kuhnle 2019). The impact of ASD is far-reaching: It is a social disease affecting not only patients, but also their families, friends, public schools, the workplace, and society. It’s estimated that U.S. families spend >\$60,000 per year caring for autistic children (Amendah et al. 2011). Autistic children become autistic adults. Consequently, it is reported in the U.K. that 40-80% of autistic adults are unemployed. In the U.S. the statistic is 80-90% unemployment or underemployment. That is 500,000 high-functioning adults who can’t get a job or stay in a job because they cannot appropriately communicate and socialize with their faces.

Many ASD individuals are unable to make or interpret facial expressions, or cannot respond automatically to the facial expressions of others (a crucial part of socialization and communication). Sato et al. (2017) reported that ASD individuals experience difficulties interpreting facial expressions: “specifically perception of form, motion, dynamic facial expressions, autonomic responses to facial expression, subliminally facial expressions, and facial mimicry”. ASD individuals exhibit deficits in expressing facial emotions in general (McIntosh et al. 2006). Additionally, (McIntosh 2006) reported impaired smile mimicry. These authors examined automatic and voluntary mimicry of emotional facial expression among adolescents and adults with ASD and neurotypical controls. Here, they reported impaired automatic mimicry in ASD. A structural MRI study (Hadjikhani et al. 2006) bolstered the observation of diminished facial mimicry in ASD. These authors described cortical thinning in brain regions corresponding to the mirror neuron system (MNS) of high-functioning ASD adults compared to matched controls. The literature suggested that impaired mimicry results in an inability to return a facial display, thus diminishing socialization and communication in ASD individuals.

The mechanism for dysfunctional facial expression in ASD is believed to arise from deficits in specific regions of the brain, altered neural interconnectivity between these

regions, and changes in the neurochemical moderating system. The literature reflects that at least four face-processing regions of the brain function differently in autistic individuals: the face patches, the amygdala, the inferior frontal gyrus (IFG)<sup>67</sup> and the temporo-parietal junction (TPJ)<sup>68</sup>.

Several investigations documented altered functional connectivity within the facial expression-processing regions of the brain. Using fMRI, Khan et al., (2013) demonstrated abnormalities in inferior frontal gyrus (IFG) activation, and reduced connectivity between the right fusiform face area (FFA) and the left anterior cingulate cortex (ACC) in ASD. In a magnetoencephalography (MEG) study, Mamashli et al. (2021) reaffirmed the alterations in connectivity between the FFA and the precuneus, the IFG, and the ACC in autism spectrum disorder versus neurotypical children. Additionally, using resting state fMRI, Dichter (2022) reviewed numerous studies showing anomalous functional connectivity in the face-processing areas of the brain in autistic individuals.

Also, many studies have reported neurochemical disturbances in dopamine, serotonin, noradrenalin, and oxytocin (essential emotion and socialization chemicals) in ASD patients (Daly et al., 2012; Kato et al., 2021; Kubota et al., 2020; Lew et al., 2020; Nakamura et al., 2010; Pavál, 2017). In summary, autistic individuals do not have an intact neuromuscular mechanism to create smiles, nor the cognitive tools to recognize or appropriately respond to the smiles of others.

To summarize the key clinical features of ASD: 1) autistic individuals have a limited repertoire of facial expressions used to communicate and often display inappropriate facial expressions in social situations. 2) Individuals with ASD have difficulties navigating social interactions because a critical neurological deficit prevents them from understanding the vocabulary of human facial expression.

The last disease in this section on impactful pathoses is major depressive disorder (MDD). MDD, a significant health problem, gives rise to a considerable global health burden

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<sup>67</sup> Specifically, the pars opercularis of the IFG. Considered a principal site of the mirror neuron system (MNS).

<sup>68</sup> The TPJ is a secondary site of MNS.

(“Depression” n.d.). Curiously, MDD is a psychiatric disorder closely tied to happy and sad facial expression. Bomfim, Ribeiro, and Chagas (2019) reported that older adults with major depression demonstrated impaired recognition of happy faces and enhanced recognition of sad and angry faces. Rehman et al. (2010) showed that depressed individuals have impaired ability to generate a smile. Arnold & Winkielman, (2021) recently reported that depressed patients displayed reduced spontaneous smile mimicry.

The neuroanatomical perturbations of recognizing happy facial expressions in MDD are noteworthy. Blom et al. (2015), using an fMRI protocol, reported the differential activation in the left anterior/middle insular cortex during sad versus happy face-processing in adolescent subjects with MDD. The authors further reported that there was less pronounced activation in the left anterior/middle insular cortex during sad versus happy face-processing in subjects with MDD than in healthy controls. They described greater functional connectivity between the left anterior insula and the right fusiform gyrus, left middle frontal gyrus, and right amygdala/parahippocampal gyrus (PHG) during happy/sad face-processing in the MDD group.

In a recent fMRI study, Liu et al. (2021) reported the accuracy of facial expression recognition in MDD patients was lower than that of the healthy control group. In particular, the ability to distinguish happy faces from fearful or surprised facial expressions was impaired in MDD patients. Moreover, happy expressions tended to be discerned as neutral. Compared with the control group, the investigators reported decreased activation in the left parahippocampal gyrus, left thalamus, the putamen bilaterally, and right angular gyrus. They noted increased activation in the left superior frontal gyrus, left middle temporal gyrus, left medial superior frontal gyrus, and right medial superior frontal gyrus.

Of particular note was an fMRI study of facial mimicry by (Wild et al. 2003), wherein healthy subjects showed remarkable activation of the putamen bilaterally when viewing happy faces. Ho et al., (2016a) reported that relative to the control group, adolescents with MDD showed hypoactivation in bilateral anterior insula and left fusiform gyrus/lingual gyrus, as well as hyperactivation in a cluster encompassing the right parahippocampal cortex, amygdala, and lentiform nucleus, hyperactivation in bilateral middle temporal gyri, and hyperactivation in the left middle occipital cortex.

