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Emotion

Paula M. Niedenthal, University of Wisconsin-Madison

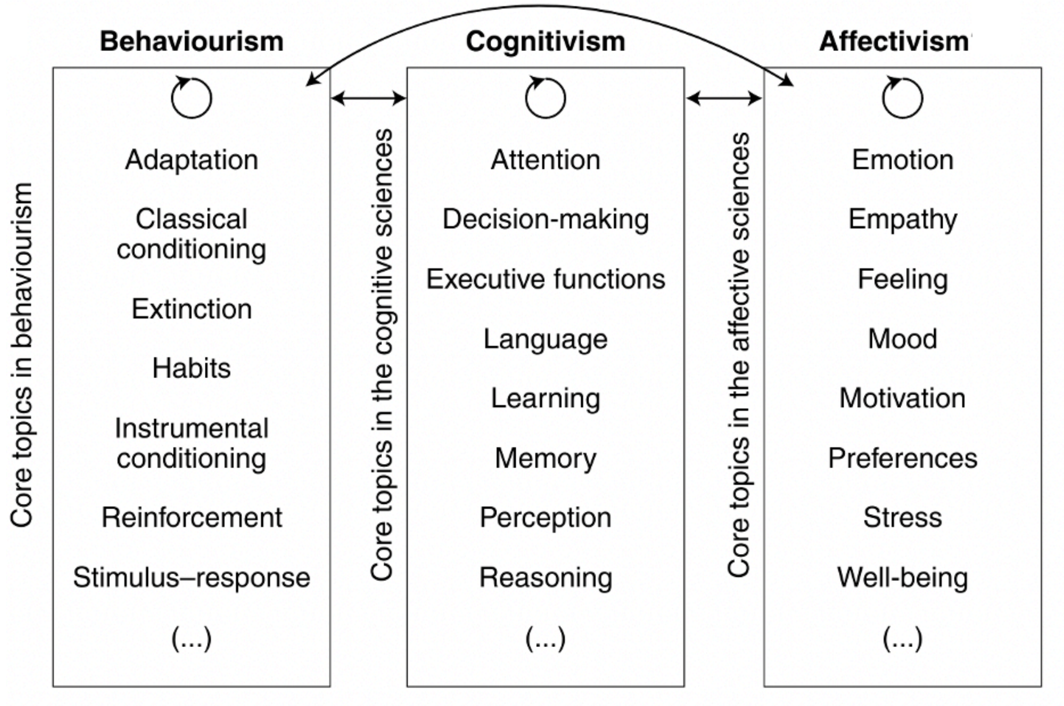
Maital Neta, University of Nebraska-Lincoln

Adrienne Wood, University of Virginia

Emotions are the fuel that motivates behavior, and without well-developed theories of emotion, our understanding of human psychology is incomplete. For several decades in the 20th century, behaviorists, and then cognitivists, tried their best to model human behavior without considering emotion at all, but these approaches fell short (for an overview, see Lazarus, 2000). Towards the end of the century, psychologists remembered that even if we understand behavioral and cognitive processes (e.g., how an organism learns, processes, and represents information), an organism without affect will not do anything with that information (Frijda, 2010; Reis & Gray, 2009; Shadmehr & Ahmed, 2020). There is now a thriving field dedicated to the empirical study of emotion known as affective science (Gross & Barrett, 2013). Indeed, some psychologists have dubbed the turn of the 21st century "the era of affectivism" (see Figure 1; Dukes et al., 2021).

In the present chapter, we review contemporary perspectives and research in affective science. "Affect" refers to any psychological process that is valenced—experienced as either good or bad. "Emotions" are a specific type of organized, goal-directed affective states. Emotions have been a topic of investigation in psychology and neighboring disciplines for over a century, and many comprehensive summaries of affective science exist (Fox et al., 2018; Keltner & Lerner, 2010). The focus is thus mainly on 21st-century research and on recent and exciting research questions.

***Figure 1*: The Rise of Affectism**



Note: Behaviorism, which avoided mental processes as explanations for behavior, dominated empirical psychology for the first half of the twentieth century. Cognitivism arose in the 1950s and renewed psychology's focus on how the mind works. Affectivism, an era proposed as beginning in the 1980s, emphasizes the motivational processes that direct cognition and behavior. Arrows indicate that each domain (behavior, cognition, affect) informs the other and they are inseparable aspects of psychology. Reproduced from Dukes et al. (2021).

We begin the chapter with a definition of emotion and a description of its properties. Having defined our concepts, we then introduce the dominant theoretical perspectives in affective science. Next, we examine how emotions are instantiated in the brain and body, which produces functional changes to cognition, communication, and behavior. In the section that follows, we review recent work on interoception and language that shows how conscious experiences of emotion can change the emotion state itself. Then we consider emotions in social contexts and ask how people infer, and sometimes match, the emotion states of others. In the final section, we highlight exciting trends in affective science that have only recently been made possible thanks to technological advances.

WHAT ARE EMOTIONS?

Affective states, and the more specific goal-directed responses known as emotions, are woven into every aspect of cognition and behavior. An affect-less organism could sense and perceive the world, but it would not know what information to prioritize and attend to. Attitudes—the affective tags associated with specific concepts, such as *crème brulee = very good* and *ex-boyfriend = trouble*—draw the organism's attention and cognitive resources to things that matter to its survival (Barsalou, 1991; Smith & Medin, 2013; Dubey et al., 2022). An affect-less organism could also remember information and put information into categories, but all information would be given equal priority. Memory and learned concepts would contain a random sampling of events and stimuli the organism encountered, most of which would be irrelevant to the survival of the organism. Affect guides memory to prioritize objects, events, and relationships that are relevant to its survival—things that are rewarding or punishing (Tyng et al., 2017; Bechler et al., 2021; Corneille & Stahl, 2019). An affect-less organism would have the *ability* to execute behaviors, but beyond reflexes, it would not have the motivation to act. And there would be no anticipated rewards or punishments to shape its choices.

Imagine, now, that the organism not only has valenced (good and bad) experiences, attitudes, and memories that help it approach good things and avoid bad things, but it also has efficient behavioral response templates that generalize across goal-relevant situations. When it recognizes a situation as having similar relevance to a goal as prior situations, it can enact a similar action plan (Frijda, 2016). This is what emotions are. Emotions are automatic, behaviorally flexible responses, that prioritize goals (Adolphs & Anderson, 2018; Scherer, 2009).

Let's flesh out that definition. Emotions are automatic in that they override planned behavior and require effortful control to inhibit (Frijda, 2010). They are therefore efficient and fast—desirable properties when self-relevant goals are at stake. Emotions are behaviorally flexible, and more flexible than reflexes (e.g., a person closing their eyes when something flies at their face or putting their hands out when they fall), which are often impossible to inhibit and are less responsive to context and learning. Because of their level of abstraction, emotions are therefore useful behavioral guides even in new contexts. A person who is afraid is driven to escape the threat, and they may do it by running or scootering or putting on a fake mustache, depending on the context. Evolution cannot anticipate all possible challenges and opportunities that people might encounter in their unpredictable, complex environments, nor what behavioral responses will be optimal, so relying solely on reflexes is impossible. Any organism that has a large array of possible behaviors and lives in a changing, heterogeneous environment benefits from having emotions.

Emotions prioritize certain outcomes over others (Adolphs & Andler, 2018; Tooby & Cosmides, 2008). When an organism recognizes a situation as subjectively important, for instance, "someone has taken something valuable from me," anger will prioritize the goal of punishing the offender. A strong emotion overrides less urgent needs (e.g., for harmonious interaction) and reorganizes attention, perception, and memory in preparation for handling the eliciting event (e.g., the reward of retrieving the stolen item). The stronger or more imminent the expected reward or punishment, the more vigorously the organism will act (Mobbs et al., 2020; Shadmehr et al., 2019). The body prepares for this action by halting less urgent processes (e.g., digestion) and redistributing resources to action-relevant systems (e.g., sending blood flow to the muscles).

Finally, and most importantly, emotions are about goals (Moors & Fischer, 2018; Scherer, 2009). All organisms seek rewards and avoid conditioned and unconditioned punishments. Emotions are abstract behavioral templates for how to seek rewards and avoid punishments depending on the properties of the situation at hand (Frijda, 2010). Is the threat an immobile object or an active agent? Does the potential reward come from another organism or is it somewhere in the environment? Is the loss of a valued item in the past or the future? Goals are unique to an individual's values, experiences, and needs, so two people might have very different emotions in the same situation if the situation is relevant to their goals in different ways.

To prepare for seeking the relevant goal, an emotion alters the brain (e.g., attention, perception, memory) and the rest of the body (e.g., autonomic nervous system, hormones, digestion) in ways that prepare the person to achieve that goal. These alterations tend to persist even after the goal has been resolved: Even after a fear-inducing threat has gone away, the person will remain vigilant and easily startled. This is another way in which emotions differ from more automatic reflexes, which only occur when the eliciting stimulus is present. Also, unlike reflexes, emotions scale, becoming more intense as the goal becomes more immediate and consequential and as the decision to act or becomes more goal relevant (Adolphs & Andler, 2018; Mobbs et al., 2020; Shadmehr & Ahmed, 2020). As emotions become more intense, their measurable effect on brain and body states becomes stronger, resulting behavior becomes more likely and more vigorous, and the associated feeling overwhelms conscious experience.

Emotions are associated with "emotion expressions," or behaviors that can signal the emotion state to others, such as speech, nonverbal vocalizations, facial expressions, or body movements. Emotion expressions do not always accompany emotions, however. Functionally, they should only occur when communicating one's emotion state to others serves the relevant goal. People can also intentionally produce (at least some) emotion expressions as communicative signals in the absence of emotion (Scarantino, 2017).

Emotions are also accompanied by changes to conscious experience—in other words, emotions are usually accompanied by feelings. The function of feelings is far less obvious than the functions of the other components of emotion, and yet feelings receive outsized attention in theories of emotion. Feelings provide affective coloring to conscious experiences, including not only emotion states but also affectively laden states such as hunger, pain, and orgasm. They are an important and salient consequence of emotion states, but Adolphs and Andler (2018) make a strong case for not centering them as affective scientists develop theories of emotion. Because feelings are measured using self-report, they are especially influenced by individual variation in meta-cognition, emotion vocabulary, developmental stage, and culture, making comparisons between individuals, groups, and species difficult. We go into greater detail on the various components (neural states, physiological changes, communicative behavior, feelings) in later sections.

Distinguishing Emotions From Related Constructs

Emotions are different from affect, attitudes, moods, and drives, although the lines between scientific categories are often fuzzy. "Affect" is a general term that refers to any psychological processes or states that are evaluative, meaning they are experienced as good or bad, as rewarding or aversive. As previously noted, organisms are motivated to repeat affectively positive states and to avoid affectively negative states. Within this general notion of affect as "attitudes," which are affective properties associated with specific concepts. Liking radishes is an attitude, as are disliking immigrants and preferring to read romance novels rather than mystery novels. When a person encounters an instance of a concept with a strongly associated attitude—when they see a radish in their salad, for instance—they will experience an emotion that motivates a goal-congruent response to the stimulus. In this case, ecstatic anticipation of the radish's crisp bitterness will drive the person to devour it.

Moods occur on a slower timescale and are less goal-directed than emotions. A positive mood builds with the accumulation of positive emotion experiences, but it will also make positive emotional responses to future events more likely by biasing how new information is evaluated (Loeffler et al., 2013). If emotions are like discrete weather events, such as tornadoes and rainstorms, then moods are like climate (Kontaris et al., 2020). Eldar and colleagues (2016) describe moods as the affective "momentum" a person is experiencing: a positive mood results from the evaluation that they are generally making progress towards their goals, and a negative mood results from the evaluation that they are not.

Finally, emotions are different from "drives"—such as hunger, itch, pain, and thirst—although they share several common features (Anderson, 2022). Emotions and drives have valence: they are about seeking good and/or avoiding bad. At least in humans (and probably other organisms, Damasio & Carvalho, 2013; van Kleef, 2022), they are often consciously experienced as feeling states. Both emotions and drives prioritize goal-relevant behaviors. But they differ in several ways that make it scientifically useful to separate them (c.f. Craig, 2003; Gilam et al., 2020). First, whereas emotions motivate behavioral responses to external threats and rewards in the environment (and, in the case of humans, thoughts about past/future/hypothetical external cues), drives motivate behavioral responses that regulate the body's functioning (Miller et al., 2022; Schulkin & Sterling, 2019). Second, drives usually cease to influence behavior once the underlying needs are met, but because emotions generalize and linger, they can continue to influence behavior even after the eliciting stimulus is gone (Kennedy et al., 2020). Third, emotions can generalize to many situations and stimuli (Wang et al., 2022), but a narrower range of interoceptive inputs generate drives.

And yet, emotion researchers cannot and do not ignore drives. Because drives define an organism's current goals, emotion states can result from deviations from those goals. For instance, the expectation of upcoming pain can generate fear, the satisfaction of hunger can generate contentment, and someone else spilling the last bottle of water during a hike in the sweltering desert heat can generate anger. Drives and emotions can also interact in complex ways: for instance, feeling hungry potentiates anger should an anger-inducing event occur (MacCormack & Lindquist, 2019), and positive and negative emotions modulate brain responses to pain (Orenius et al., 2017).

There is one other source of confusion that is worth addressing. Emotions are not the same thing as emotion concepts, which are learned mental representations of emotions (Winkielman et al., 2018). Emotion concepts guide how people understand the emotions of themselves and others, whether and how they label them, and whether they attempt to regulate them. Like concepts for other cognitive processes, emotion concepts are "meta-cognitive", meaning they are thoughts about mental states. Meta-cognition can influence the very mental states about which it is concerned (e.g., Camos & Barrouillet, 2011; Lupyan et al., 2020; Teng & Kravitz, 2019). As we shall see later in the chapter, this is also true for emotion: people can alter their emotion states by thinking about and labeling them (Kross & Ayduk, 2011; Lieberman et al., 2007; Lindquist et al., 2015b; Mauss et al., 2011; Ong et al., 2015; Smidt & Suvak, 2015).

Even though emotion concepts can shape emotion states (and, obviously, vice-versa), an understanding of the difference is vital (Adolphs & Anderson, 2018). Animals and pre-verbal humans may not have well-developed emotion concepts, but that does not mean they do not have emotions—that is a separate question (Griffiths & Scarantino, 2001). A person with semantic dementia can lose their ability to distinguish emotions cognitively (Lindquist et al., 2014), just as they lose their ability to distinguish cats from dogs. They have not necessarily lost the ability to experience emotion states any more than they have erased the real-world differences between cats and dogs. Emotion concepts support our meta-cognition about emotions, but they can and should be separated from emotions.

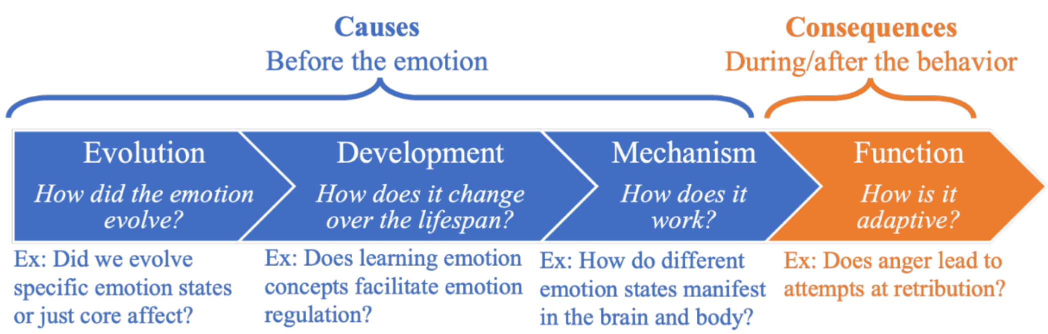
Now that we have defined emotions and distinguished them from related concepts, we discuss the types of questions researchers ask about emotions and how emotion theory has grown and changed to accommodate the answers.