The prefrontal cortex (PFC) has emerged as one of the regions most consistently impaired in MDD (Pizzagalli and Roberts 2022). For example, in an fMRI study, Xie et al. (2021) reported decreased activity in the medial orbitofrontal cortex (a subregion of the PFC) of adolescents compared to healthy controls. Intriguingly, a publication by O’Doherty et al., (2003) may connect the medial orbital frontal cortex (mOFC) to impaired happy face recognition in both MDD *and* schizophrenia. In this fMRI study, the authors, in contradistinction to Xie, observed that in healthy individuals, the mOFC distinctly activates when the experimental subject observes a smile. Correspondingly, one should note that many of the anatomic regions described in MDD are implicated in face-processing (Zeichner, Radlanski, and Zeichner 2021).

Additionally, the literature supported the idea that dysfunctional smile production in MDD individuals may correlate with perturbations of the brain’s “reward network”. That is, mOFC activation generally has been associated with response to reward stimuli (the smile is considered a social reward). Correspondingly, the mOFC is linked to the limbic-cortico-striato-pallidal-thalamic circuit (LCSPT), which is based on connections between the orbital and medial prefrontal cortex, amygdala, hippocampal subiculum, ventromedial striatum, mediodorsal and midline thalamic nuclei, and the ventral pallidum (Drevets, Price, and Furey 2008). Many of the aforementioned downstream elements of the LCSPT circuit have been demonstrated to be part of the face-processing network. Interestingly, Peters, Dunlop, and Downar (2016) reported that the LCSPT circuit was impaired not only in MDD, but also in schizophrenia and substance use disorders. In addition to the reported disruption of the LCSPT pathway in MDD, there appears to be aberrant functional connectivity in the circuit. Using diffusion MRI and resting-state BOLD fMRI, Pisner, et.al. (2018) demonstrated functional connectivity deficits in the emotional salience network in patients with depressive rumination. The emotional salience network identified by Pisner et al. (2018) is a frontostriatal network interconnecting the dlPFC to the ACC via the superior corona radiata white matter tract to the amygdala. This is in alignment with the findings of van den Berg et al. (2021), that patients with stroke in this region showed decreased recognition of happy faces. After integrating the literature, I suggest that a likely mechanism for dysfunctional face-processing in MDD may be aberrant frontostriatal functional connectivity.

Wang et al. (2019) reported yet other lapses in functional connectivity involving specific components of face-processing that impact on mirroring facial expressions. They investigated the whole-brain voxel-based hypothalamic resting-state functional connectivity in fifty-five patients with major depressive disorder and forty age and sex-matched healthy controls. The results showed that major depressive disorder patients had a significant decrease in resting-state functional connectivity of the bilateral hypothalamus with the right insula, superior temporal gyrus, inferior frontal gyrus, and Rolandic operculum compared with healthy controls. As cited in Chapter III, these regions have been implicated with deficits in facial recognition, discriminating emotions, and understanding meanings and intentions.

Additional studies appear to support the role of the key neuropeptides involved in emotional facial expression—serotonin, dopamine, noradrenalin, and endorphins in depressive disorders with respect to dysfunctional facial expression (Kaufman et al., 2015; Yim, 2016). Yim connected the ability of facial muscles associated with happy facial expressions (laughing and smiling) to neuropeptide concentrations found in blood samples. In turn, these reported observations suggested that induced or voluntary smiling or laughing is a beneficial therapeutic in depressed patients. Thus, it is not surprising that multiple investigations reflected that induced, or voluntary smiling, is a beneficial therapeutic in depressed patients (see (Akimbekov and Razzaque 2021) for review, also (Cho and Oh 2011; Ko and Youn 2011)).

In short, recent clinical and neuroimaging literature has supported the notion that MDD is accompanied by deficits in facial expression production and emotional face perception that point to multifactorial etiologies. The literature reviewed focused on happy and sad facial expressions of emotion. The focus does not necessarily mean that happy and sad facial (Cho and Oh 2011) expressions are the only facial displays altered in MDD patients. It should be considered that the reviewed literature merely reflects the directions investigated by the researchers.

## **x. Psychiatric Disorders**

The literature reviewed supported impaired smiling in obsessive compulsive disorder (OCD.) A study by Haq et al. (2011) reported that deep brain stimulation (DBS) of the

internal capsule and the nucleus accumbens region of the brain produced smiling and laughter in test subjects. In another study using single-photon emission computed tomography (SPECT), Figeo et al. (2014) found that DBS induced striatal dopamine release from the nucleus accumbens in patients with OCD. Dopamine release has been associated with happy facial expressions (cited earlier). Further studies correlated impaired facial muscle activity in patients with obsessive compulsive disorders (Mergl et al., 2003). The investigators hypothesized that basal ganglia dysfunction, such as observed in Parkinson's disease, underlies the dysfunctional smiling/laughter in OCD. Moreover, it was further postulated that there may be a disturbance in neurotransmitter systems involving serotonin, dopamine, and acetylcholine. Underscoring the connection between dysfunctional face-processing and OCD, fMRI studies have shown that several face-processing regions of the brain, including the amygdala, fusiform, and the left anterior insula, are perturbed in patients with OCD (Cardoner et al. 2011). Additional investigations disclosed dysfunctional facial mimicry in OCD (Bersani et al., 2012).

Schizophrenia has been implicated in dysfunctional facial expression. In a high-resolution MRI study, (Onitsuka et al.) reported neuroanatomic abnormalities of the fusiform gyrus that impaired the recognition of facial expressions in schizophrenic patients. Du et al. (2022) observed impaired ability to produce voluntary facial expressions in schizophrenic patients.

Happy facial expressions received particular attention in the literature. For example, Kohler et al. (2008), reported inappropriate smiling in the affected individuals. Del-Monte et al. (2013); Falkenberg, Bartels, and Wild (2008) described the inability in schizophrenic individuals to suitably interpret the smiles of others during social interactions. She et al. (2017) reported that the accuracy of detecting a happy face among neutral faces is lower in schizophrenia than healthy controls, implying that smile detection may be impaired in patients with schizophrenia.

Several studies point to structural and functional abnormalities in schizophrenia that are implicated in dysfunctional facial expression Arnold, (2000); Chua et al. (1997); Schneider et al. (1998). In a fMRI study, Wild et al. (2003) reported that subjects viewing happy faces showed significant activation in the hippocampus, amygdala, parahippocampal region, fusiform gyri, the right occipitoparietal junction, the right central region, the median

supplemental motor area (SMA) and cingulate, and in both inferior frontal opercula and the right insula. The authors further noted numerous structural and functional abnormalities in the amygdala, the hippocampus and the parahippocampal region in patients with schizophrenia.

These findings suggest a mechanism by which schizophrenic patients exhibit deficits in facial mimicry and misinterpret the facial expressions of others. Additionally, a recent review by Acharya and Kim (2021) offered a pathophysiological mechanism by which impaired smiling results from a dysregulation of dopamine pathways. The pathogenesis of schizophrenia, like PD, OCD, ASD, and MDD appears to involve dysregulation of neuropeptides to impair the processing of happy facial expressions.

Borderline personality disorder (BPD) is a personality disorder affecting approximately 6% of the population of western countries (Volkert, Gablonski, and Rabung 2018). This disorder is characterized by dramatic shifts of mood, intense anger, transient delusional or paranoid ideation, marked impulsivity, and fear of abandonment (Zeichner 2013). BPD has been linked repeatedly to the limbic system (New et al. 2007), the same system that is demonstrably integrated with facial expression.

It is not surprising that several investigations have described dysfunctional facial affective behavior in BPD. In a study of thirty inpatients diagnosed with BPD, Dammann et al. (2020) reported that these patients exhibited a higher proportion of negative facial expressions of emotion—particularly disgust and contempt. On the other hand, BPD patients showed a lot of smiles. However, these were insincere (social) smiles rather than genuine (Duchenne) smiles. Not only do patients with BPD produce aberrant smiles, but also, they misinterpret the positive expressions of emotion of others in social situations. For example, Fenske et al. (2015) reported that BPD patients correctly identified positive facial expressions less often than healthy controls. The authors suggested, such misperception of facial expression may be attributed to limbic hyperactivation in concert with deficits in the regulatory function of the caudate cortex (particularly the anterior cingulate cortex) that has been associated with BPD. Similarly, Ferreira et al. (2018) observed that women with BPD showed impaired recognition of happy faces—both failing to identify happy faces and underestimating the intensity of the happy expression when compared to controls. In a recent facial electromyographic study, Steinbrenner et al. (2022) reported decreased facial reactivity and mirroring in women with BPD. In particular, patients with BPD showed a smaller

increase of mimic activity in response to happy faces in the zygomaticus major muscle than in healthy controls. These findings suggested that there are both motor and smile-mimicry deficits in BPD. Molecular imaging studies, Kolla et al. (2020) linked functional impairments in BPD to insula cortex, hippocampus, ventral striatum, dorsal putamen, and dorsal caudate—regions known to be implicated in the perception of happy affect.

In summary, the literature that addressed facial pathology in BPD pointed to significant dysfunction in interpreting and producing facial expressions. This manifested as impairment of the facial communication system leading to social impairment. The literature further suggested that the impairment involved the interconnection of brain regions responsible for face-processing with the limbic system (the brain regions responsible for emotional regulation).

#### **4.1. Summary/Conclusions Chapter IV**

Chapter IV highlighted more than twenty disorders of facial communication. Rarely are these disorders viewed by the medical profession as abnormalities of the face. Nonetheless, by studying the neurocorrelates of these conditions, comparing and synthesizing the findings of diverse investigations, this thesis offers interesting insights.

Some of the more informative observations derive from “lesion studies”<sup>69</sup>. Parvisi’s work with a temporal lobe epilepsy patient, whose treatment entailed electrical stimulation of a brain region immediately proximal to the right mFus-face and pFus-faces area, cemented the concept that the right FFAs were central to face-processing. This observation that the subject’s perception that Parvisi’s face morphed momentarily during stimulation, explained the etiology of prosopagnosia, face blindness.

Other lesion studies offered considerable insight into the relationship of the face to the “social brain”. For example, patients with Williams syndrome (WS) have a chromosome deletion that alters both brain structure and the production of the neuropeptide, oxytocin. The

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<sup>69</sup> “Lesion studies” are a staple of neuroscience research. In the lesion studies, patients with brain lesions are examined to determine which brain regions are damaged and how this influences the experimental subject’s behavior.

regions involved correspond to key sites of face-processing. Thus, individuals with WS demonstrate a fascination with the human face. WS individuals are noted for their smiling faces, and are drawn to the smiling faces of conspecifics. They engage conspecifics without fear or social inhibition, and these individuals are known for empathy. Thus, individuals with WS, manifest a behavioral phenotype characteristic of the lesions observed experimentally.

Other heritable diseases provided insight into the mechanisms of facial expression recognition and facial expression production. Studies of patients with Angelman syndrome, characterized by hyper-sociability and smiling faces, delineated the involvement of the insula in discriminating happy facial expressions and the role of the prefrontal-amygdala pathway in social disinhibition.

The studies of patients with Huntington's chorea show significant impairment both in recognizing and producing facial expressions. This research suggested an intervening loop between the neural pathways that perceive facial expressions and the pathways that produce a facial response (in other words, a codependence of two neural circuits). Particularly noteworthy were the fMRI findings that pointed to disruption of the pSTS, a key component of the mirror neuron system. The MNS is the pathway which enables humans to mirror and acknowledge gestures (including facial gestures) of others during nonverbal communication. This observation gives insight to why patients with neurodegenerative disorders who lack the ability to use the muscles of their faces, concomitantly cannot comprehend the facial expressions of conspecifics.