THEORIES OF EMOTION

Are emotions learned or innate? Do they vary across cultures? Are they conserved across species or are they species-specific? What are they for? What brain networks generate emotions? Can we separate emotion from cognition? These are some of the questions that affective scientists have been debating for decades. To come to consensus about the answers to these questions, affective scientists must first agree what type of evidence would constitute a satisfying answer. When two seemingly incompatible camps believe the data support their own perspective, they may both in fact be right. They may simply be trying to answer different questions without realizing it.

In 1963, the behavioral ecologist Niko Tinbergen suggested that all questions about animal (and human) behavior are one of four types: evolutionary questions (how did it evolve?), developmental questions (how does it emerge over the lifespan?), mechanistic questions (how does it work?), and functional questions (how is it adaptive?). Recently, Bergman and Beehner (2021) simplified Tinbergen's framework by placing the four questions onto a timeline, with evolutionary questions in the far past, developmental questions in the near past, mechanistic questions in the present, and functional questions in the future (see Figure 2). The first three—evolutionary, developmental, and mechanistic—are questions about what causes the behavior, while functional questions address the consequences of the behavior. A complete understanding of any behavior requires answers to all four questions.

***Figure 2*: Bergman and Beehner's (2021) Reformulation of Tinbergen's Four Questions, Applied to Emotions**



Note: Tinbergen proposed that all scientific questions about behavior are instances of one of these four.

Note that evidence addressing one type of question does not necessarily address the others. For instance, evidence that self-conscious emotions (e.g., shame and pride) emerge later in development than other emotions (e.g., fear and happiness; Lagattuta & Thompson, 2007) does not say anything about whether self-conscious emotions are the product of learning or genes. In theory, an evolved and genetically encoded behavior emerges only through interaction with an environment and when the organism has the cognitive and motor capacities to produce it. Likewise, such evidence would say little about the cognitive or physiological mechanisms that underlie the emotion, or how or whether the emotion is adaptive. And two hypotheses made at different levels of analyses cannot be pitted against each other: It is nonsensical to ask, "Do self-conscious emotions emerge late in development or are they evolved adaptations?" or "Are self-conscious emotions caused by stress hormones or by the perception that one's social standing has changed?" In both instances, one, neither, or both explanations may be correct. Animal ethology benefited and became more cumulative when researchers clarified the level of analyses their work addressed (Bergman & Beehner, 2021), and affective scientists will similarly benefit from identifying which of Tinbergen's questions they are answering.

There are too many theories of emotion to do them all justice (for overviews, see: Fox, 2018; Gendron & Barrett, 2009; Izard, 2010; Moors, 2009; Scarantino, 2023). The focus here is on the most enduring and dominant theories, which are the basic emotions, constructionist, appraisal, and functional theories. Each family of theories might better be described as a "metatheory." As defined by Witherington and Crichton (2007), a metatheory "serves as a general ontological model, set of beliefs, or worldview about what constitutes reality rather than as a specific theory with testable hypotheses" (p. 628). Other affective scientists have described emotion theories as "research programs," meaning they are less competing descriptions/explanations of the world than they are different methodological agendas with different assumptions as starting points (Barrett & Russell, 2015; Scarantino, 2015). Indeed, each theoretical tradition emphasizes a different Tinbergenian question, which may be why these sparring theoretical camps have not been able to move on after a century of debate (Lindquist et al., 2013). Perhaps they are asking different questions (e.g., Adolphs et al., 2019).

Basic Emotions Theories: Questions Of Evolution

Charles Darwin is the great-grandfather of the first theoretical tradition, so it should not be surprising that these theories are concerned with questions of evolution. Sometimes referred to as "basic emotions theories," these perspectives state that a finite set of specific emotions evolved over thousands or even millions of years to solve challenges repeatedly encountered by humans and their evolutionary ancestors (Izard, 2007; Keltner et al., 2019; Scarantino, 2012; Shiota, 2023; Tracy, 2014; Tracy & Randles, 2011; Tooby & Cosmides, 2008). According to these theories, many of the basic emotions are shared with other species, mammalian or otherwise (there is some evidence for a state akin to fear in fruit flies, for instance; Gibson et al., 2015). Basic emotions theorists often reference the environments and lifestyles of early humans and pre-human hominids to hypothesize which emotions we would have evolved (Sznycer et al., 2017).

An early version of Ekman's taxonomy of basic emotions is the most well-known and includes fear, anger, disgust, sadness, happiness, and surprise (Ekman, 1999). This list of six emotions continues to be the basis for everything from the most common facial expression stimuli sets (Tottenham et al., 2009) to Pixar movies ("Inside Out") to the development of emotionally intelligent robots (Faria et al., 2017). But critics argue the basic emotion list was not systematically developed, was based on folk concepts from the English language, and gave too much emphasis to facial expressions as the basis for identifying discrete emotions (e.g., Crivelli & Fridlund, 2019).

Contemporary researchers have expanded the list to include additional emotions, including pride (Tracy & Robins, 2004), gratitude (Algoe & Haidt, 2009), awe (Shiota et al., 2007), and embarrassment (Keltner & Buswell, 1997). A data-driven approach has identified upwards of 27 basic emotions by building large sets of emotion expressions or emotionally evocative videos, having people rate them on a variety of dimensions, and then counting how many clusters emerge (Cowen & Keltner, 2017). With that said, there is a growing acceptance that emotions are not categorically distinct states characterized by unique patterns of neural, bodily, and communicative changes, but are instead "networks of causally connected emotion components" and that "the causal networks of different emotions overlap" (Lange & Zickfeld, 2021, p. 157).

The challenge for basic emotions researchers, who are making a fundamentally evolutionary claim, is that studies addressing mechanism (e.g., how does a particular emotion change the body and brain?) or function (e.g., how many emotions are there and how are they adaptive?) do not directly speak to evolutionary questions (Bateson & Laland, 2013). Critics of basic emotions theories point out that discrete and functionally unique emotion states could emerge through learning and interaction with the social environment (Scherer, 2009). Observing a set of discrete emotions with unique brain states, communicative displays (e.g., facial expressions, vocalizations, body movements), or behavioral tendencies (e.g., aggression, play, cooperation) tells us about the mechanisms and functions of those emotions, but not where they came from (Lindquist, 2013; Mesquita et al., 2016).

Basic emotion researchers therefore look for evidence of universality—that regardless of the environment and cultural context, humans everywhere experience the same emotion states (Matsumoto & Yoo, 2007). This would provide indirect support for emotions as evolved states that persist across contexts. Ideally, the cultures being compared are as different as possible and have minimal interaction with each other. This is increasingly difficult in our globalized world. Researchers traipse to remote communities that are living indigenous lifestyles, and that are ideally isolated from the rest of the world (e.g., Cordaro et al., 2016; Gendron et al., 2014). The researchers show Westerners' communicative displays of emotion, such as videos of facial expressions and audio recordings of vocalizations, and they then ask the indigenous participants to interpret the displays. They also ask the indigenous participants to make their own communicative displays (Cordaro et al., 2018). And, of course, researchers use self-report methods to examine cultural differences in the frequency and co-occurrence of emotion states in daily life (Scollon et al., 2004).

Consistently, researchers find evidence of both cross-cultural consistency and variability, depending on whether they focus on the signal or the noise in their data (Cordaro et al., 2019; Elfenbein et al., 2007; Gendron et al., 2018; Jack et al., 2012). All human cultures appear to have some affective processes in common: For instance, laughter seems to be universally associated with close relationships and positivity (Bryant et al., 2016; Sauter, 2010). But cultures also vary in terms of when specific emotions are likely to occur (de Leersnyder et al., 2011; Imada & Ellsworth, 2011), how they manifest (Butler et al., 2009), how they are expressed (Gendron et al., 2018), and whether and how they are regulated (Ford & Mauss, 2015).

Such research tends to focus on the universality and cultural relativity of emotion expressions and emotion concepts, and thus cannot speak directly to whether emotions states are evolved, universal processes. Societies may independently culturally evolve similar ways of categorizing and conveying emergent motivational states (Nölle et al., 2021) without those states being the product of evolution. Conversely, emotions could be evolved and universal states of action readiness, and yet their communication and conceptualization might vary across cultures (Frijda & Parrott, 2011). Furthermore, evidence for universality only indirectly bolsters the evolutionary basic emotions perspective (Samuels, 2004). Humans around the world wear shoes, but no one thinks humans evolved to wear shoes.

More direct evidence that emotions are evolved adaptations comes from cross-species comparisons (e.g., Anderson, 2022; Clark, 2013; Papini, 2003). The first self-described "affective neuroscientist", Panksepp, developed his own list of basic emotions by observing functionally equivalent states across species and identifying the subcortical brain regions and neurotransmitter systems that seemed to give rise to those states (Panksepp & Biven, 2012). He argued that rage, fear, lust, care, play, seeking, and panic/grief are emotions that are conserved across mammals, that lead to functionally equivalent and adaptive behaviors, and that arise from homologous neural processes. Panksepp's list of basic emotions differs from Ekman's original one in several ways. First, he based his categories on animal behavior and neuroanatomy and Ekman based his on human facial displays. This means that Ekman did not include any emotion states that might be communicated in other ways, such as through touch, posture, or voice, or emotion states for which there is no communicative display because it would presumably not serve the emotions' adaptive functions. Second, only three of Panksepp's seven basic emotions are negative in valence and function to address threats (rage, fear, and panic/grief), while five of Ekman's six are negative. Basic emotions researchers will benefit from continuing to incorporate research on animal behavior and comparative neuroscience into their evolutionary arguments (Anderson, 2022; Crivelli & Fridlund, 2019) to ensure that they do not neglect positive emotions (Shiota et al., 2017).

Basic emotions theories will also benefit from continuing to incorporate ideas from contemporary evolutionary biology (Anderson, 2022; Jablonka & Lamb, 2014)—for instance, the notion that traits or representations of traits are not directly inherited, genetically or otherwise, but are instead reconstructed during development by a range of interacting resources (genetic, environmental, cultural, social) that the organism inherits (Oyama et al., 2001). Scientists will never find genes that encode the tendency to experience fear. If fear is indeed an evolved capacity, it emerges developmentally when the inherited social and physical environment interacts with gene expression and behavior. Evolved capacities do not exist separately from the environmental niche (Griffiths & Scarantino, 2001; Hochman, 2013).

Constructionist Theories: Questions Of Development

How does experience with the world build emotion states? This developmental question is central to constructionist theories of emotion. Constructionists have long argued against the basic emotion view of emotions as discrete, functionally distinct, and separately evolved states (Barrett, 2006; Mesquita et al., 2016; Russell, 2003). They propose that humans are born with the capacity to experience positive and negative affect at varying levels of arousal, or intensity. This two-dimensional space of valence (positive to negative) and arousal (high to low) is known as core affect (Russell, 2005). According to constructionists, all emotion states are points in this continuous space, rather than the biologically and functionally discrete categories proposed by basic emotion theorists. But how can two emotions, such as fear and anger—which are both high arousal, negatively-valenced states—be adjacent in the core affect space, and yet people experience them as different emotions (Yik et al., 2011)? Constructionists say that the subjective experience of feeling angry or afraid arises when people interpret their core affect state (high arousal negativity) with additional information gleaned from the context ("Am I in a haunted house or a fight with my spouse?") and culturally relative knowledge gained through learning and socialization (people in a haunted house experiencing high arousal negative affect are "afraid"). The related "affect as information" theory suggests people attach their current affective state to whatever is most salient at the time, be it a person, an event, or their own thoughts, thus using their feelings to discover their attitudes about the salient stimulus (Clore et al., 2018). Core affect parsimoniously accounts for much of the variability in the subjective experience and conceptualization of emotion states, even across cultures (c.f., Cowen & Keltner, 2020; Jackson et al., 2019).

Any claim that constructionism is about Tinbergen's questions of development is, of course, a simplification. Constructionist theories, such as Barrett's psychological constructionist theory, also address issues of mechanism, such as how emotions emerge in the brain from more basic neural processes (Barrett, 2013; Hoemann & Barrett, 2019; Lindquist & Barrett, 2012; Wager et al., 2015). In their opposition to basic emotions theories, these perspectives further take a stance about the evolution (or lack thereof) of emotions (Lindquist et al., 2013). However, at the heart of constructionist theories are hypotheses about development. Only when people learn their cultures' emotion concepts and how to apply them to affective experiences do they go from merely existing in the core affect space to experiencing specific emotions (Lebois et al., 2020). Emotions are a construction of people's minds that emerge from their interactions with the world and the categorization of their own experiences. In support of this perspective, research has shown how strongly culture (Mesquita et al., 2016), age (Nook et al., 2018), language (Lindquist et al., 2015a), and individual differences (Ogren & Johnson, 2020) shape people's understanding, experience, and communication of emotion. Constructionism emphasizes the role that meta-cognition plays in the differentiation of emotions, and some versions of this perspective suggest animals lacking such meta-cognitive capacity do not have emotions[1] (instead, they have only core affect; Barrett, 2012).

Basic emotions and constructionist perspectives can be viewed as more compatible than their proponents typically suggest because each perspective focuses on a different Tinbergenian question. The "hundred-year emotion war" between the two camps (Lindquist et al., 2013) is an instantiation of the nature-nurture debate, with evolved basic emotions on the nature side and developmental constructionism on the other. But modern biology has largely moved on from the nature-nurture debate (Bergman & Beehner, 2021; Jablonka & Lamb, 2014; Oyama, 2002). Even behaviors for which humans have clearly evolved, such as bipedal walking (Adolph & Hoch, 2019; Caballero et al., 2019), seeing with eyes (Purpura & Tinelli, 2020), and coexisting with others in social groups (Almeida et al., 2021; Atzil et al., 2018), require interaction with the environment to emerge, and they continuously adapt to contextual constraints (Gomez-Marin & Ghazanfar, 2019). Humans did not need to evolve genetically determined abilities to walk, see, or socialize, because the environments that help "construct" those behaviors have been consistent throughout human and pre-human evolution. It would be genetically inefficient to encode a predisposition towards those behavioral programs when they can emerge from goal-driven interaction with the environment (Clark, 1998). All evolution had to do was give people the bodies and brains that, under the right environmental conditions, can do those behaviors. Walking, seeing, and living in groups are nearly universal to all humans, they are adaptive behaviors, they have shaped human biological and cultural evolution, and they have helped create the human niche. But their development is not deterministic—it is dependent on the environment and experience (Hochman, 2013; Lickliter & Honeycutt, 2003).

What if emotions are the same? Using the modern perspective on evolution and development there is a plausible theoretical perspective that accepts the core tenets of both basic emotion theories and constructionism. Perhaps having emotions is functional and adaptive, and therefore evolution selected for brains and bodies that, in the right environments, tended to wind up generating the same basic emotions (with some variability). Although around the world and across time, humans have encountered different environments and created different societies, many environmental and societal features remain the same. All humans need to eat, sleep, co-exist with other humans, care for offspring, escape mobile and immobile threats, and gather information. The same goal-relevant behavioral templates (what we call emotions) could appear again and again as each unique person encounters the world (as basic emotions theorists have taught us). Their solutions to those goal-relevant contexts appear similar across individuals and groups because people repeatedly rediscover the "best" behavioral solutions (Oudeyer & Smith, 2016; Scherer, 1994). This is analogous to toddlers stumbling (pun intended), through trial and error, onto the same maximally efficient walking gait (Adolph & Hoch, 2019). And just as some people walk with a limp or use a wheelchair, there would be individual variability due to differences in people's brains and bodies (as the constructionists have taught us). There would also be individual- and culture-level variability resulting from differences in the physical and social environment (Lebois et al., 2020). And just as people adjust their walking gait when wearing stilettos or walking barefoot on gravel, emotions demonstrate functional within-person variability across contexts.