To date, the essential role of the MNS has not received emphasis with regard to facial communication. However, new evidence from the meta synthesis of data from this chapter revealed a thread common among the facial pathologies presented here. That is, the diseases showed an abnormality in at least one of the four principal components of the MNS or disruption of the neural pathways leading to or among the anatomic components of the MNS.

Also notable was the volume of people having facial communication disorders arising from stroke, Parkinson's disease, autism spectrum disorders, and major depressive disorder. The scope of the associated health, economic, and social burdens are considerable.

In conclusion, by systematically assessing the contemporary literature on facial pathology, this thesis establishes key anatomic regions and/or neural circuits in the brain, that

when affected by lesions, result in characteristic dysfunction in facial communication or face-related socialization.

## CONCLUSION

The primary contribution of this thesis to the field of communication sciences is that until now, there has been no comprehensive, “big picture” examination of the anatomy, physiology, and pathology of the human face with respect to facial communication and socialization. Nor has facial communication been viewed from the perspective of a written or spoken language. This thesis has led to key conceptualizations.

Firstly, this thesis introduced the concept that facial communication has linguistic parallels. For example, by integrating the literature from diverse fields of study, I have illustrated that facial communication has vocabulary (including facial expression “emblems” that convey full concepts rather than individual words) and a “dictionary” that codifies the words. Additionally, “the language of the face” has punctuation, context, social rules (pragmatics), accents, and dialects. Furthermore, facial communication is gender-, age-, culture-, and family-dependent. Remarkably the facial gestures unique to a family (“that certain smile”) are not learned: The distinct muscle movement is inherited. Equally remarkable is that the vocabulary of facial language is larger than the average adult working-vocabulary.

Facial emotional expression is an interplay between the muscles of facial expression and a collection of neurons within the brain. This system enables humans to both express emotions in their faces and perceive emotions in faces of others. The distinctive neuroanatomy is central to human survival both as individuals and as a species. The review and analysis of the anatomic literature revealed noteworthy takeaways. That is, the muscles of facial expression are skeletal muscle with uniquely distinct attributes. The muscle fibers are fine with multiple sites of innervation that allow for the subtle movement needed to achieve many movement variants—essential for a broad “vocabulary” by which to communicate facially. Also, these muscle fibers are “fast twitch” fibers—uniquely suited for allowing fleeting “micro expressions” that are essential in facial communication.

In addition, this thesis illuminated an often-overlooked, but essential, triad of face muscles essential to human survival. These muscles respond to pathogens, toxins, or pleasant taste, thus telegraphing to other humans a safe food supply, the danger of disease, or the

presence of poisons. Curiously, these primitive facial signals of disgust, distaste, or gustatory pleasure, in modern times, extend to contemplating a pleasurable meal or thinking about moral disgust and distaste, such as the concepts of dishonesty, death, disease, or culturally-unacceptable sex acts.

This thesis further brought to the fore the concept of a distributed neural network comprised of multiple face-processing sites distributed throughout the brain. Although many of the anatomic sites have been known for decades, the data analysis in this thesis extended the known network. More than fifty face-processing nodes were tabulated in this thesis.

Viewing scores of brain MRIs led to an interesting anatomic relationship previously unreported in the face-processing literature. That is, there was a contiguous series of gyri extending from the occipital lobe to the frontal lobe. These gyri contained fourteen nodes identified with face-processing. The most striking finding is that these gyri interconnect all four principal sites in the mirror neuron system. This may explain why most of the diseases of the face investigated in this project exhibited abnormalities in the mirror neuron system (MNS).

This dissertation addressed several little-known findings about the extraordinary physiology by which humans leverage faces for communication and socialization. Some of the more interesting aspects included: 1) That humans are incredibly sensitive to faces, to the point at which they see faces within inanimate objects. 2) That there are intrinsic neural mechanisms linked to faces that rapidly segregate” in-social group” from “out-social group”. These complex neural circuits activate the “emotional brain”, triggering negatively-valenced emotions toward out-group faces and prosocial behaviors toward in-group individuals. Several investigations suggested that face-processing is at the core of racial or ethnic prejudice. 3) Facial age discrimination is central to human social structure. Via rapid neural mechanisms for age assessment, society limits aggression toward members with older faces and very young faces, nurtures and protects members with child-like facial features, and permits copulatory behaviors with females whose facial features signal they are of reproductive age or males with mature facial features that represent sufficient stature to support offspring. 4) There is evidence that humans communicate with facial displays while

copulating. Furthermore, investigators have codified these facial gestures. 5) The neural mechanism by which primates, and especially human primates, innately and involuntarily mimic facial expressions, plays a vital role in communication. This dissertation explained the physiology of the mirror neuron system, the core of facial mimicry. The mirror neuron system also is fundamental to the critical social/communication conceptualization of Theory of Mind. One cannot communicate effectively if one has no conception or understanding of the state of mind of the person with whom one is communicating. The physiology of the human face allows for this essential insight. Also, this thesis explained the far-reaching effects of the human smile. Not only is interpreting or generating a smile an important part of human communication and socialization, but also smiling was shown to relate to human health status and physiological processes such as immunity, cardiovascular function, metabolic disease, and several neuropsychiatric disorders.

Chapter III (Physiology of the Face) proposed a network map derived from the data collected in this project. A data analysis led to a new proposed neurophysiological mechanism for the physiology and pathophysiology of smiling—an integral process in facial communication. The proposed mechanism involved twenty-six nodes and six interconnected hubs on a distributed neural network. Other key findings of Chapter III included: a contemporary discussion of the neurophysiology for facial identity determination, age/gender/race/health discrimination, mating-related facial mechanisms, and responses thereto.