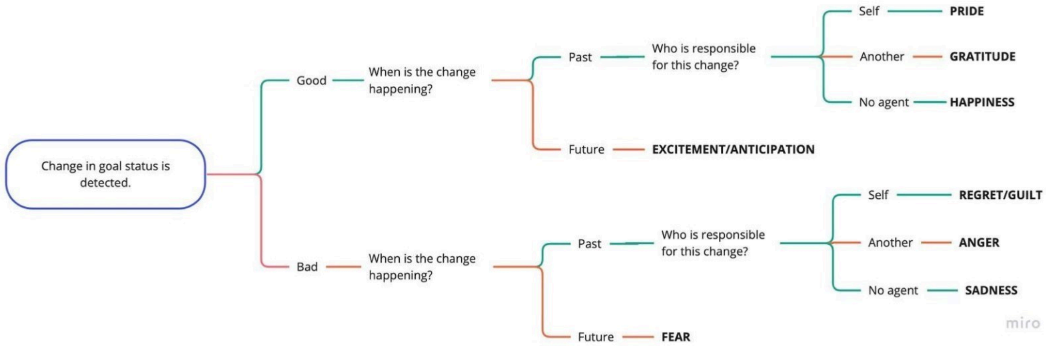
Time will tell if such claims are correct. But the point is that both basic emotions and constructionists might provide right answers to different questions. It might be true that, on a long timescale (millennia) humans evolved to have some number of specific emotion states, and that those states emerge from more basic neural processes over the course of development (a single generation), leaving room for learning and culture to shape them (and cultural evolution shapes which cognitive capacities will be acquired during development; Heyes, 2020). By treating evolution and development as interdependent causal processes that operate on different timescales (Hochman, 2013; Oyama et al., 2001), rather than mutually exclusive explanations, affective science can benefit from the contributions of both the basic emotions and constructionist perspectives (for a similar argument about behavior more generally, see Gomez-Marin & Ghazanfar, 2019).

Appraisal Theories: Questions Of Mechanism

The first two theoretical positions, basic emotions theories and constructionist theories, are often packaged with mechanistic explanations of how emotions are instantiated in the brain and body. The "classic" basic emotions theories proposed that distinct emotions are generated by distinct modules in the brain (Panksepp & Biven, 2012), while constructionists argue no such modules exist (Lindquist & Barrett, 2012). But the core evolutionary and developmental propositions of the theories persist even when their preferred mechanisms change. For instance, when it became clear to basic emotions researchers that there aren't anatomically distinct modules in the brain generating each emotion (e.g., Touroutoglou et al., 2015), researchers began using functional connectivity and dynamic state-based approaches to identify the neural systems underlying emotions (Berridge, 2019; Wang et al., 2020).

One family of theories, known as appraisal theories, focuses more directly on mechanistic causes of emotion (Cunningham et al., 2013; Ellsworth & Scherer, 2003; Lazarus, 1991; Moors et al., 2013). Appraisal theories catalog the possible goal-relevant construals, or appraisals, people can make about a situation, and then predict which emotion states will result from combinations of those construals (Figure 3). For instance, research by Kuppens and colleagues found that "anger" is a motivational state resulting from a cascade of appraisals about a goal being frustrated (1) unfairly (2) by another agent (3) who is perceived as arrogant and entitled (4), which elicits an antagonistic action tendency towards the offending agent (Kuppens et al., 2003). Evidence suggests, however, that no single appraisal is necessary or sufficient for the experience of anger; instead, they all co-occur probabilistically with anger (Kuppens et al., 2003). Importantly, appraisal theories are not stimulus-response mappings between agreed-upon features of a situation and an emotion state; the situation is appraised by the individual in relation to their goals, and different stimuli can therefore elicit different emotions across individuals (Siemer et al., 2007).

***Figure 3*: An (Incomplete) Example of an Appraisal Theory in the Form of a Decision Tree**



> *Note: For the sake of space, here we represent as categorical outcomes the following appraisal dimensions: valence, time, and agency. Other common dimensions include novelty, outcome probability, magnitude of expectation violation, control, and urgency (e.g., Ellsworth & Scherer, 2003).*

Common appraisal dimensions proposed by appraisal theories include valence (is the event good or bad for me/my goals?), novelty/surprisal (how unexpected is the event?), agency (who caused the event?), control (how much agency do I have to change the situation?), and fairness (Ellsworth & Scherer, 2003). Recent theories add a dynamic component to appraisal approaches (Cunningham et al., 2013), which have historically framed appraisals in static terms. Dynamically, both positive and negative moods result not only from the absolute distance from a goal but also from a person's experience of their current velocity towards/away from a goal (Lawrence et al., 2002). Future updates to appraisal theories may also more explicitly incorporate prediction errors: Positive and negative affect result less from positive and negative outcomes, but from outcomes that are better or worse than expected (Villano et al., 2020).

Appraisal theories represent a mechanism-focused perspective because they describe which appraisals cause which emotion state (Moors et al., 2013). Appraisal theorists sometimes also posit how brains instantiate the appraisal process, which is another mechanistic question (e.g., Sander et al., 2005). Appraisal theories are straightforward to translate to emotional artificial agents (Gratch et al., 2009; Malatesta et al., 2009) because they describe the rules by which features of a situation, as construed by the organism, translate into specific emotions and, thus, actions.

Appraisal theories are compatible with basic emotions theories in at least two forms: either by positing that evolution shaped and selected for the core appraisal dimensions, rather than discrete emotion states (Frijda, 2016), or, for each possible branch of the appraisal decision tree, adding a discrete emotion to the list of "basic emotions." According to some appraisal theorists, the components of an emotion—the associated physiological, cognitive, or communicative states—are not a unified package. Instead, the individual components are linked to specific appraisal dimensions (Scherer & Moors, 2019). This is where componential appraisal theories can disagree with basic emotions perspectives that emphasize discrete, prototypical emotions (Tracy & Randles, 2011). Appraisal theories are also mostly compatible with constructionism (Ortony & Clore, 2015) so long as the assumed developmental process is one in which emotions are learned and constructed through the acquisition of emotion concepts (which may include the appraisal dimensions).

Functionalist Theories: Questions Of Function

Finally, functionalist theories focus on understanding what emotions are for—what their utility is for the organism (Campos et al., 1994; Keltner et al., 2022). While the first three Tinbergenian questions and their associated emotion theories are about causes of emotion, functionalism is about the consequences. The aim of a functionalist theory is "to elucidate pattern in organism-environment relations, not to identify causal antecedents [of emotions]" (Witherington & Crichton, 2007, p. 630). The function is inductively inferred from observations about when the emotion occurs and how it changes physiology, cognition, and behavior; then, the hypothesized function deductively generates new predictions about other consequences that would be expected. Functional approaches aim to identify which emotions (if any) are distinct, natural kinds. Emotion states belong to the same scientific category if they have equivalent goal-relevant consequences (Farb et al., 2013).

Consider the emotion of fear. An example of a functional definition of fear is "the motivation to avoid harm." Many stimuli can elicit fear: a scary movie, watching a child step into traffic, or being followed by someone while walking home at night. Avoiding harm with each of these stimuli requires different behaviors: covering your eyes, grabbing the child, or walking faster and calling the police. These behaviors are examples of threat responses shared across species, including humans: freezing, fighting, and fleeing (Blanchard et al., 2001; Keay & Bandler, 2001). These distinct fear-based behaviors are reflected in distinct neural and physiological profiles (Roelofs, 2017). Despite such differences, if all versions of fear cause functionally equivalent outcomes—attempts to avoid harm—then functionalist accounts place them in the same emotion category.

Note how abstractly functions are defined (Adolphs & Anderson, 2018). Functions purposefully do not specify the eliciting stimulus (animate or inanimate), the underlying mechanisms (a human, a cat, or a sentient AI could all, in theory, love), or the specific behaviors that are motivated by the emotion. Merely the function of those behaviors. A person's emotional response to a situation is a product of their unique goals, how they interpret the situation in relation to their goals, and their available action repertoire. The behavioral, cognitive, and physiological components of an emotion also vary across instantiations as a function of how the person chooses to act upon their environment (Witherington & Crichton, 2007).

Humans tend to categorize objects according to function as a default (Barsalou, 1991), and Adolphs and Andler (2018) argue that categorizing emotions by their functions is the most tractable approach to building a taxonomy of emotion states. Functions translate more easily across individuals and species than do particular brain states, behaviors, or subjective feelings. We could define anger as a response to specific elicitors (such as an outgroup member) or as a cause of specific actions (such as hitting or biting), but this list would be ever-expanding and specific to the individual. We might also define anger according to the physiological, neural, and communicative changes associated with it (e.g., Lang, 2010), but we would have to treat individual, contextual, and cultural differences as noise. Or we could define it by how we think it evolved (Clark, 2010). Functionalist theories are sometimes accused of being teleological (Barrett, 2017), implying that behaviors were "designed" for a "purpose." But when function is truly separated from evolution (as consequences and causes, respectively), then functionalist questions are about the current utility of a behavior (Bateson & Laland, 2013; Bergman & Beehner, 2021), not its past value in an imagined ancestral "environment of evolutionary adaptedness" (Cosmides & Tooby, 2000). Even learned behaviors have current utility value and lend themselves to functional analysis.

As previously stated, theories that focus on different Tinbergenian levels of analysis are not in direct conflict with one another. Functionalism fits easily with a basic emotions perspective if the basic emotions constraint that each emotion has a prototypical neural, bodily, and communicative profile is relaxed. Evolutionary and functional analyses go together because both are about "ultimate" explanations: Here is how this emotion evolved, and here is what it evolved for. Functionalism is also compatible with appraisal accounts (cf. Griffiths & Scarantino, 2001). Indeed, functionalist perspectives often explicitly include appraisals as components that determine which emotion state will occur and how it will affect behavior (Campos et al., 1994; Witherington & Crichton, 2007).

Finally, functionalism has the potential to fit with constructionism. The two perspectives agree that emotions vary tremendously across individuals and contexts. For instance, no one brain state is specific to, or diagnostic of, a given emotion (e.g., Doyle et al., 2022). Constructionists attribute this variation to individual and cultural differences in emotion concepts that are essentially interchangeable, whereas functionalists attribute the variation to individual and situational differences in the optimal strategy for achieving goals. Given a person, their goals, and their understanding of the situation, they will experience a predictable emotion state, and there is an optimal way for that emotion to manifest (optimal in relation to their goal). For instance, the function of fear—avoiding an active threat—may be best achieved by freezing, escaping, or fighting, depending on situational affordances (Mobbs et al., 2015). Conversely, a behavior such as laughter could accompany any emotion state as long as communicating a lack of seriousness and diffusing social tension serves the associated goal (Wood & Niedenthal, 2018). People can laugh when they are in a playful emotion state to encourage their social partners not to take them seriously (Gervais & Wilson, 2005), but they can also laugh when they are embarrassed to signal that they do not take themselves seriously (Keltner & Anderson, 2000).

Constructionism has revealed the immense variability within emotion states, while functionalism (a different level of analysis) suggests why and how that variability is useful. One way to merge these theories is with a dynamical systems framework, which describes how stable emotion states emerge (i.e., are constructed) over the course of development from the interaction of goals, appraisals, and bodily and environmental constraints (Witherington & Crichton, 2007).

We have provided an overview of the dominant theoretical perspectives in affective science. The assignment of each of the theoretical families to a Tinbergenian level certainly oversimplifies matters, as theorists from each of the four research programs have plenty to say about the other levels of analysis. But the point of this exercise is to point out that evolutionary, developmental, and mechanistic causal explanations of emotion are rarely mutually exclusive, and they are rarely in conflict with functional descriptions of the consequences of emotions. For an understanding of emotion to be complete, affective scientists must consider all four levels, as well as their interactions. Now that we have surveyed the theories that guide emotion research, we can finally turn to the empirical literature and see what contemporary affective scientists have been up to in the last decade or so.

COMPONENTS OF EMOTION

As is obvious in our treatment of theories of emotion, emotions or "emotion episodes" (Russell, 2003), involve many processes, sometimes called emotion components. Having provided a definition of emotion, which includes the putative functions of emotion, we therefore turn to discussing what is known to this point about the components of emotion—both those external manifestations that can be visually observed and those internal events that can only be scientifically measured. It should be noted at the outset that theorists do not always agree on whether a component of emotion is a cause, part, or consequence of the emotion. For instance, while many appraisal theorists believe that appraisals are causes of emotions, others consider appraisals a component of the emotion; a process that constitutes the experience or episode (Moors, 2013 for discussion). In what follows, we are agnostic to this point and try to represent advances in the discoveries about each component.

Given the variety of emotion theories and disagreements about which components of emotion are most central, there may be no ground truth for validating an emotion state. Many theorists hold that the self-report of subjective feelings validates the occurrence of an emotion—and the nature of that emotion. Indeed, some theorists suggest that the conscious, reportable experience of emotion is the very definition of emotion (Barrett, 2015; LeDoux 2012; 2017). But, as we have mentioned, and discuss in greater detail later in the chapter, the framework we use here stems from the notion that conscious experience and self-report of emotional states are decoupled from emotion more broadly (Berridge, 2003; Dolan, 2002).

In this section, we explore the neural, psychophysiological, and expressive components of emotion. Subjective, conscious experience is covered in a subsequent section. After a discussion of the components of emotion, we review the state of the research on coherence among the components. We end the section with an examination of the form and function of cognitive processes during emotion (i.e., the interplay between emotion and processes of attention, perception, and memory).

Neural Components

The science of the neural basis of emotion—affective neuroscience—has expanded in the past decade along with the development of new methodological approaches to studying emotion. It is a necessary subfield of affective science because the brain coordinates all other components of emotion. In this sense, the brain could be considered the conductor of the orchestra comprising the other components.

The simplest way to study the neural basis of emotion is to examine the relationship between a single brain region (or set of regions) and a functional outcome. Indeed, much of the early work examining the neural responses to emotion, both in animals and in humans, identified a crucial role for a relatively small set of regions, including the amygdala, hypothalamus, insula, ventromedial prefrontal cortex, and the periaqueductal gray (Adolphs, 2017). Early insights were gleaned from studying patients with brain lesions, beginning with the famous case of Phineas Gage in 1848. Gage, a railroad foreman, survivied an accident in which a metal rod was driven through his head, thereby destroying a large portion of his left frontal lobe. Consequent changes in Gage's personality were consistent with the conclusion that prefrontal cortex was in part responsible for the ability to regulate emotions. Subsequently, studies of amygdala lesions in monkeys (i.e., Kluver-Bucy syndrome; Kluver & Bucy, 1937; Weiskranz, 1956) and humans (e.g., patient SM; Adolphs et al., 1994; Feinstein et al., 2011), revealed profound alterations of emotional – especially fear-based – behavior. Feinstein et al. (2013) reported that patient SM, who has complete bilateral amygdala destruction due to a rare disease—Urbach-Wiethe Disease—in which bilateral calcifications of the medial temporal lobe selectively destroys the amygdala, shows intact fear responses to an interoceptive threat (CO2 inhalation), but blunted responses to threatening stimuli in the external environment. These findings suggest that the amygdala plays a crucial role in initiating a learned fear response but is not the region of the brain where the subjective experience of fear occurs.

More recently, human neuroimaging techniques, such as fMRI (functional magnetic resonance imaging), have provided a window into the neural mechanisms associated with human emotion in healthy, non-lesioned brains. Much of this work has also examined the role of specific regions—for example, noting that the amygdala might be part of a rapid threat detection system (Ohman, 2005), or serve as part of an "information gathering system" (Whalen et al., 1998). One study examined recognition of happy, disgusted, and fearful expressions in blindsight patients—individuals that, despite lesions in primary visual cortex, can unconsciously recognize low-level visual features—and found evidence that the amygdala and the insula are crucial for the experience and recognition of fear and disgust, respectively (e.g., Gerbella et al., 2019). The cingulate gyrus (Shackman et al., 2011), ventromedial prefrontal cortex (Phelps et al., 2004; Schiller & Delgado, 2010), and hypothalamus (Karlsson et al., 2010; Vandewalle et al., 2011) have also received some attention in this domain of research, with evidence suggesting links to various functions such as emotion control, learning, and generation, respectively.

Despite enormous growth in the field of affective neuroscience over the last several decades, there are notable limitations to consider, as addressing these limitations will likely shape the next decade of research. First, most (if not all) neuroimaging research is correlative rather than causal. Thus, the fact that the amygdala is recruited during the experience of fear does not alone indicate that the amygdala causes the experience of fear. It is, of course, equally possible that amygdala activation and the experience of fear co-occur in response to some eliciting event. For this reason, the use of creative experimental designs and triangulating an effect with multiple measures are necessary.

A second limitation in the field arises from low specificity, sometimes referred to as "degeneracy" (Price & Friston, 2002). A particular brain region is involved in many functions and a particular function is carried out by many brain regions (see Pessoa, 2017). The regions that have largely been the focus of emotion research (the amygdala, the insula, and the cingulate), for example, are activated by many emotions and emotion processes, and even by many non-emotional processes, including sensation, perception, and other cognitive operations (Yarkoni et al., 2011; LeDoux, 2012). Therefore, conclusions that the activation of any given brain region on its own is necessary or sufficient to determine that a specific emotion, or even that any emotion at all, has occurred (often referred to as "reverse inference"), are usually not warranted.

A third limitation—one that is more specific to the study of emotion—is that there is relatively low consistency in the brain mechanisms implicated in a specific emotion state. Perhaps a major cause of the low consistency is that much of human neuroimaging conflates different aspects of affective processing: the functional state (e.g., fear), the conscious experience (e.g., feeling afraid), the conceptualization of emotion (e.g., thinking about fear), and emotion perception and attribution (e.g., perceiving fear in others; Adolphs, 2017). Many neuroimaging studies of emotion are in fact studies of the latter – how the brain processes or responds to emotion in others (e.g., using emotional facial expressions as stimuli). Even in studies that do attempt to study emotion by inducing an emotion state, methods of emotion induction are highly variable (e.g., threat of an electric shock, exposure to a tarantula, autobiographical memory, imagery, watching cinematic films or listening to instrumental music; Damasio et al., 2000; Mobbs et al., 2007; Mobbs et al., 2010; Kassam et al., 2013; Kragel et al., 2016). A problem of interpretation arises when the different studies using different methods implicate different brain regions in an emotion state: Are there differences because there truly is no consistent neural signature for the emotion, or is it because the methods changed the emotion state in unrecognized ways, or both?

As the field of affective neuroscience evolves, new methods are advancing the understanding of the neural basis of emotion. Some such methods have been used to tackle the limitations described earlier. For example, optogenetics is a research tool that permits fast, targeted manipulation of subpopulations of neurons in the brains of freely moving mammals. Using methods of genetic engineering, a family of proteins called microbial opsins that react to light, can be selectively inserted into a subpopulation of neurons in the brain. Using fiberoptics or another light-guiding tool, light can then be directed on the identified neurons and only that population will be activated or deactivated. Thus, optogenetics supports stronger causal claims about the roles that neuron populations play in emotions (e.g., Berridge & Kringelbach, 2013). Recent work that relies on these innovative techniques demonstrates a finer-grained approach to understanding, for instance, the role of the amygdala and its interconnected regions in emotion—playing a key role in processing both fearful and rewarding stimuli (Janak & Tye, 2015; for a review, see LaLumiere, 2014). For example, experimental manipulation of neuronal activation revealed that the nucleus accumbens produces both positive/appetitive and negative/aversive emotion states (Berridge and Kringelbach, 2013). And light-induced excitation of amygdala projections—from basolateral to central nucleus— in mice has been shown to produce acute anxiolytic effects, demonstrating a crucial role for these connections in anxiety control (Tye et al., 2011).

Further, research in human neuroimaging has been increasingly focused on identifying the distributed brain systems that support emotion (Pessoa et al., 2012; Wager et al., 2015; Kragel et al., 2016; Pessoa, 2017; for a review, see Malezieux et al., 2023). In a study that used a hierarchical Bayesian model, Wager and colleagues (2015) demonstrated that neuroimaging data could be used to classify five emotion categories (anger, disgust, fear, happiness, and sadness) with roughly 66% accuracy (chance was 20%; i.e., classification of anger was on the lower end at 43%, but the classification for disgust and fear were much higher, at 76% and 86%, respectively). They also found that classification relied not on any single region or system, but on configurations across multiple systems that include cortical-subcortical interactions. The consideration of distributed regions is not an entirely new approach (see Papez, 1937; MacLean, 1949), but is one that has benefited enormously from the recent technological advances in the field. For example, a system-level approach—which leverages multivariate pattern analysis, machine learning, and network analysis—has contributed to our understanding of the distributed regions in the human brain that are important for emotion (Lindquist & Barrett, 2012; Kragel & LaBar, 2014; Pessoa, 2017).

Findings from the last decade demonstrate that although a specific emotion category cannot be localized to a specific swath of brain tissue (see also Barrett & Satpute, 2019), distinct emotion states can be decoded from complex neural models (Chang et al., 2015; Kragel et al., 2016; but this again relies on correlational findings). Widespread neural activation makes sense given that emotions mobilize the brain and body—via autonomic, neuroendocrine, and musculoskeletal systems—so large-scale coordination of these systems is likely necessary. Notably, some of the structures previously identified appear to be important hubs for the distributed cortical-subcortical systems (defined based on both structural and functional connectivity; Pessoa, 2017). Together, there is some agreement that emotion states are highly distributed and map onto functional networks of the brain (Chang et al., 2015; Kragel et al., 2016; Pessoa, 2017). Continued work in this domain will be crucial for determining the extent to which the brain signatures are dynamic and context-dependent or more generalizable across tasks and conditions (see also Wager et al., 2015; Pessoa, 2018). Such developments will be important as they will lend further insight into the dynamic nature of emotion states, and how these states interact with and influence other related processes (e.g., attention, perception, interoception).

Toward the goal of understanding the interplay between different processes, advances in multivariate approaches have shed new light here as well. For example, representational similarity analysis (RSA) is a popular technique in neuroimaging that enables investigation of the informational content encoded in brain activity by comparing patterns of activity across different regions, or within a given region across different stimulus categories/processes (see Popal et al., 2019 for a guide to implementing RSA in social neuroscience). RSA can thus be used to compare psychological (e.g., conceptual knowledge) and neurobiological (e.g., patterns of brain activity) information about emotion. This can be done either for a specific region (e.g., the amygdala: Jin et al., 2015; Puccetti et al., 2021) or across the whole brain (Chikazoe et al., 2014; Chen et al., 2020).

Participants in a study by Puccetti and colleagues viewed affective images followed by a neutral facial expression, and RSA was used to characterize the similarity in amygdala activation patterns across images and faces. Persistence in amygdala activity—which represents the tendency toward more frequent or longer-lasting emotional experiences—was operationalized as high similarity in activation patterns. The findings revealed that greater persistence (i.e., greater pattern similarity for affective images and subsequent neutral faces) was associated with less positive and more negative daily affect, and with lower psychological well-being (Puccetti et al., 2021). This suggests that variability in the dynamics of one's emotional experiences is associated with important psychological outcomes such as better overall daily affect. Another study used RSA to identify mechanisms that process emotion across audiovisual (i.e., emotional speech and dynamic facial expressions) modalities (Xu et al., 2021). In this way, RSA has helped to address debates in emotion theory, for example, showing that both categorical and dimensional models explain neural representations of emotion but along very different spatiotemporal scales; categorical models explain early processing (within the first 200 milliseconds) in fronto-temporal regions, and dimensional models explain relatively later processing (200-500 milliseconds) in limbic-temporal regions (Giordano et al., 2021).

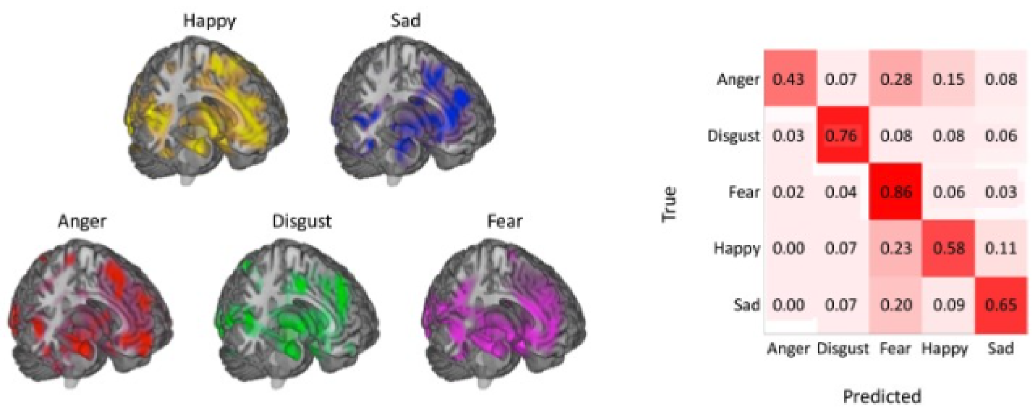
In addition to comparing different processes or comparing responses across modalities, RSA is useful for comparing different individuals or groups of individuals and for characterizing individual differences in emotion responses. For example, some work revealed that, in response to watching erotic and neutral film clips, neural representations distinguished people according to their sociosexual desire versus self-control preferences (Chen et al., 2020). That is, people who cluster together around a particular preference orientation show similar patterns of neural responses, suggesting they are processing information about the videos more similarly. Another study examined variability in response to emotional ambiguity, with the prediction that more negative evaluations are the default and that more positive evaluations are supported by an emotion regulation process (Petro et al., 2018). The findings revealed that negative evaluations were associated with a pattern of amygdalar activity in response to ambiguity that was similar to maintaining one's natural (unregulated, or default) response to negative images.

The field of affective neuroscience continues to expand. Extensive work in animals and in humans has identified a specific set of brain regions that are crucial for emotion. But recent advancements have emphasized the importance of whole-brain systems and brain organization. The current state of the research suggests that there are widespread brain systems that support emotion (see Figure 4), and that future work will move further away from single-region theories. In addition, with more sophisticated techniques, we are moving toward a greater appreciation for multimodal datasets that will allow us to address some of the big questions of emotion in new and exciting ways. For example, some research is beginning to think outside of the proverbial dark tube (MRI) by demonstrating that individual differences in neural responses to reward in the MRI are predictive of real-world emotion using experience sampling methods (Heller et al., 2015).

When considering the innovations in methods available to emotion researchers, there are a few important issues to keep in mind. First, we should not be so moved to take advantage of the new methodological advances that we lose sight of the questions. There remain some important questions in affective neuroscience that can be addressed with univariate—rather than multivariate—approaches and we should always use the best approach for answering the primary research question. Second, recent concerns have been raised about the test-retest reliability of fMRI tasks (Elliott et al., 2020) that will likely influence many design considerations (Kragel et al., 2020; Chen et al., 2021).

There is also some debate about the sample sizes necessary for establishing reliable estimates of brain-behavior relationships (Gratton et al., 2022; Marek et al., 2022; Rosenberg & Finn, 2022). But with the proper respect and appreciation for methodological strengths and limitations, future research will almost surely address some of the theories described earlier—defining emotion states, distinguishing emotion states from other related processes (e.g., emotion perception, attribution, conceptualization, etc.), and examining the generalizability of effects across different conditions, tasks, and samples.

***Figure 4*: Whole-Brain Models of Discrete Emotions (Adapted from Kragel & Labar, 2016)**



Note: Intensity maps developed from the peak coordinates of 148 neuroimaging studies of emotion (Wager et al., 2015), indicating expected activations assigned to each emotion category. The confusion matrices indicate correspondence between ground truth and predicted labels; most entries fall along the diagonal indicating good performance, with few errors between similarly valenced emotions (e.g., fear, anger, and sadness). Reproduced, with permission, from Wager et al., 2015 and Kragel & LaBar, 2016.

Physiological Components

The autonomic nervous system (ANS) coordinates a large number of physiological responses (Bernston & Cacioppo, 2000), and includes the sympathetic and parasympathetic branches that are associated with activation and relaxation, respectively. Although ANS activity is not exclusive to emotion—the ANS oversees many other bodily functions, such as digestion and homeostasis (Bernston & Cacioppo, 2000)—there is little doubt that an emotional state is associated with measurable changes in ANS activity.

The most common ANS indices that have been examined in the context of emotion are electrodermal (i.e., sweat gland activity which represents a sympathetic measure of physiological arousal; Hamm et al., 1993; Dawson et al., 2007) and cardiovascular (e.g., heart rate, from which measures of both sympathetic and parasympathetic activity can be derived; Mendes et al., 2008: Berntson et al., 2007). In addition, many studies measure the magnitude of the eyeblink responses to intense sensory stimuli such as loud sounds, bright lights, or puffs of air known as the startle responses (i.e., an autonomic reflex that is modulated by the amygdala; Vrana et al., 1988; Davis, 1989). Additional biological indices can illuminate broader or more tonic measures of affect, such as hormones and metabolites in saliva, blood, and urine (e.g., stress-induced arousal; Uchino et al., 1996; Zoccola, 2018).

The notion of ANS discriminability among emotions began with William James in 1884, who argued that, contrary to intuition, an emotion-eliciting stimulus first causes a suite of physiological responses, which then causes an emotional experience (James, 1884; 1890). This idea is consistent with a functional theory of emotion in that, in response to a potential threat, physiological responses (e.g., increased heart rate) enable us to fight or flee (Finger, 1994). Evidence in support of James's notions indicates that certain emotions can be distinguished based on autonomic responses (Levenson, 1992), particularly when considering a suite of autonomic measures in tandem (Kreibig et al., 2007; Stephens et al., 2010; Siegel et al., 2018).

However, much evidence also contradicts James's notions (e.g., Lang, 1994). A swift and lasting critique (Cannon, 1927; Bard, 1929) countered that the response to threat—either fight (which may be more likely in instances of anger) or flight (which may be more likely in instances of fear) —is associated with overlapping physiological responses (but see Ax, 1953; Larsen et al., 2008; Levenson, 2014). There is now evidence to suggest that cognitive interpretations of environmental cues modulate the link between physiological responses and subjective experience of emotion (see more on this in the section on Feelings of Emotion; Schachter & Singer, 1962; see also MacCormack & Lindquist, 2017). And more recent findings are inconsistent with the basic assertion that autonomic activity discriminates among specific emotions at all (Siegel et al., 2018). Results of a meta-analysis point to the same conclusion (Cacioppo et al., 2000), and the authors note that autonomic responses are better viewed in terms of broad dimensions of emotion responding (e.g., valence and arousal; see also Russell & Barrett, 1999).

Integrating central and autonomic nervous system responses, increasing attention has been paid to the vagus nerve, the tenth cranial nerve, which is broadly responsible for the regulation of internal organ function (e.g., maintaining a resting heart rate of roughly 70 beats per minute) and certain reflexes (e.g., swallowing, coughing; Breit et al., 2018). The bulk of the signals conducted via the vagus nerve are afferent, transporting critical information about the state of the body to the brain (Levenson, 2014). According to Polyvagal theory (Porges, 2001; 2007), the vagus nerve is the key phylogenetic substrate that supports emotion recognition in a manner that promotes safety and survival. Several studies using transcutaneous vagus nerve stimulation (tVNS), a technique for non-invasive brain stimulation that uses a mild electrical current to cause vagus nerve firing, found evidence implicating the vagus nerve in emotion recognition (Sellaro et al., 2018; Steenbergen et al., 2021) and emotion regulation (i.e., cognitive reappraisal ability; DeSmet et al., 2021). Relatedly, there is emerging evidence that suggests tVNS may be a promising therapeutic option for treatment-resistant depression (Fang et al., 2016; Koenig et al., 2021).

The vagus nerve also establishes important connections between the brain and the gastrointestinal tract (i.e., brain-gut axis), situating it as an important target for psychiatric (Evrensel & Ceylan, 2015;

Leclerq et al., 2016) and gastrointestinal disorders (Bonaz et al., 2017). Indeed, an early translational study found that lactic acid bacteria (i.e., Lactobacillus rhamnosus) produced an anxiolytic effect in mice, but not in those that were vagotomized, identifying the vagus as a crucial link between the gut and brain (Bravo et al., 2011; see also Kane & Kinzel, 2018 for a review). Future work will likely continue to shed light on this important connection between central and peripheral nervous systems, as they relate to emotion responses.