Chapter IV, “Pathology of the Face”, highlighted functional abnormalities of the human face in diseases that conventionally are not considered “diseases of the face”. The chapter also drew attention to the social and economic significance of facial disorders. Comparing and synthesizing the findings of diverse investigations in twenty diseases of the face, offered interesting insights that may not be well appreciated by non-specialists or single-discipline scholars. Specifically, the findings from temporal lobe epilepsy lesion studies cemented the concept that the right fusiform face areas (FFAs) were central to face-processing.

Other lesion studies offered considerable insight into the relationship of the face to the “social brain”. For example, patients with Williams syndrome have a chromosome deletion that alters both brain structure and the production of the neuropeptide, oxytocin. Analyzing

the data from multiple published studies of WS, this thesis correlated anatomic and neurochemical abnormalities to key sites of face-processing thus explaining the characteristic behavioral phenotype of individuals with WS.

New evidence from the meta synthesis of data from this thesis investigation revealed a thread common among the facial pathologies presented here. That is, the diseases showed an abnormality in at least one of the four principal components of the mirror neuron system or disruption of the neural pathways leading to or among the anatomic components of the MNS. The analysis led to the novel conclusion that the mirror neuron system, the essential pathway which enables humans to mirror and acknowledge gestures (including facial gestures) of others during nonverbal communication, was implicated in most of the diseases investigated. This observation gives insight to why patients with facial communication disorders, who lack the ability to use the muscles of their faces, concomitantly cannot comprehend the facial expressions of conspecifics. Finally, by systematically assessing the contemporary literature on facial pathology, this thesis established key anatomic regions and/or neural circuits in the brain, that when affected by lesions, result in characteristic dysfunction in facial communication or face-related socialization.

As expected with scientific inquiries, this project opened the doors to more questions than answers that it produced. Some areas of future inquiry might be mapping additional emotion-processing routes, such as those associated with the facial expression of sadness, disgust, anger, and fear. Preliminary assessment of these parameters suggested paired neurocorrelates of happiness and sadness, and parallel neurocorrelates for anger, disgust and fear. These hypotheses merit further investigation. The data from the present investigation beg further investigation of the mirror neuron system. It is significant that dysfunction in any portion of the four anatomic sites of the MNS disrupts most facial communication. This merits further exploration.

In conclusion, this dissertation project put together the fragmented science of facial communication to better elucidate the intricate processes by which humans communicate with their faces. The thesis proposed new, or expanded existing schemata for neural networks involving self-identity, gender, race, and age determination, and the recognition or generation of specific expressions of facial emotion. Additionally, the thesis explored possible mechanisms for heretofore unexplained or partially-explained disease processes. The thesis

also offered scientific insight into how the activation of specialized muscles in the face can act systemically on the rest of the body to moderate metabolism, immunity, cardiovascular health, and pain tolerance.

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## APPENDIX

Table 1. List of Action Units (AUs) and Action Descriptors (ADs) (with underlying facial muscles). Table adapted with permission of the publisher. Courtesy of Bryn Farnsworth, Ph.D, <https://imotions.com/blog/facial-action-coding-system>.

Main Codes		
AU number	FACS Name	Muscular Basis
0	Neutral face	
1	Inner brow raiser	<i>frontalis (pars medialis)</i>
2	Outer brow raiser	<i>frontalis (pars lateralis)</i>
4	Brow lowerer	<i>depressor glabellae, depressor supercilii, corrugator supercilii</i>
5	Upper lid raiser	<i>levator palpebrae superioris, superior tarsal muscle</i>
6	Cheek raiser	<i>orbicularis oculi (pars orbitalis)</i>
7	Lid tightener	<i>orbicularis oculi (pars palpebralis)</i>
8	Lips toward each other	<i>orbicularis oris</i>
9	Nose wrinkler	<i>levator labii superioris alaeque nasi</i>
10	Upper lip raiser	<i>levator labii superioris, caput infraorbitalis</i>
11	Nasolabial deepener	<i>zygomaticus minor</i>
12	Lip corner puller	<i>zygomaticus major</i>
13	Sharp lip puller	<i>levator anguli oris</i>
14	Dimpler	<i>buccinator</i>
15	Lip corner depressor	<i>depressor anguli oris</i>
16	Lower lip depressor	<i>depressor labii inferioris</i>
17	Chin raiser	<i>mentalis</i>
18	Lip pucker	<i>incisivii labii superioris and incisivii labii inferioris</i>
19	Tongue show	
20	Lip stretcher	<i>risorius with platysma</i>
21	Neck tightener	<i>platysma</i>
22	Lip funneler	<i>orbicularis oris</i>
23	Lip tightener	<i>orbicularis oris</i>
24	Lip pressor	<i>orbicularis oris</i>
25	Lips part	<i>depressor labii inferioris, or relaxation of mentalis or orbicularis oris</i>
26	Jaw drop	<i>masseter; relaxed temporalis and internal pterygoid</i>
27	Mouth stretch	<i>pterygoids, digastric</i>
28	Lip suck	<i>orbicularis oris</i>

Table 2. List of movement codes.

Head Movement Codes		
AU Number	FACS Name	Action
51	Head turn left	
52	Head turn right	
53	Head up	
54	Head down	
55	Head tilt left	
M55	Head tilt left	The onset of the symmetrical 14 is immediately preceded or accompanied by a head tilt to the left.
56	Head tilt right	

M56	Head tilt right	The onset of the symmetrical 14 is immediately preceded or accompanied by a head tilt to the right.
57	Head forward	
M57	Head thrust forward	The onset of 17+24 is immediately preceded, accompanied, or followed by a head thrust forward.
58	Head back	
M59	Head shake up and down	The onset of 17+24 is immediately preceded, accompanied, or followed by an up-down head shake (nod).
M60	Head shake side to side	The onset of 17+24 is immediately preceded, accompanied, or followed by a side-to-side head shake.
M83	Head upward and to the side	The onset of the symmetrical 14 is immediately preceded or accompanied by a movement of the head, upward and turned or tilted to either the left or right.