Methodological advances have enabled new insight into the relationship between physiological responses and subjective experience of emotion. As in the study of neural components, RSA (described in the previous section) has been used to examine the correspondence between four physiological measures—skin conductance, heart rate, startle eyeblink, and corrugator electromyography (i.e., a measure of activity in the corrugator supercilii, which is the facial muscle that extends across the top of both brows and shows bidirectional effects of valence)—and subjective reports of valence and arousal in response to pictures, sounds, and imagery (Ventura-Bort et al., 2022). By and large, the physiological responses did not predict subjective experience, except for the relationship between skin conductance and self-reported arousal. Future work will surely continue to explore the physiological components of emotion (Levenson, 2014), including greater consideration of some factors that have been largely overlooked (e.g., effects of experimenter), and provide further insight into the coherence and specificity of these responses. In addition, new ambulatory measures of physiological processes will enable increasing external validity, creating new avenues for exploring these important questions (Gordon & Mendes, 2021; Newman, Gordon, & Mendes, 2021).

Expressive Components

As already noted, functionalist approaches emphasize the behavioral output of emotions, as they assume that the neural and physiological components of emotion are ultimately in service of behavior. We turn next to focus on one set of behaviors, namely, the outward expression of emotion in the face, body, and voice.

During the first part of the 20th century, the basic emotion perspective popularized the notion that specific emotions cause fixed and specific expressive behaviors that can be measured or recorded and that this behavioral output is sufficient for classifying an emotional state. Many affective scientists, particularly of the psychological constructionist persuasion, disagree, emphasizing the notable within- and between-person variability in how (and whether) emotions are outwardly expressed (e.g., Barrett et al., 2019). The lively back-and-forth between basic emotions and functionalist theories, on the one hand, and constructionists, on the other hand, continues.

We suspect that both sides are partly correct: There are recognizable behaviors that are probabilistically associated with distinct internal states, but there is also much variability due to knowledge of contextual meaning and cultural rules. And just as speech utterances are often incomprehensible out of context even though words have some consistency in meaning (otherwise they would not communicate anything), taking dynamic facial, bodily, and vocal expressions out of context deprives them of some of their recognizability and meaning.

Facial Expression

Facial expressions that are assumed or observed to accompany emotion states have been variously described as designed for survival and communication (Burrows et al., 2011; Shariff & Tracy, 2011; Susskind, & Anderson, 2008). These complex functions are served by a complex design: Around two dozen muscles on each side of the face operate, many quite independently, not just to help us blink, chew, and sniffle, but also to signal information to others. Facial muscles are the only muscles in the body that are anchored to skin, which means that every muscle twitch translates to visible movements of the skin. The fact that most human faces are relatively hairless makes these movements all the more visible to observers.

According to Darwin (1872/1998), facial expressions in humans evolved from movements that were adaptive for their ancestors because the movements solved challenges to survival. For instance, Darwin reasoned that the expression of anger involves the lowering of the eyebrows to protect against strikes to the eyes in aggressive encounters. More recent studies have provided evidence for some of Darwin's speculations, although he thought that the initial utility of facial expression was no longer needed in the present, and that the association between challenges and opportunities and specific facial expressions largely has come to serve a communication function.

Careful studies do, however, suggest that the form of some facial expressions still serves the proposed distal survival function (Susskind & Anderson, 2008). For instance, when experimental participants make facial expressions of fear, they take in visual and olfactory information more efficiently than when they make neutral expressions (Lee, Susskind, & Anderson, 2013; Susskind et al., 2008). Specifically, the size of people's visual field increases, they can localize visual targets in space more quickly, and they can take in more air more rapidly through their nasal passages (West et al., 2011). And the surprised expression seems to have similar sensory processing benefits to that of fear (Susskind & Anderson, 2008). Findings also indicate that the disgust expression has the opposite effect. Compared to a neutral expression, the disgust expression tends to close off the senses to external input. In particular, the visual fields contract and inhalation through the nasal passages is more restricted. Since fear arises during threat and disgust arises during exposure to contamination, these relations seem functional even today (Krusemark & Li, 2011). Do all expressions have a demonstrable adapted utility? Future research efforts will no doubt address this question.

According to basic emotion theories, a small set of underlying emotion states are reliably expressed by contractions of facial muscles that vary around a prototype: a typical and recognizable facial signal (Ekman & Friesen, 1971; Ekman, Sorenson, & Friesen, 1969). For example, in theory, people scowl when angry and smile when happy. Cultural differences in facial expression have typically been understood in terms of variations around the prototypes (i.e., expression "dialects"; Elfenbein & Ambady, 2002; 2003) or the degree to which intentional suppression of expressions occurs in specific contexts. However, affective scientists now acknowledge that facial expressions communicate not just the internal emotional state of the expresser but also what the expresser might do next and what the expresser needs from other people in the social environment (Crivelli & Fridlund, 2019; Fridlund, 1991; Scarantino, 2019). Because facial expressions convey information to others, they, like speech, are shaped by social feedback and should therefore be able to communicate a full range of social intentions and needs, including, but not limited to, emotion (Scarantino, 2019).

The specific design of facial expressions contributes to the success of their communication. The wide eyes of fear, for instance, have been shown in careful studies to be excellent signals to the spatial location of threat. For example, studies show that observers can extract gaze information very efficiently from the typical shape and size of the eyes made in the expression of fear (Lee et al., 2013). Findings demonstrate that the wide eyes of the fearful expression increase attentional orientation to threat. They also delay attentional disengagement from threat (Carlson & Reinke, 2014). The behavioral findings are complemented by findings from neuroimaging studies that suggest that the wide eyes of fear alone (Hardee, Thompson, & Puce, 2008), and even just the eye-whites of the fear expression (Whalen et al., 2004), are associated with increased activation in the amygdala.

The discovery of potentially coherent signals of other emotions, beyond the six basic expressions initially proposed by Ekman, proceeds apace. Advances in this accounting have been inspired by social-functional theories of facial expression, which draw on theory in behavioral ecology and deemphasize the internal cognitive and affective states of the expresser (Adams, Albohn, & Kveraga, 2017; Fischer & Manstead, 2008; Fogel et al., 1997; Keltner et al., 2006; Morris & Keltner, 2000; Sherrif & Tracy, 2011). In this approach, facial expressions are assumed to serve the function of regulating social interactions in order to accomplish basic, perhaps universal, tasks. For example, Niedenthal and colleagues (2010) rely on social-functional theories of emotion and the behavioral ecology view of facial expression (Fridlund, 2014) in proposing that in addition to signaling positive underlying emotion, the human smile also conveys the smiler's orientation toward the perceiver (Johnston, Miles, & Macrae, 2010).

Niedenthal and colleagues point to three basic tasks of human social living and propose that each task can be solved by a physically distinct smile expression. The three tasks include reinforcing desired behavior in the self and others (Reward smile), communicating non-threat (Affiliation smile), and communicating superior status (Dominance smile). Reward smiles are described in similarly to the "true" (i.e., of experienced positive affect) or Duchenne smile in that the smile causes expressers and perceivers to feel pleasure (Bernstein et al., 2010), most likely because the smiles stimulate reward centers of the brain (Bhanji & Delgado, 2014; Ekman, Davidson, & Friesen, 1990). Affiliation smiles, in contrast, can signal safety and openness to engagement without being associated with an internal state of positive affect (Cashdan, 2004; Fridlund 1991; 2002; Schneider & Josephs, 1991). Such smiles may include expressions shown in "greeting" (Eibl-Eibesfeldt, 1972) as well as the smile component of the embarrassment gesture (Keltner, 1995; Ambadar, Coh, & Reed, 2009). Finally, so-called Dominance smiles are also distinct from positive emotions and appear to share features of contempt while still be classified as smiles (e.g., Martin et al., 2018).

Recent empirical studies bolster the proposed social-functional classification of smiles by confirming 1) three hypothesized task-specific motivations for smiling, 2) three physically distinguishable smile gestures that communicate the proposed functional meanings, and 3) predicted physiological responses to the smiles in context (Martin et al., 2017; 2018). To provide an analysis of the task-specific motivations, Rychlowska and colleagues asked respondents from nine countries to rate the extent to which a list of motives and internal feeling states are accompanied by a smile (Rychlowska et al., 2015). Exploratory factor analysis revealed a three-factor solution corresponding to the tasks of rewarding, signaling non-threat or appeasement, and communicating superiority. In a second series of studies, Rychlowska and colleagues (Rychlowska et al., 2017) then modeled the three smiles using a data-driven procedure to identify the physical appearance of each gesture represented by computer animations. Their discoveries are encoded by the actor seen in Fig. 5. Other studies have linked the smiles to predictable physiological responses (Martin et al., 2018).

Figure 5: **Example Smiles of Reward, Affiliation, and Dominance, Based on the Modeling of Rychlowska et al. (2017)**

An exciting new direction in affective science concerns the observation that in addition to the action of facial muscles, facial coloration can serve as an efficient and honest signal of underlying emotion (Benitez-Quiroz, Srinivasan, & Martinez, 2018; Thorstenson et al., 2018). Emotions that involve reducing circulation of blood to the periphery (i.e., vasoconstriction) slow cutaneous blood flow (Drummond & Quah, 2001). This gives skin the appearance of being bluer and greener, detectable in most skin types, because of accumulating blood volume and deoxygenation of the blood cells. Emotions that involve flushing the periphery with rapid circulation of oxygenated blood (i.e., vasodilation) result in redder and yellower skin appearance. For example, happiness and anger are both associated with increased redness and yellowness (Nakajima, Minami, & Nakauchi, 2017; Young et al., 2013). Facial coloration has also been shown to disambiguate ambiguous facial expressions for the perceiver (Thorstenson et al., 2019). While the limits of this research direction are becoming clear (Peromaa & Olkkonen, 2019; Wolf et al., 2021), we expect to see further developments in the coming decade.

Vocal Expression

Emotions are expressed by nonlinguistic aspects of the voice that together are called prosody. People can use their tone of voice purposefully to communicate emotion, but prosodic changes to the voice are often automatic and uncontrollable. The properties of vocalization that contribute to the expression of emotion include pitch, loudness, rhythm, tempo, phonation features like breathiness and nasality, and the variability and unpredictability of all those properties over time.

Physiological arousal has a direct influence on the quality of one's voice and results of initial studies suggested that prosody largely conveys information about emotional arousal, such that higher pitch is associated with greater arousal (Bachorowski, 1999; Kappas, Hess, & Scherer, 1991; Pittam, Gallois, & Callan, 1990; Sherer et al., 2003; but see Goudebeek & Scherer, 2010). Other possible dimensions of affect, such as valence, and discrete emotion states, have been more elusive to description in terms of acoustic properties. Anger and joy, as an example, are associated with similar increases in pitch and loudness, presumably because they are both high arousal states (Johnstone & Scherer, 2000).

However, the strength of conclusions depends on the physical properties of the voice that are analyzed (Juslin, 2013). Regarding the lack of differentiation between anger and joy just mentioned, it may be that combinations of other features of sound are more diagnostic of specific emotions. For example, anger vocalizations appear to have a more abrupt onset than happy ones (greater attack) and may sound more irregular with slight perturbations in pitch (higher jitter; Juslin & Scherer, 2005). And smiling perceptibly changes how the voice sounds, but partly by changing how vowels (formants) sound (Lasarcyk & Trouvain, 2008). Indeed, when researchers examine a full range of acoustic properties, including irregularities in speech patterns and changes in phonation, researchers find that the combination of features can distinguish emotions, at least when vocalizations are produced by actors (Johnstone & Scherer, 2000).

Although analysis of the physical features of prosody is useful for investigating the expression of emotion in vocalizations, crowd-sourcing responses is also a useful way to answer questions about the expression of emotion in the voice. Results of a meta-analysis, for example, suggest that consensus about the emotion expressed by the voice is quite high for the expression of anger, fear, happiness, sadness, and tenderness and that this accuracy is moderated neither by the perceiver's cultural background nor the spontaneous versus posed nature of the vocalizations (see also Sauter et al., 2010; cf., Gendron et al., 2014). In a large-scale study, judges could correctly identify 22 different emotions, including emotions such as shame, compassion, and embarrassment (Simon-Thomas et al., 2009).

Bodily Expression

If one function of emotion is to prepare a person for appropriate action in response to a stimulus, then it would seem almost definitional to consider the body as a channel of emotional expression. Observation of many species suggests that when experiencing fear, one is likely to freeze, cower, or prepare for rapid flight; when angry, one might make themselves appear big and make powerful movements of approach; and when experiencing joy, one typically moves in an open and playful manner. Indeed, these behaviors appear to match the theoretical functions of the emotions—to escape a threat, to aggress against a transgressor, and to explore and socially engage, respectively.

As with the voice, researchers have investigated the physical properties of movement as they relate to emotional states (Castellano, Villalba, & Camurri, 2007). For a very basic assessment of the movement-emotion connection, some innovative researchers used animated bouncing balls to identify the specific dynamic features of movement that convey specific emotions (Sievers et al., 2012). They found for instance that erratic, rapid, and downward focused movement conveys anger.

Another approach is to use minimal visual descriptions of human bodily movement in the assessment of the bodily expression of emotion. The most useful method to distill information from the body is the point-light display method (e.g., Brownlow et al., 1997). In one study, researchers filmed actors in a darkened room, portraying disgust, fear, anger, happiness, and sadness with body movements while wearing full-body suits with reflective material at a few important locations on the body (e.g., the wrists and head, Atkinson et al., 2004). The actors tended to convey anger with erratic movements, shaking fists, and stamping feet. They conveyed fear by cowering, contracting movements, and sometimes raised hands protectively. Happiness was associated with playful movements such as skipping, jumping, and pumping the air with the arms. And sadness often involved a slumped posture and self-soothing gestures such as face covering or self-hugging. In displays of disgust, actors covered their mouths and noses, turned away, and waved their hands in front of their faces as if to dispel a toxic smell (Atkinson et al., 2004). Naïve observers correctly categorized the intended emotion at greater than chance accuracy.

Other work has drilled into distinct bodily gestures that appear to be regularly associated with specific emotions. For example, work by Tracy and colleagues has shown that pride is displayed by an expansive body posture, often with arms raised (Tracy & Robins, 2004; Tracy & Matsumoto, 2007). Similarly, past research suggests that embarrassment is displayed with a shrinking posture, putatively intended to minimize one's presence, along with very specific movements of the face and hands (Keltner & Buswell, 1997).

The conclusion that bodies express specific emotions is not, however, supported by the results of other studies (Zacharatos et al., 2014). For example, one analysis suggested that bodies mostly convey information about valence and arousal (Senecal et al., 2016). Another study that examined the bodily movements of 10 professional actors displaying 12 discrete emotions found that while a few emotions were associated with a prototypical body display (e.g., hot anger), most emotions were expressed in a highly variable manner (Dael et al., 2012).

Much more work is needed in this domain, including study of the ways that emotional signals from the face, voice, and body interact during the experience and expression of emotion (see de Gelder et al., 2015; Aviezer, Trope, & Todorov, 2012). Future work can also be directed at further linking the findings in bodily expression of emotion to broader biological motion cues that serve as universal signals across cultures and species (Sievers et al., 2013; Parkinson et al., 2017).

Coherence Across Components

As is now evident, emotion involves a suite of coordinated changes across neural, physiological, and expressive (as well as experiential) response systems, which is consistent with many theories (e.g., Tomkins, 1962; Plutchik, 1980; Scherer, 1984; Lazarus, 1991; Ekman, 1992; Davidson, 1992; Levenson, 1994; Panksepp, 1994). For instance, an emotional stimulus might trigger covarying changes including increased amygdala activity (neural system), increased heart rate (physiological system), facial expressions (expressive system), and subjective experience of emotion (experiential system). The different systems are thought to cohere to the extent that they are characterized by covariation in emotion response systems across time (Mauss et al., 2005). Thus, coherence is defined as positive associations between components activated in response to an emotion state across various neural, physiological, and expressive components. For example, high coherence is evidenced by a state of amusement evoking a suite of coordinated responses including increases in skin conductance, heart rate, activity in zygomaticus major— the facial muscle associated with expressing a smile—and distributed neural activity associated with amusement. In contrast, low coherence might be evidenced by a state of amusement that is accompanied by self-report, but no associated changes in skin conductance, heart rate, or other physiological or neural signatures.