<b>Eye Movement Codes</b>		
<b>AU Number</b>	<b>FACS Name</b>	<b>Action</b>
61	Eyes turn left	
M61	Eyes left	The onset of the symmetrical 14 is immediately preceded or accompanied by eye movement to the left.
62	Eyes turn right	
M62	Eyes right	The onset of the symmetrical 14 is immediately preceded or accompanied by eye movement to the right.
63	Eyes up	
64	Eyes down	
65	Walleye	
66	Cross-eye	
M68	Upward rolling of eyes	The onset of the symmetrical 14 is immediately preceded or accompanied by an upward rolling of the eyes.
69	Eyes positioned to look at other person	The 4, 5, or 7, alone or in combination, occurs while the eye position is fixed on the other person in the conversation.
M69	Head or eyes look at other person	The onset of the symmetrical 14 or AUs 4, 5, and 7, alone or in combination, is immediately preceded or accompanied by a movement of the eyes or of the head and eyes to look at the other person in the conversation.

<b>Visibility Codes</b>	
<b>AU number</b>	<b>FACS Name</b>
70	Brows and forehead not visible
71	Eyes not visible
72	Lower face not visible
73	Entire face not visible
74	Unscorable

<b>Gross Behavior Codes</b> (These codes are reserved for recording information about gross behaviors that may be relevant to the facial actions that are scored)		
<b>AU Number</b>	<b>FACS Name</b>	<b>Muscular Basis</b>
29	Jaw thrust	
30	Jaw sideways	

31	Jaw clencher	<i>masseter</i>
32	[Lip] bite	
33	[Cheek] blow	
34	[Cheek] puff	
35	[Cheek] suck	
36	[Tongue] bulge	
37	Lip wipe	
38	Nostril dilator	<i>nasalis (pars alaris)</i>
39	Nostril compressor	<i>nasalis (pars transversa) and depressor septi nasi</i>
40	Sniff	
42	Slit	<i>orbicularis oculi muscle</i>
43	Eyes closed	relaxation of <i>levator palpebrae superioris</i>
44	Squint	<i>corrugator supercilii</i> and <i>orbicularis oculi</i> muscle
45	Blink	relaxation of <i>levator palpebrae superioris</i> ; contraction of <i>orbicularis oculi (pars palpebralis)</i>
46	Wink	<i>orbicularis oculi</i>
50	Speech	
80	Swallow	
81	Chewing	
82	Shoulder shrug	
84	Head shake back and forth	
85	Head nod up and down	
91	Flash	
92	Partial flash	
97*	Shiver/tremble	
98*	Fast up-down look	

Table 3. The Periauricular Muscles. Descriptive anatomy of the three periauricular muscles and the principle facial expressions in which they participate.

Name	Origin	Insertion	Innervation	Action	Principle Expression
<b>1) Superior auricular</b>	galea aponeurotica	Back of the auricle in area of the eminentia scaphae & eminentia fossae triangularis, spina heliis	Temporal branches & auricular branch of the posterior auricular nerve of CN VII	Pulls ear upward & backward	Heightened interest & attention to sound.
<b>2) Anterior auricular</b>	temporalis fascia, galea aponeurotica	major helix	Temporal branches VII	Pulls ear forward & upward	Responds to emotional facial
<b>3) Posterior auricular</b>	mastoid	eminientia conchae of auricle	Temporal branch VII	Pulls ear backward	displays & signals

Table 4. The Orbicular Muscles. Descriptive anatomy of the three muscles of the eye and the principle facial expressions in which they participate. The orbicularis oculi is subdivided into three pars, and the pars palpebralis is further subdivided into three components.

Name	Origin	Insertion	Innervation	Action	Principle Expression
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<b>1) <i>Obicularis oculi</i></b>			Temporal, zygomatic & buccal branches VII		wink, concern, perplexion
<i>1) Pars Orbitalis</i>	frontal & maxillary bones	Neighboring muscles		Tightly closes eyelids	
<i>2) Pars Palpebralis</i>	medial palpebral ligament	lateral palpebral ligament		Gently closes & pulls on lacrimal sac, creating suction for removal of lacrimal fluid from medial angle of eye	
<i>i) pretarsal</i>	medial canthal tendon	lateral canthal tendon			
<i>ii) ciliary</i>					
<i>iii) preseptal</i>	medial canthal tendon	lateral canthal tendon		Expresses tears	
<i>3) Pars Lacrimalis</i>	crista lacrimalis of lacrimal bone	lacrimal canaliculi into the palpebral part		Drains tears	
<b>2) <i>Palpebrae superioris</i></b>	lesser wing of sphenoid bone	anterior surface of superior tarsal plate	Oculomotor CN III	Raises superior eyelid	Surprise, fear
<b>3) <i>Corrugator supercilii</i></b>	nasal process of the frontal bone	frontalis & orbicularis muscles & deep surface of skin	Temporal branches VII	Draws eyebrow downward & medially	Frowning, suffering

Table 5. The Nasal Muscles. Descriptive anatomy of the 3 muscles of the nose and the principle facial expressions in which they participate.

Name	Origin	Insertion	Innervation	Action	Principle Expression
<b>1) <i>Nasalis Transverse</i></b>	canine eminence	aponeurosis at bridge of nose	Zygomatic branches VII	Compresses nostril	anger
<i>Alar part</i>	superior to lateral incisor	greater alar cartilage		Dilates nostril	
<b>2) <i>Depressor septi nasi</i></b>	Incisive fossa of maxilla	cartilaginous part of nasal septum	Zygomatic & buccal branches VII	Depresses nasal septum & dilates nostril	More involved speech than expression
<b>3) <i>Procerus</i></b>	nasal bone, lateral nasal cartilage	skin overlying the glabella	Zygomatic branches VII	Depresses medial end of eyebrow	Distain or combined w/ corrugator supercilii =sadness

Table 6. The Oral Muscles. The descriptive anatomy of the ten muscles of the mouth and the principle facial expressions in which they participate. The oral muscles are arranged in three groups of three around the central obicularis oris muscle.

Name	Origin	Insertion	Innervation	Action	Principle Expression
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<b><i>Obicularis Oris</i></b> 1) <i>Deep part</i>  2) <i>Superficial part</i> <i>Upper bundle</i>  <i>Lower bundle</i>	Modiolus  Fibers of depressor anguli oris	contralateral modiolus  ANS, nostril sill  philtral ridge	Zygomatic, Buccal & Mandibular	Closes the mouth & puckers the lips	pouting
<b>1) <i>Levator labii superioris</i></b>	infraorbital margin of the maxilla above the infraorbital foramen	skin of the upper lip and wing of the nose, o. oris	Zygomatic & buccal branches VII	Elevates upper lip	distaste
<b>2) <i>Levator labii superioris alaeque nasi</i></b>	frontal process of the maxilla	upper lip, skin of the nasal wings	Zygomatic & buccal branches VII	Elevates upper lip & wing of the nose, Dilatates the nostril	snarl, 'Elvis muscle' disgust
<b>3) <i>Levator anguli oris</i></b>	Maxilla below infraorbital f.	Corner of mouth	Buccal branch VII	Elevates corner of mouth	gustatory pleasure
<b>1) <i>Zygomaticus major</i></b>	Lateral zygomatic process	Corner of mouth	Zygomatic & buccal branches	draws lip outward & superiorly	smile
<b>2) <i>Zygomaticus minor</i></b>	Medial zygomatic process	Lateral part of upper lip	Zygomatic branches	draws upper lip superiorly	smile or sadness or pain
<b>3) <i>Risorius</i></b>	Fascia over parotid & masseter	Skin angle of mouth	Buccal branch VII	retracts corner of mouth laterally	insincere smile
<b>1) <i>Depressor anguli oris</i></b>	Inferior border mandible	Skin corner of mouth	Mandibular branch	draws mouth downward & laterally	sadness
<b>2) <i>Depressor labii inferioris</i></b>	Inferior border mandible-oblique line	Skin and mucosa lower lip & fibers of oo	Mandibular branch of VII	depresses, draws laterally & everts lower lip	sorrow, doubt, irony
<b>3) <i>Mentalis</i></b>	Incisive fossa of mandible	Skin of chin	Mandibular branch of VII	protrudes & everts lower lip, wrinkles chin skin	doubt or distain

Table 7. Other Facial Muscles not associated with a specific facial region. The descriptive anatomy of the 3 uncategorized muscles and the principle facial expressions in which they participate.

Name	Origin	Insertion	Innervation	Action	Principle Expression
<b>1) <i>Platysma</i></b>	Fascia of superior chest	Mandible & fascia of lower face	cervical branch of VII	Draws lower lip laterally, wrinkles skin of neck	Horror, surprise, disgust
<b>2) <i>Occipito-frontalis</i></b> <i>frontal belly</i>  <i>occipital belly</i>	Epicranial aponeurosis  Occipital & mastoid regions	Fibers of o. oculi, CS & skin of brow  aponeurosis	Temporal branch of VII  Posterior auricular branch VII	Elevates brows	Surprise or horror  Worry or disgust

<b>3) Buccinator</b>	Alveolar process of maxilla, mandible & pterygomandibular raphe	Lower lip & upper lip	buccal branches of VII	Pulls commissures laterally & compresses cheeks	exasperation
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Table 8. Face-processing nodes within the limbic system.

<i>Limbic system</i>		
<b>Structure</b>	<b>Anatomic relationships</b>	<b>Role(s)</b>
Amygdala (hemisphere not specified)	In medial temporal lobe anterior to the hippocampus	Exhibits overall response to faces. Diminished in TLE <sup>70</sup>  Contributes to facial recognition. Preferential response to eye features  Impaired recognition mostly fear  Resolves ambiguous expressions  Responds to race (RFC) <sup>71</sup>  Responds to infant faces  Disgust perception in racial faces  Diminished volume in Angelman's syndrome
Right amygdala		Greater functional connectivity in MDD <sup>72</sup>
Hippocampus	Abuts the posterior amygdala	In facial recognition, codes for specific faces.  Imparts social judgement to the features of faces.  Responds to race  Responds to infant faces  Involved in self-recognition  Less responsive to faces in TLE  Part of LCSPT <sup>73</sup> circuit impaired in MDD,

<sup>70</sup> TLE=temporal lobe epilepsy

<sup>71</sup> RFC=reactive fear circuit

<sup>72</sup> MDD=major depressive disorder

<sup>73</sup> LCSPT= limbic-cortico-striato-pallidal-thalamic circuit

		schizophrenia, and substance abuse disorders
Hippocampus subiculum	Tail of the hippocampus	Part of LCSPT. Involved in impaired smiling
Parahippocampus	Inferior to subiculum Surrounds hippocampus	Less responsive to faces in TLE. Greater fc <sup>74</sup> in happy/sad face-processing Diminished recognition of happy faces associated with decreased activation left parahippocampal gyrus
Thalamus	Directly superior to the brainstem. Bounded anteriorly by insula. Inferiorly by hypothalamus.	Left hemisphere correlated with diminished recognition of happy faces
Mediodorsal & midline thalamic nuclei	Within the thalamus	Part of LCSPT implicated with impaired smiling
Hypothalamus	Inferior to the thalamus	Responds to race via (CFC) <sup>75</sup> Decreased fc in MDD
POMC cells of hypothalamus	In paraventricular nucleus	Modulator linked to $\beta$ -endorphins, mood elevation
Insula (anterior)	Proximal to ACC,	Diminished volume in Angelman's Implicated in self-recognition Responds to infant faces Happiness perception Gender perception Responds to race via (RFC) Disgust perception in racial faces No perception of disgust in Huntington's