Many emotion theorists (particularly those of the basic emotion persuasion) view coherence as the defining feature of the emotion episode. For example, a state of self-reported amusement that does not produce coordinated changes in neural, physiological, and expressive systems might not in fact be a true state of amusement, whereas a state of amusement that is evident throughout the brain and body can be more reliably defined as an emotional experience. Indeed, coherence might support more effective responses to environmental challenges (i.e., adaptive function), associated with greater well-being. However, there is a paucity of robust and reliable evidence for coordinated changes suggestive of emotion coherence.

By and large, most work that has examined emotion coherence has relied on subjective experience (i.e., self-report) as the gold standard for classifying something as an emotion, and as a particular emotion (LeDoux, 2012; Barrett, 2015), or the "ground truth" to which other measures of emotion are compared. It could be, therefore, that weak evidence for emotion coherence is an indication that self-report measures do not serve as ground truth – and perhaps there simply isn't one. Some interesting work has examined the link between neural, physiological, and endocrine responses to dishonesty, a behavioral construct that, by definition, lacks valid self-report, and thus, self-report cannot be used as ground truth (see ten Brinke et al., 2015 for a review). The findings point to a suite of coordinated changes in the brain and body associated with negative health outcomes of dishonesty— depletion of the brain regions that support executive control, increased heart rate and blood pressure, and increased cortisol reactivity. That is, there may be better evidence of coherence when self-report is not relied upon as the ground truth.

Perhaps future research will overcome this reliance on self-report by exploring emotion coherence through relationships between the various response systems. In other words, the simultaneous recording of neural and physiological measures (Heller et al., 2011; Lindner et al., 2015), will pave the way for new evidence of coherence that is agnostic to subjective experience and the processes used to attend to and report it (Heller et al., 2014). For example, one study found coordinated responses in the brain and physiology (facial electromyography), such that trial-wise increases in corrugator muscle activity— indicative of experienced negativity— in response to negatively valenced images tracked increased amygdala and decreased ventromedial prefrontal activity. Future work can leverage multivariate approaches mentioned earlier (e.g., representational similarity analysis, or RSA) to explore similarities in emotion representations across neural, physiological, cognitive, expressive, and subjective experiences of emotion. These findings will also help to address the possibility that weak coherence arises because coherence is constrained to a certain type of response across systems. For example, there is some evidence for greater coherence as a function of whether the responses across systems are considered automatic versus reflective (Evers et al., 2014).

Alternatively, it could be that the weak evidence for emotion coherence stems from variability across individuals. Indeed, recent work has reported evidence that coherence varies as a function of age (Lohani et al., 2018), body awareness (Sze et al., 2010), and psychological (Brown et al., 2020) and physical well-being (Sommerfeldt et al., 2019). In particular, coherence tends to be higher in older adults, individuals with higher body awareness (e.g., meditators or dancers), and those with higher self-reported well-being (e.g., lower levels of anxiety, depression, proinflammatory biomarkers). However, more work is needed to determine the extent to which these moderating effects are stable and generalizable.

In the next sections, we turn from examining the neural, physiological, and expressive components of emotion, to examining the cognitive consequences of emotions (e.g., how attention, perception, and memory are modulated). Notably, although many assume that emotion and cognition are categorically distinct mental faculties with their own neural circuitries (e.g., Shafritz, Collins, & Blumberg, 2006), evidence now largely suggests that emotion and cognition involve, at least in part, shared substrates that should not (or cannot) be teased apart (Pessoa, 2008; Bechtel & Richardson 2010). Regardless of whether separating cognition from emotion is scientifically useful, emotion states are accompanied by changes in how people attend to, perceive, and remember information.

Emotion And Attention

As the capacity of the human brain is limited, people cannot process all information entering their senses. They must select a subset of information to prioritize (at the cost of other information). Interestingly, internal affective states can be powerful modulators of this attentional spotlight. For example, hunger is a state that modulates attention by increasing sensitivity to sensory cues associated with food, such as taste and smell (Sengupta, 2013). Similarly, an emotion state shapes the spatial and temporal scope of attention. There is an attentional bias toward emotionally relevant information that is thought to unfold in a two-stage process involving bottom-up signals from the amygdala and top-down influences from the frontal cortex (Compton, 2003), ultimately allowing for more efficient detection of emotional information and preparation of an adaptive response (Pourtois et al., 2013). However, there can be adverse consequences of attentional prioritization of emotion, such as prioritizing emotional information that is task-irrelevant over other task-relevant information (i.e., emotion-induced blindness; see Goodhew & Edwards, 2022 for a review)

Extensive research has shown that the appraisal of a stimulus as emotionally relevant causes a rapid allocation of attention toward that stimulus (Brosch et al., 2008; see Yiend, 2010 for a review). Much of the early work relating emotion and attention used experimental paradigms, such as visual search and dot-probe tasks, to show that a person's attentional spotlight prioritizes negative—particularly fearful—information (e.g., Hansen & Hansen, 1988; Mogg & Bradley, 1999; Ohman et al., 2001). The threat superiority effect has been demonstrated for evolutionarily based threatening stimuli (e.g., snakes) as well as more modern threats (e.g., guns; Blanchette, 2006; Carlson et al., 2009). Perhaps one of the most famous demonstrations of this effect is the *weapon focus effect*, which is the finding that a weapon (e.g., gun) creates a spotlight of heightened attention resulting in a decrease in attention to the periphery (e.g., the perpetrator holding the gun; Loftus et al., 1987; Fawcett et al., 2013).

Although threat appears to be prioritized in attention, more recent work has demonstrated that the effects on attention—broadening versus narrowing—may depend on the type of threat conveyed. For example, a comparison of two negatively valenced facial expressions—fear and anger—revealed that fear results in a broadening of attention, whereas anger has a narrowing effect. Such a finding may seem inconsistent with the weapon focus effect, but considering the mechanism directing attention, the effects are compatible. Specifically, the widened eyes in fearful expressions are thought to signal that there is a potential threat in the environment, directing attention outward (i.e., "I am detecting a threat and you would do well to detect it too!"), whereas the narrowed eyes in the anger expression identify a certain and direct threat (i.e., "*You* are the threat I am detecting in the environment; *you* are my problem." —similar to the effect imposed by the presence of a gun). As a result, neutral information that is presented surrounding a fearful face receives greater attention (and is later remembered more often) than information that is presented surrounding an angry face (Davis et al., 2011; Taylor & Whalen, 2014).

Alternative explanations for the weapon focus effect include the arousal hypothesis, which holds that heightened arousal results in a narrowing of attention focus (e.g., Wegner & Giuliano, 1980; Schimmack, 2005). That is, seeing a weapon induces heightened arousal, and it is this arousal that narrows the focus of attention on the weapon. Some evidence for the arousal explanation comes from accumulating evidence that positive emotional stimuli can also attract attention, particularly when the stimulus is highly arousing, and when relevant to ongoing concerns (e.g., hunger; Kemps & Tiggemann, 2009; Pool et al., 2016; though there is some evidence that the attentional bias to positive stimuli is weaker than to negative; Smith et al., 2003). For example, chocolate attracts our attention – perhaps via frontostriatal circuits (Padmala & Pessoa, 2011)—despite being rather uninteresting, visually speaking, and regardless of the extent to which a person might wish to avoid attending to the temptation (Hübner & Schlösser, 2010; Pool et al., 2014). That said, the evidence described previously that suggests a broadening—rather than narrowing—of attention in response to fear and positive emotion (Fredrickson, 2001; see Fredrickson, 2013 for a review) runs counter to this hypothesis.

Still another explanation that has been offered for the weapon focus effect is the unusual object hypothesis (Mitchell et al., 1998), which posits that a rare or unexpected stimulus attracts attention more than common or expected items (Johnston et al., 1990; Henderson et al., 1999). For example, most people see cars driving on the road and think nothing of it. But if a car was overturned, resting on its back, it would stand out as unusual and attract greater attention. The culmination of some rigorous testing of these alternative hypotheses (Flowe et al., 2013) has lent credence to the unusal object explanation in demonstrating that a weapon does not have greater access to attention than a non-threatening but unexpected object (e.g., pocket watch). Thus, it appears that context is a powerful determinant of attentional allocation: in a context where a gun is expected (e.g., shooting range), it does not elicit heightened attention (Pickel, 1999). And, of course, a combination of these explanations is also possible, such that a gun attracts attention because it is both threatening and unexpected.

Notably, the effects of emotion on attention are bidirectional; emotion can modulate attention, as evidenced by the broadening and narrowing of attention described earlier, but attention can also modulate emotion. For example, attentional deployment strategies are an effective form of emotion regulation (Gross, 1998; Webb et al., 2012; Sheppes et al., 2014) that circumvents cognitive demands (Mauss et al., 2007). For example, people often cover their eyes during a scary movie scene to avoid having to experience the intended emotion. Indeed, a number of interventions that rely on attention modification, including cognitive behavior therapy and mindfulness, have been shown to be effective in treating and even preventing anxiety (MacLeod & Mathews, 2012; Crowe & McKay, 2017), depression (Cuijpers et al., 2013; van Zoonen et al., 2014; Crowe & McKay, 2017; Krejtz et al., 2018), and other related affective disorders (see Hofmann et al., 2012 and Goldberg et al., 2018 for reviews).

Emotion And Perception

As widely evident from popular music lyrics, emotions color perception. Affective science also finds that to be the case. Of course, the effects on attention and perception are highly interrelated given that attention limits the information that can be processed, then enhancing the perception of some information while reducing the perception of others (Brosch et al., 2008).

Although the effects of emotion on perception are likely fraught with confounds (e.g., fearful faces are prioritized because the widened eyes are higher contrast and thus easier to detect; Firestone & Scholl, 2015; Niedenthal & Wood, 2019), there is good evidence that emotions modulate visual perception. Gayet and colleagues (2016) used simple perceptual stimuli—colored circles—that were fear-conditioned, allowing for manipulation of threat independent of the perceptual features of the stimuli. The researchers found that fear-conditioned circles received the same perceptual prioritization as inherently threatening stimuli (fear faces). Such perceptual effects are largely a result of the extensive efferent amygdala projections that reach nearly all levels of the visual cortical hierarchy (Amaral et al., 2003), allowing for emotional stimuli to override perception/attention deficits, for example, in blindsight patients (de Gelder et al., 1999; Celeghin et al., 2015).

It is now clear that visual processing occurs in a context that is shaped by signals in the amygdala, as well as other brain regions associated with emotion processing (e.g., orbitofrontal cortex; Vuilleumier & Pourtois, 2007; Pessoa & Adolphs, 2010; Freeman & Ambady, 2011). Thus, rather than vision representing a separate or isolated process, it is colored by emotion even at the level of the primary visual cortex (Padmala & Pessoa, 2008).

A growing body of research further demonstrates that visual processing (e.g., object perception) is characterized in part by initial predictions about the basic gist of perceptual information that feeds back to the visual cortex (Schyns & Oliva, 1994; Bar et al., 2006). These predictions are thought to stem from learned stimulus-response associations that include affective value (Barrett & Bar, 2009) and allow for cognitive and affective penetrability of perception (O'Callaghan et al., 2017). For example, a blurred representation of an object (e.g., an image emphasizing the low spatial frequencies) activates initial guesses useful for identifying that object, but top-down information (e.g., contextual cues indicating a dark alley, a hair salon, or a tool bench) can shape the recognition process toward identifying the object as a gun, a hair dryer, or a power drill (Bar & Neta, 2008). Similarly, predictions during visual perception can carry affective value, and this affective penetrability is part of the initial perceptual experience, supported by the orbitofrontal cortex.

As evidence for the affective penetrability of perception, low-level perceptual properties that have learned associations with danger or threat can drive preferences for novel percepts (Bar & Neta, 2006; 2007). In a series of experiments, Bar and Neta found that sharp transitions in contour— even in novel visual objects—are sufficient to trigger a negative bias and increased amygdala activation, compared to the same objects with curved contours. Likewise, low-level perceptual properties that are associated with positive outcomes can color preferences (Palmer & Schloss, 2010). Further, a person's affective state (e.g., negative mood) has been shown to result in speeded visual perception during early stages of perceptual processing (Kuhbandner et al., 2009; Panichello et al., 2017). As noted earlier in the discussion of attention, the micro-valences that are computed during perception, as well as mood effects on perception, may serve an important role in guiding approach and avoidance motivation, allowing for a more adaptive interaction with our environment (Lebrecht et al., 2012; Kveraga et al., 2015; O'Callaghan et al., 2017).

Again, the effects of emotion on perception are bidirectional. Just as affective states and predictions influence early perceptual processing, low-level perceptual processing can influence emotion. For example, some research has demonstrated that there are stable and reliable individual differences in a person's tendency to appraise an emotionally ambiguous stimulus (e.g., a surprised facial expression) as having a more positive or negative meaning (i.e., valence bias; Neta et al., 2009; Harp et al., 2022). Using eye-tracking methods, this work found that individuals who look longer at the eyes—a feature that is highly overlapping with more negatively valenced expressions of fear—show a more negative valence bias, but those who look faster to the mouth—a feature that discriminates surprise from fear—show a more positive bias (Neta et al., 2017). Notably, follow-up work controlled the perceptual input using a moving window that appeared as a spotlight around the visual features that were fixated by the most positive and the most negative participant. The findings revealed that viewing the faces 'through the eyes' of the most positive or negative participant was sufficient for shifting the (otherwise stable) valence bias in new participants (Neta & Dodd, 2018). In other words, perceptual input can shape one's emotional response to the environment.

Emotion And Memory

An emotion state can shape not only attention and perception, but it can also have long-term effects on memory. The prioritization of emotionally relevant information in memory is often attributed to increases in the autonomic nervous system brought about by stimulus appraisals (McGaugh, 2000).

The physiological consequences can manifest as modulations at the encoding, consolidation, or retrieval stages of memory (through a series of functional and structural connections between the amygdala, hippocampus, and prefrontal cortex; e.g., McGaugh, 2000; Smith et al., 2006 and Denkova et al., 2013; Kensinger & Ford, 2021), though we focus here on retrieval given that effects at earlier stages are somewhat overlapping with effects on perception and attention. The fact that an emotion-eliciting stimulus (e.g., a gun) can capture attention in a way that limits attention to peripheral information (e.g., the face of the robber) has consequences on encoding and consolidation of this event (Talmi et al., 2013).

Concerning retrieval, memories of emotional events are usually characterized by a persistence (McGaugh, 2004; LaBar & Cabeza, 2006) and vividness (Todd et al., 2012) that non-emotional memories appear to lack. Some work has shown that emotion augments the confidence in recollection, independent of its accuracy (Talarico & Rubin, 2003; Hirst & Phelps, 2016). For example, Talarico & Rubin (2003) asked a group of Duke students, on September 12, 2001, to record their memory of the previous day – the terrorist attack on the World Trade Center in Manhattan – and to record a recent neutral event. After some time (1, 6, or 32 weeks later), they were asked to recall the same events. The researchers found that memory deteriorated to the same extent for the emotional and neutral events, but that participants were much more convinced that their emotional memories were accurate. This suggests that emotional memories have characteristics that lead us to *believe* they are better memories (i.e., to be recalled with greater accuracy) — and this increased sense of recollection is associated with increased amygdala activity (Sharot et al., 2004) — but they in fact may not be.

It is worth noting that other research exploring the effects of emotion on memory has demonstrated that emotional events are remembered with greater accuracy than non-emotional events (Reisberg & Hertel, 2005). The relative inconsistency in these findings could be attributed, at least in part, to differences in the details that are being remembered. For example, Rimmele and colleagues (2012) demonstrated an enhancement in recollection accuracy that was specific to the spatial and temporal context of an emotional event (e.g., remembering where you were when you learned about the terrorist attacks on 9/11), but not for other details of the event.

Other work has shown that emotion might either augment or interfere with retrieval and that these effects vary as a function of physiological arousal (Mather & Sutherland, 2011; Loeffler et al., 2013) and memory details (Kensinger & Ford, 2020). Arousal-biased competition (ABC) theory, for example, suggests that emotional arousal—regardless of whether it is evoked by external stimuli, internal motivation, or hormones—enhances memory for high-priority, salient stimuli and suppresses memory for low-priority, non-salient stimuli (Mather & Sutherland, 2011; Lee et al., 2014). Further, work examining memory details that modulate retrieval found that negatively valenced events and details (Kensinger, 2009; Bowen et al., 2018) and details that are consistent with a person's emotion goals (Holland & Kensinger, 2013) are remembered more accurately (Kensinger & Ford, 2020). Along these lines, socioemotional selectivity theory posits that emotion goals change with age such that older adults show an increasing emphasis on positive over negative emotions (Carstensen & Charles, 1998). Relatedly, older adults tend to remember more positive than negative events, consistent with these goals (Mather, 2006). And these effects might even interact, such that arousal associated with memory details may have downstream consequences on the accuracy of memory as a function of how the features are associated, or bound together (Mather, 2007).

As is the case for attention and perception, the effects of emotion on memory are bidirectional. Indeed, although generally emotional stimuli are highly memorable, patients with amygdala damage show impaired retrieval of emotional events (Buchanan et al., 2005; 2006). In contrast, patients with post-traumatic stress disorder (PTSD) experience powerful negative emotions that are triggered by the involuntary retrieval of traumatic memories (Roszell et al., 1991; Hall et al., 2018). It appears therefore that brain regions that play a critical role in the retrieval of emotional memories (e.g., the amygdala and the prefrontal cortex) may be, in a way, recreating the original emotional experience (see Buchanan, 2006). In one study, participants recalled positively valenced autobiographical memories in the MRI, and their recall of this information was sufficient to induce a positive emotion state, along with associated reward-related activity in the striatum and medial prefrontal cortex (Speer et al., 2014). Of note, although recall can often recreate the original emotion, it can also bring about new or different emotional experiences. For example, recalling negative emotions, if done so with a particular narrative frame (e.g., learning a lesson, identifying a silver lining) or to repair mood, can induce a positive emotion experience (Loeffler et al., 2013; Kensinger & Ford, 2021).

Feelings Of Emotion

When asked how they are feeling, or even the degree to which they are feeling a specific emotion, most people can reply swiftly and confidently (Barrett, 2004; Cowen & Keltner, 2017): People communicate about how they are feeling by using emotion terms or metaphors (Lakoff, 2016). People also readily rate the extent to which they feel joyful or angry on Likert-type scales anchored by the statements "not at all joyful (or angry)" and "very joyful (or angry)." Such ratings represent the individual's interpretation of their mental and bodily states, supported by dedicated, integrated neural circuits (LeDoux, 2020; Oosterwijk et al., 2012). Just what are people reporting on? What causes variation in these reports? And what function does the feeling serve?

The mechanisms that support feelings of emotion, as distinct from states related to other homoeostatic processes of the body (e.g., "feeling" thirst) or cognitive assessments (e.g., "feeling" prepared), are the subject of many theories past and present. For William James, for example, the conscious perception of afferent feedback from the autonomic nervous system to the central nervous system constituted the "emotion" and thus his theory was ultimately a theory of conscious feelings of emotion (James, 1890; Prinz, 2005). Other theories hold that feelings, are a "component" of emotion, participating in what is sometimes referred to as an emotion "episode" (Russell, 2003). But even asserting that feelings are a component of emotion does not require that subjective feelings be accommodated within a single, overarching theory of emotion.

Although there are reasons to object to a theoretical distinction between feelings and emotions—a distinction that has been made at various times in various ways over centuries (e.g., Bull, 1945; Dewey, 1895; McDougall, 1908/1921)—there are also good reasons to maintain the distinction. One is that unlike the components discussed in the previous section, feelings are neither observable nor directly quantifiable, as is heart rate; they are communicated through self-report, usually via language. Terms for emotion vary across language groups and culture (Harkins & Wierzbicka, 2010; Jackson et al., 2019; Russell & Sato, 1995); there are individual differences in people's learning and use of language for emotions (Barrett et al., 2001; Hoemann, Barrett, & Quigley, 2021; Kashdan, Barrett, & McKnight, 2015); there are within individual changes in the terms used to name emotion states over development (MacCormack et al., 2021; Nook et al., 2018); and there are subclinical conditions, notably alexithymia, associated with limitations on the ability to label emotions at all (Kooiman, Spinhoven, & Trijsburg, 2002; Luminet, Bagby, & Taylor, 2018).

As we discuss later, there are also individual and cultural differences in attention to and precision in monitoring bodily states (Ainley et al., 2016; Garfinkel et al., 2015; Ma-Kellams, 2014), and people have beliefs about internal states that they use in the interpretation and therefore reporting of their bodily states (i.e., interoceptive beliefs; Chua & Bliss-Moreau, 2016; MacCormack, Bonar, & Lindquist, 2021; Ondobaka, Kilner, & Karl Friston, 2017). In bringing together the input into reports of feelings, Robinson and Clore (2002) propose that experiential knowledge (i.e., attention to one's current internal state), episodic memory, situation-specific beliefs (i.e., knowledge about the emotions that are usually experienced in specific situations), and identity-related beliefs (i.e., knowledge about the emotions that the self usually experiences in specific situations) all inform reports of one's feelings.

People's attention to and ability to report on physiological bases of feelings, and the influences on these processes exerted by personality, context, language, and culture are very important and productive areas of research. However, a systematic accounting of the variety of influences also suggests that reports of feelings need not be tightly correlated with indicators of other components of emotion across individuals or even within individuals over development.

LeDoux (2020) provides justification, from a neuroscience perspective, for developing theories of feelings separately from theories of emotion more generally. With specific reference to fear, LeDoux writes, "When one faces certain kinds of danger, defensive responses like fleeing or freezing can co-occur with feelings of fear, not because the neural processes underlying these two kinds of events are intimately entwined in the amygdala, but instead because the events have the same starting point—a threatening stimulus that enters the brain through the visual (or some other sensory) system. From there, the paths underlying the responses and feelings diverge." This account is reminiscent of Cannon's counter proposals to James' theory of emotion (Cannon, 1927; 1931). Damasio and Carvalho (2013) similarly distinguish "emotion" which they define as an adaptive, patterned neural response, from "feeling," which they define as internal sensations resulting from the neural responses and input from interoceptive processes.

How Feelings Arise

Adolphs and Anderson (2018) propose several basic conditions for the experience called feeling. One is that the feeling person is conscious, that is, able to be aware of their internal states and make them the subject of focal attention. What people are consciously aware of, in this view, involves access to somatic content, the emotion as a state of the body, and cognitive content such as the understanding that an action should be taken or that an event or stimulus is relevant to themselves. Further elaboration of the content of feelings has been developed in several recent theories. Here we review recent advances in two recent answers to this question: constructionism and the feelings-as-goals hypothesis.

Constructing Feelings From Core Affect And Concepts

Schachter and Singer (1962) famously proposed that exciting events cause non-specific autonomic arousal that, when disambiguated by reference to the arousing situation, generates specific feelings that can be labeled sadness, disgust, joy, and so forth. The researchers conducted a study in which participants were injected with either epinephrine, which caused a state of arousal, or a placebo, which had no physiological effect. Participants were then exposed to a confederate of the experimenter who either displayed euphoria or anger, impliciting providing a label for the participant's aroused state. The findings of the study were in fact quite weak but did point to the possibility that labeled arousal gives rise to specific emotions. More generally, Schachter and Singer's theory pointed future researchers toward an integration of interoception, arousal, and conceptual processes in the unfolding of and specificity of feeling states. These constructs have been elaborated in constructionist theories which, as we have seen, hold that an emotion is a "situated subjective state that emerges from the combination of more basic constitutive parts" (MacCormack & Lindquist, 2017). A full account of the constituents and the process of their integration to produce feelings is a major aim of the theory.

According to constructionist theories, the fundamental constituent of feelings is not non-specific autonomic arousal but rather "core affect," a state of the organism that can be described in terms of its pleasantness (valence) and its activation (arousal; Barrett, 2006; Clore & Ortony, 2013; Lindquist, 2013; Russell, 2009; Russell & Barrett, 1999). The two dimensions represent an integration of sensory information from the external environment with interoceptive and homeostatic information internal to the individual. Understanding the information in context, sometimes called "situated conceptualization," further generates conscious feelings of discrete emotions such as fear and sadness or whatever emotion concepts exist in an individual's culture (Lindquist & Barrett, 2008). So, the nature of feelings arises from the way in which core affect is given meaning by a particular individual in a particular situation in a particular culture. The meaning is thus derived from experience (such as having been fearful in a similar situation in the past and labeling it as such) and explicit learning (such as having been taught that a state called fear arises when one is in a situation of danger).

By some constructionist accounts, representations of past feelings are used as predictions of likely feelings in a specific context and determine the probability of having a feeling at all as well as its intensity. The construct of interoceptive inference has been linked to specific neural mechanisms, notably the insular cortex, which appear to support the integration of current interoceptive and exteroceptive information. The sources of information can be compared to each other (Gehrlach et al., 2019; Livneh et al., 2020) and the comparison can result in the detection of prediction errors. Erroneous predictions, representing a difference between the expected state and interoceptive feedback, contribute to the content and awareness of current feelings (Saxe & Houlihan, 2017; Seth & Friston, 2016).

Feelings-As-Goals Hypothesis

The feelings-as-goals hypothesis is an account of feelings as a subject of theory and experimentation explicitly separate from the other components of emotion (Kron & Weksler, 2022). The account extends the notion, developed most notably by Frijda (e.g., 2004, 2005), that feelings are "felt action tendencies" to make the novel claim that feelings are action goal representations (Kron & Weksler, 2022). More formally, feelings, in this view, are the content of a type of mental representation that includes a desired goal and the motivation to attain that goal that comes to mind when faced with an emotion-arousing stimulus (Mitchel, 2020).

The function of feelings is thus to drive an organism to take adaptive action within the constraints of a particular context. To be adaptive, therefore, the mental representation can not contain a rigid motor program; it should be "non-motoric." The reason the representation must be non-motoric is because otherwise, action taken to reach the desired goal would be reflexive and unresponsive to changing conditions. If the feeling represents the action goal rather than the action tendency, then behavior can be flexibly altered during goal pursuit. So, the goal and the resulting motor responses are decoupled, which permits a one-to-many relationship in which the emotion-arousing stimulus is associated with many different possible goal-serving responses. A one-to-many relationship means that a feeling can bring about different types of behavioral responses, depending upon which one is most useful within the constraints of the specific situation.

As an example of a one-to-many relationship, imagine a person who feels intensely afraid of a snake. If the fear is felt in a zoo and is generated by seeing the reptile enclosure up ahead, a person might circumvent the enclosure altogether. If is the snake is lying across a hiking trail, the fear could cause very fast fleeing beahvior. Finally, if fleeing were not possible at all because the snake is encountered in an enclosed area, fear might cause the person to try to club or otherwise harm the snake. A final claim made by this account is that feelings need not have a conceptual format for their function to be achieved. Semantic information is not required to provide a guide to achieving the goal.

We have reviewed three productive accounts of the content of feelings of emotion: as products of the conscious perception of bodily changes, as conceptualizations of core affect, and as representations of action goals. In all cases, there is some role for interoception, or the ability to direct conscious awareness to bodily signals including heartbeat, respiration, satiety, and the autonomic nervous system sensations related to emotions in general (Craig, 2002; Mehling et al., 2012). In the next section, we review new, accumulating findings in the area of interoceptive mechanisms and biases.

Interoception

When people attend to their bodily states and signals, such as rapid breathing or a flushed face, they are engaged in interoception. Interoception is the perception of the physiological states and signals of the body, which contributes to the regulation and maintenance of homeostasis (Craig, 2009). Interoceptive processes are distinct from the perception of external conditions (i.e., exteroception) and are also distinct from proprioception, which refers to sensing the body's muscles and joints in space (Craig, 2015).

Damasio and colleagues (2000) mapped the neural basis of interoception and found that it involves both first-order structures such as the somatosensory cortices and the insular cortex and second-order structures such as the cingulate cortex and the nuclei in the brainstem. The anterior cingulate cortex has also been demonstrated to be involved in the accurate detection of emotional signals perceived through interoception (Lane et al., 1998). In conceptualizing input to self-reports of feeling, most theorists assume that interoception informs such reports, but there are substantial individual differences in sensitivity to, accuracy in perceiving, and beliefs about interoceptive cues, and therefore in the relationship between bodily changes and reports of feelings via interoception.

Garfinkle and colleagues propose the following distinctions and measurements of the variety of interoceptive processes: (1) interoceptive accuracy, measured by performance on objective tasks such as heartbeat detection, (2) interoceptive sensitivity, measured by self-report of attention to bodily states, and (3) interoceptive awareness, measured with probes to metacognitive awareness of interoceptive accuracy such as the relationship between accuracy and confidence (Garfinkel et al., 2015; see also Arnold et al., 2019; Murphy, Catmur, & Bird, 2019). Here we discuss interoceptive accuracy because, including work by researchers who use different labels for it (including “interoceptive ability”), it is the most extensively studied construct. We also point to an emerging body of research on interoceptive beliefs.

Interoceptive Accuracy

People might be aware that something is happening in their body but be wrong about what that something is. So interoceptive accuracy varies continuously across people. Individual differences in interoceptive accuracy are, as mentioned, often measured using a heartbeat detection task, which presumably provides an objective measure of the extent to which awareness of bodily cues delivers a correct account (Critchley & Garfinkle, 2017; Herbert et al., 2010; Legrand et al., 2022; Lischke et al., 2020). Performance on the heartbeat detection task has been shown to be positively correlated with individuals’ self-reports of their interoceptive accuracy (e.g., Murphy, 2020).

Findings reveal that interoceptive accuracy is associated with the experience of more intense feelings (Kindermann & Werner, 2014; Pollatos, Gramann, & Schandry, 2007; Wiens, Mezzacappa, Katkin, 2000), with better emotion abilities (Critchley & Garfinkle, 2017; Koch & Pollatos, 2014), with the perception that stimuli are more emotionally arousing (Pollatos, Kirsch, & Schandry, 2005), with empathic responding (Grynberg, & Pollatos, 2015; Heydrich et al., 2021) and with better emotion regulation (Kever et al., 2015), although on this last point the findings are decidedly mixed (Zamariola et al., 2019) and the effect may be moderated by gender (Prentice, Hobson, Spooner, & Murphy, 2022). Other research also suggests that improving interoceptive accuracy is associated with better memory (Garfinkle et al., 2013; Werner et al., 2010) and more effective decision-making (Dunn et al., 2010). These relationships are interpreted in a general way as suggesting that accurate representation of internal physiological states and signals is associated with more appropriate responses.

Appropriate responses may not always be best guided by attending to internal bodily states, however. For example, Durlik and Tsakiris (2015) manipulated feelings of social exclusion using the Cyberball procedure, which is a virtual ball-toss game often used for social exclusion or rejection. Participants who had experienced exclusion showed decreases in interoceptive accuracy compared to baseline. The interpretation here is that social exclusion does (and perhaps should) shift attention from internal to external states and signals in order to repair social conditions. In integrating the findings relating interoceptive accuracy and social interaction, Arnold and colleagues hold that it is most effective to shift attention flexibly between internal, emotional signals and external, social signals (Arnold et al., 2019).

Interoceptive Beliefs

People’s idiosyncratic knowledge about how the body works can affect not only reports of their feelings but also their insights into the physiology of their own emotions. Interoceptive beliefs refer to what people think about the nature, value, or meaning of interoceptive sensations (MacCormack, Bonar, & Lindquist, 2021).

Nummenmaa and colleagues (2014) developed a nonverbal method to probe what individuals believe about the physiological basis of their feelings. The researchers created a computer-based, topographical self-report method called emBODY, which invites participants to use hot and cool colors to represent, on a human silhouette, the areas in the body that are activated or deactivated during feelings usually labeled as fear, anger, and so forth. Data can be averaged to produce illustrations of what people believe is going on in the body during each investigated emotion feeling and such averages can be compared across cultures as well. Volynets and colleagues, for example, found high similarity in interoceptive beliefs across more than 100 countries (Volynets et al., 2020). Consistent with past work, this study also found significant age-dependent reduction in the intensities of the feeling of the emotion in the body such that older people felt emotions as less intense.