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<sup>74</sup> Fc=functional connectivity

<sup>75</sup> CFC=cognitive fear circuit

		<p>Diminished perception of anger and sadness</p> <p>Greater fc in left with MDD</p>
Pituitary (anterior lobe)	Inferior to the hypothalami	Production of $\beta$ -Endorphins
Cingulate cortex (CC) unspecified	Arch-shaped medially-located cortical structure	<p>Neuroanatomical alteration myelin in William syndrome</p> <p>Diminished volume in Angelman's</p> <p>Self-recognition, responds to race</p> <p>Stroke impairs happiness recognition</p> <p>Sadness activates ACC</p> <p>Impaired happiness recognition in BPD<sup>76</sup></p>
dorsal anterior cingulate (dACC)	-	Reactive fear circuit
anterior cingulate gyrus	Anterior portion of the CC	<p>Race identification</p> <p>Disgust perception in racial faces</p>
<p>Left anterior dorsal cingulate cortex (ACC)</p> <p>Posterior cingulate cortex</p>		<p>Face recognition, part of a postulated DNN.</p> <p>Implicated in prosopagnosia</p> <p>Recognizing kin</p> <p>Selectively responds to infant faces</p>

Table 9. Face-processing nodes of the paralimbic region.

**Paralimbic**

<sup>76</sup> BPD=borderline personality disorder

<b>Structure</b>	<b>Anatomic relationships</b>	<b>Roles (s)</b>
Clastrum	Sheet-like collection of neurons medial to insula and lateral to putamen.	Part of disgust circuit
Nucleus accumbens (nAc)	Immediately rostral to the hypothalamus. The shell of the nAc extends to the amygdala, and further connects to the hippocampal subiculum	LCSPT <sup>77</sup> diminished fc <sup>78</sup> Prosocial behavior e.g., smiling, perception of happiness
Subthalamic nucleus right hemisphere	Most superior region of brainstem abutting the inferior surface of the thalamus	Self-recognition
Parahippocampal gyrus (PHG) parahippocampus	Inferior to hippocampal subiculum	Less responsive to faces with TLE <sup>79</sup> Greater fc in happy/sad face-processing Diminished recognition happy faces Correlates with decreased activation left parahippocampal gyrus
Intraparietal sulcus (IPS) left hemisphere	<i>The groove separating the superior and inferior portions of the parietal lobe</i>	Own face recognition
Angular gyrus (AG) right hemisphere	A gyrus in the parietal lobe that communicates inferiorly with the superior temporal gyrus	Diminished recognition of happy faces
Occipital parietal sulcus (OPS) right hemisphere	In anterior occipital lobe adjacent to precuneus	Identifies kin
Temporoparietal junction	<i>A broad region encompassing portions of the temporal and parietal lobes</i>	Recognizing one's self and one's past-self Diminished facial mimicry

Table 10. Face-processing nodes in the prefrontal cortical network.

<b>Prefrontal Cortex</b>		
<b>Structure</b>	<b>Anatomic relationships</b>	<b>Roles (s)</b>
Superior frontal gyrus (SFG) Left hemisphere	Most superior gyrus of the frontal lobe	Responds to infant faces Face recognition, part of a postulated DNN perturbed in prosopagnosia Increased activation in MDD <sup>80</sup>
Medial superior frontal gyrus (mSFG) both hemispheres	The medial turn (genu) of the SFG	Increased activation concurrent with diminished recognition of happy faces in MDD
Inferior frontal gyrus (IFG)	<i>Most inferior gyrus in the frontal lobe. Contained in the inferior frontal cortex</i>	Gender perception Diminished facial mimicry Decreased fc in MDD

<sup>77</sup> LCSPT= limbic-cortico-striato-pallidal-thalamic circuit

<sup>78</sup> Fc = functional connectivity

<sup>79</sup> TLE+ temporal lobe epilepsy

<sup>80</sup> MDD= major depressive disorder

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pars opercularis of the IFC	“leg” of Inferior frontal gyrus	Responds to animated faces. Stroke impairs sadness perception
pars triangularis of the IFC	“leg” of Inferior frontal gyrus	Facial identification
Anterior prefrontal cortex Left (APFC)	<i>The most rostral part of the frontal lobe</i>	Face recognition, part of a postulated DNN prosopagnosia
Medial prefrontal cortex		Impaired smiling in LCSPT <sup>81</sup> circuit
Orbital frontal cortex (OFC)	<i>Most ventral part of the frontal lobe. Situated medially overlying the floor of the orbits.</i>	Neuroanatomic alterations in William syndrome Diminished volume in Angelman syndrome Diminished facial identity in Alzheimer’s
Inferior frontal-orbital cortex (iOFC)		Gender perception Poor sadness perception in stroke Disgust perception in racial faces
Posterior medial orbital frontal cortex (pmOFC)		Stroke impairs happiness recognition
Medial orbital frontal cortex (mOFC)		Neuroanatomic alterations in William syndrome Activates when observing happy faces Responds to facial beauty & sexual relevance of faces Responds to gender and sexual orientation
Ventral lateral prefrontal cortex (vlPFC)	Within the lateral frontal cortex	Perceiving fearful, surprised, sad, and disgusted faces. Responds to race (CFC) <sup>82</sup> Activated in fathers viewing infant faces. Expressing pleasure, gratification and/or satiation via the face Identifying self Responds to race (CFC)
Dorsal lateral prefrontal cortex (dlPFC)	<i>Located below the vlPFC</i>	Stroke impairs happiness recognition
right inferior frontal face area (riFFA)	Proximal to the junction of the right inferior frontal and middle frontal gyri.	Facilitates view-invariant representation of identities

<sup>81</sup> LCSPT= limbic-cortico-striato-pallidal-thalamic circuit

<sup>82</sup> CFC=cognitive fear circuit