The importance of interoceptive beliefs is becoming more evident with the emergence of new research that compares the influences of the different components of interoception referred to previously. MacCormack and colleagues (2022) collected measures of interoceptive sensitivity and interoceptive beliefs from participants who also completed a heartbeat detection task to measure interoceptive accuracy. The interoceptive beliefs of interest concerned the intensity, danger, and difficulties posed by interoceptive information (i.e., the value of those sensations). In a second session, participants underwent a stressful task while their sympathetic and parasympathetic nervous system reactivity were continuously measured with electrocardiography and impedance cardiography. Self-reports of emotional arousal during the task were acquired immediately after the task. Results showed that higher sympathetic nervous system reactivity, lower interoceptive accuracy, and less positive interoceptive beliefs (i.e., the belief that interoceptive information is dangerous) predicted more intense high-arousal emotions during the stressor. However, interoceptive belief was the only component of interoception that moderated the correspondence between physiological and emotional arousal. Specifically, participants who held more positive beliefs about interoceptive sensations showed greater coherence between sympathetic nervous system reactivity and emotional arousal.

In sum, although interoceptive sensations have been considered the primary input into feelings of emotion by many theorists, interoception is composed of multiple components. Refining definition and measurement of these processes has been called for by many affective scientists and we expect the next decade to see major theoretical and empirical advances in this area (Garfinkel, Schulz, & Tsakiris, 2022).

Labeling Feelings

From Schachter and Singer's classic 1962 paper through recent advances in theories of constructionism, the idea that labeling one's feelings affects the psychological, behavioral, and even physiological unfolding of an emotion has been a compelling one. Labeling an emotion, as in replying that one feels "sad" in response to a query about how one is doing, can serve to make feelings more discrete and sometimes easier to regulate. These effects make sense in light of our understanding of the general effects of applying categorical labels to objects, events, and experiences (Lupyan, 2012; Lupyan, Rakison, & McClelland, 2007).

Labels Make Feelings More Discrete

Earlier, we distinguished the feeling states generally labeled as sadness, joy, and so forth from moods along several dimensions, one of which is their specific character. Although emotions are specific and intentional, moods are more diffuse in tone. Some recent research suggests that putting feelings into words makes their character more discrete; in other words, the label turns an affective (mood) state into a discrete emotional experience. Indeed, it is a fundamental claim of constructionist theories of emotion (Barrett & Bar, 2009; Barrett & Bliss-Moreau, 2009; Barrett & Satpute, 2013; Lindquist & Barrett, 2012; Lindquist et al., 2012) that when core affect is put into words, a more specific feeling state (an emotion) is experienced (Barrett, 2006; Clore & Ortony, 2013; Cunningham, Dunfield, & Stillman, 2013; Lindquist, 2013; Russell, 2003). In this view, labels shape the perception of interoceptive sensations because they name concepts that provide information and help generate predictions that are brought to bear in interpreting the feeling. Labels for emotions vary by language and culture and the linguistic variation is thought to be responsible for–not merely reflective of–individual and group differences in emotion experiences (Lindquist et al., 2022).

Various lines of research support the claim that putting affect into words produces more discrete emotional experiences. For example, some findings reveal that labeling a stress response with an adaptive emotion term such as “excitement” causes different emotional experience, physiology, and behavior than labeling the response with a maladaptive emotion term such as “fear” (e.g., Jamieson, Mendes, & Nock, 2013 for a review). Similarly, Lindquist and Barrett (2008) primed concepts of either fear or anger (or did not prime any emotion concept) in their participants. They then induced either an unpleasant and aroused state or neutral state in the primed participants. To indirectly probe changes in emotion, they measured participants’ risk aversion, which increases when people are fearful. Consistent with a labeling account, participants primed with fear that experienced an aroused, unpleasant state rated risks as higher than those primed with anger, indicating that they saw the world in a more threatening light.

Although the research is in its early days, we expect that the manner in which putting emotions into words helps to differentiate the state (e.g., distinguishing feelings of fear and anger for example) will be a topic of rigorous experimentation in the coming decade.

Labeling As Emotion Regulation

Emotion regulation is a multifaceted construct that includes understanding and acceptance of one’s emotions, as well as the ability to change one’s emotions according to situational demands and goals (Gratz & Roemer, 2004). By that definition, there are at least two ways in which labeling can serve to regulate emotion: first, labeling could reduce the intensity of one’s emotions, and second, labeling could influence or potentiate explicit emotion regulation strategies that are available.

While applying a label to an emotional state may serve to enhance its specific character, shaping it from a vague state of core affect to a discrete emotional experience, this does not mean that a labeled emotion is more intense than an unlabeled one. Much research suggests that emotional intensity is reduced when feelings are labeled, which gives credence to a parent’s intuition to ask their distraught child to put their feelings into words. The idea is also enshrined in theories of psychotherapy and treatments for traumatic experiences (Fratteroli, 2006; Pennebaker, 1997; Pennebaker & Beall, 1986). Still, there are some mixed findings regarding the effects of labeling, suggesting the need for more research on moderating variables (Matsuguma et al., 2020; McRae et al., 2010; Ortner, 2015).

Recently, findings from several methodological approaches have converged around the notion that ongoing negative feelings are reduced by the application of a label, suggesting this could be a method of “implicit emotion regulation” (Torre & Lieberman, 2018; Braunstein et al., 2017). For example, research in affective neuroscience has repeatedly demonstrated that labeling an affective response is associated with reduced amygdala (Foland et al., 2008; Lieberman et al., 2007), and increased ventrolateral prefrontal activity, suggesting a regulatory outcome. Other work has found that self-reported distress (Lieberman et al., 2011) and skin conductance (Tabibnia, Lieberman, & Craske, 2008) are both lower when people generate or view emotion (but not neutral) labels for aversive images (see also Constantinou et al., 2013; 2014, 2015). Labeling also decreases cardiovascular responses after an anger induction (Kassam & Mendes, 2013) and reduces the intensity of negative feelings in response to tweets (Fan et al., 2019).

In addition to research exploring the underlying mechanism of labeling, other work has examined *why* labeling might reduce the intensity of negative feelings (Lieberman, 2011; Wood, Lupyan, & Niedenthal, 2016a; Torre & Lieberman, 2018). For example, applying a label to a feeling involves processes of conceptualization that make the experience more categorical. The result is an enhanced ability to reflect on the experience and draw inferences about cause and coping potential, all of which would reduce the uncertainty and therefore the urgency of the state. Inferring the cause of a feeling may also defuse it because reflecting on the state and isolating a presumed cause would indicate that the eliciting conditions can be prepared for or have been coped with (Torre & Lieberman, 2019). This latter interpretation is further bolstered by the observations that verbalizing positive feelings, which are less urgent, is not always associated with a diminished intensity of feelings (Fan et al., 2019; Vlasenko, Rogers, & Waugh, 2021).

Although labeling might be considered an implicit regulation strategy, it can also be encouraged with the explicit goal of emotional regulation by another person. The explicit social regulation of emotion by labeling occurs when one person (e.g., a therapist, a parent) requests that another person put their feelings into words. This type of co-regulation of emotion has been demonstrated in several types of studies (e.g., Fitzpatrick et al., 2019) and is central to the principles of many psychotherapeutic techniques. For instance, therapists often prompt clients to use emotion labeling in mindfulness training to bring feelings into (non-judgmental) awareness (Kabat & Zinn, 1990; Segal, Williams, & Teasdale, 2013).

Does labeling make explicit emotion regulation likelier or easier? Above and beyond serving as a method of implicit emotion regulation, labeling one's feelings might also influence or potentiate explicit emotion regulation strategies available to the person (Fitzpatrick et al., 2019). That is, having named the feeling might aid an individual in the process of intentionally regulating it themself. Recent work suggests that this is not the case. Nook and colleagues (Nook, Satpute, & Oschner, 2021) investigated the effect of labeling emotion on subsequent use of reappraisal processes (e.g., intentional reinterpretation of the emotion-eliciting event; Mcrae et al., 2012; Ochsner et al., 2012) and mindful acceptance (i.e., intentional appraisal of emotions as temporary experiences that can be reflected on and released; Kober et al., 2019; Kross et al., 2009). They found that participants who had labeled their feelings used both regulation strategies with less effectiveness (i.e., their feelings worsened). The authors interpret their findings as suggesting that putting feelings into words make the feelings "crystalized" and thus less malleable by intentional cognitive strategies.

The findings reviewed so far are not incompatible but suggest that moderating variables, time-course analyses, and investigation of both individuals and dyads are required for a full account of the effects of putting one's feelings into words. Future studies will also likely compare the feelings that arise when bi- or tri-lingual people apply words from different languages to the same feeling. Although the words may be considered faithful translations, the conceptual content may be quite different, leading to different behavioral or other response outcomes (Lindquist, 2017).

PERCEIVING EMOTIONS IN OTHERS

As is now evident, the human body reveals states of emotion in facial expression (Ekman, 1971; Cowen & Keltner, 2020), vocal prosody (Laukka et al., 2005; Schirmer & Adolphs, 2017), bodily motion (Atkinson, 2013; de Gelder, De Borst, & Watson, 2015; Witkower & Tracy, 2019), and posture (Dael, Mortillaro, & Scherer, 2012; Lopez et al., 2017). These communicative behaviors are (imperfectly) predictive of the expresser's subsequent cognitions and behaviors and may call for a response from an observer. Therefore, understanding the complex processes by which the observer reads the emotional signals of another person—which we will call emotion understanding (Spunt & Adolphs, 2019; Spunt & Lieberman, 2012)—is a critical topic in affective science. The importance of this topic is underscored by findings that accuracy in understanding others' emotions is positively associated with theory of mind (Mier et al., 2010), emotional intelligence (Mayer, Roberts, & Barsade, 2008; Salovey & Grewal, 2005), self-regulation (Garner & Waajid, 2012), and some components of empathy (Israelashvili, Sauter, & Fischer, 2020). And deficits in emotion understanding are positively associated with aggression (Schultz, Izard, & Bear, 2004) and antisocial behavior more generally (Fairchild et al., 2009; Marsh & Blair, 2008).

The understanding of other people's emotions is computationally demanding (Kragel & LaBar, 2015; Martinez, 2017). It involves flexible, context-sensitive engagement of cognitive operations that support the rapid orienting to, recognition, and integration of emotional signals, as well as the classification of the signals into categories acquired in one's cultural context (Spunt & Adolphs, 2019). As noted earlier in the chapter, most older versions of basic emotions theory posit the existence of evolved neural modules for perceiving, at least, the discrete emotions of sadness, anger, fear, surprise, disgust, and happiness in other people (Ekman & Cordaro, 2011; Panksepp & Watt, 2011). The assumption of modularity means that perceiving emotions is impenetrable by other cognitive processes such as expectations and conceptual knowledge; rather, the process is automatic and universal.

In contrast, cognitive theories assume interactive activation between perceptual and conceptual processing modes in the perception of emotion signals and content (Bower, 1981; Niedenthal, 1992; Niedenthal, Setterlund, & Jones, 1994; Niedenthal & Wood, 2019), as do more recent constructionist theories of emotion (Barrett & Russell, 2014; Lindquist, 2017; Lindquist et al., 2006; Lindquist & Gendron, 2013). On both accounts, the classification of a percept (e.g., a facial expression) is ultimately determined by bottom-up as well as top-down processes (Niedenthal & Wood, 2019; see also Bar et al., 2006). Thus, the perceiver's own emotional state, sensorimotor experience, expectations, and knowledge are potential inputs into the perceptual processes that inform emotion understanding (e.g., Halberstadt et al., 2009; Wood et al., 2015).

Detailed mappings of the neural basis of the underlying processes (e.g., Adolphs, 2002; Pessoa & Adolphs, 2010) find support for a distributed set of structures involved in the visual processing of stimuli that have emotional content including the occipitotemporal neocortex, amygdalae, basal ganglia, orbitofrontal cortex and right frontoparietal cortices. Auditory perception of emotion relies on some overlapping structures, as well as the right inferior frontal regions and regions of the auditory cortex (Adophs, 2002). Importantly, the somatosensory cortex also participates in the processing of emotion signals, suggesting a role for an observer's vicarious experience in understanding the emotions of others (Niedenthal, 2007; Niedenthal et al, 2017; Winkielman et al., 2015; Wood et al., 2016b). Results of some functional neuroimaging studies specifically suggest that areas within the right somatosensory cortex contribute to the processing of discrete facial expressions. Such studies also find evidence of somatotopy, meaning that regions of primary somatosensory cortex code for features of facial expressions that are most diagnostic of the corresponding emotion, such as the turned-up lip corners indicative of happiness (Kragel & LaBar, 2015; Sprunt & Adolphs, 2019 for discussion).

Inspired by the behavioral and neural evidence indicating that understanding others' emotions is not an encapsulated, inevitable process, the last decade of research in affective science has seen an accumulation of findings suggestive of the roles of sensorimotor simulation, especially mimicry, as well as context and language, in how people come to understand the meaning of facial expression, prosody, and bodily motion, and we discuss these advances in turn.

Mimicry: A Role For Sensorimotor Simulation

William James (1884) believed that the act of emotion perception triggered a partial or complete experience of the same emotion in the observer and that the matching experience informed emotion understanding. Contemporary theorists have also posited such a process, and research findings indicate that observing and understanding others' emotional signals sometimes relies on the same neural processes involved in producing those signals (Wood et al., 2016b). The process by which emotions of others generate a semblance of the same emotion in observers is termed "sensorimotor simulation" because activity in somatosensory and motor systems recruited in the perception of emotions in others is largely overlapping with those that are activated in the production of the corresponding emotion in the self.

Simulation sometimes, although not inevitably, includes the activation of the same muscles in the observer as those activated in the emotionally expressive person. The reproduction of correspondent motor behavior in the self is termed mimicry. Although highly debated in the last decade due to failures to replicate early foundational studies, ample empirical support for three claims needed for a full account of mimicry in emotion understanding is now available. These claims are 1) people mimic others' emotional signals, 2) mimicry of signals of emotion is functionally related to a simulation of the corresponding emotional state, and 3) simulation of the corresponding emotional state informs emotion understanding (see also the later section on affective synchrony).

Evidence of pervasive mimicry of facial expression has accumulated from the initial programmatic work of Dimberg and colleagues (Dimberg, 1988; Dimberg & Thunberg, 1998; Dimberg, Thunberg, & Elmehed, 2000) to more recent findings (Korb et al., 2014; Sato & Yoshikawa, 2007). Facial mimicry may occur even if the initiating expression is not consciously visible (Bornemann, Winkielman, & van der Meer, 2012). For instance, in patients with unilateral damage to the occipital visual cortex, who are thus phenomenally blind in the contralateral visual field, facial mimicry and matching physiological arousal occur when facial signals of emotion are presented to their lesioned hemisphere. Such findings, and those documenting mimicry even when facial expression is task-irrelevant (Cannon, Hayes, & Tipper, 2009), provide converging evidence for spontaneous facial mimicry. People likewise spontaneously mimic emotionally expressive bodies and voices (Bernhold & Giles, 2020; Moody et al., 2018).

Although spontaneous in many cases, mimicry of emotional signals is not inevitable. Numerous moderators of mimicry have been identified (Hess & Fischer, 2014; Hess, 2021; Seibt et al, 2015). These include the nature of the relationship between the expresser and the observer (Bourgeois & Hess, 2008; Weisbuch, & Ambady, 2008), attitudes (Likowski et al, 2008), hormonal states of the perceiver (Korb et al, 2016; Kraaijenvanger, Hofman, & Bos, 2017; Pavarini, et al., 2019) and social context (Philip, Martin, & Clavel, 2018). For instance, in studies by van der Schalk and colleagues (2011), participants mimicked the anger and fear expressions of people who they thought were studying the same discipline at the university as they were (i.e., ingroup members) more than the expressions of people studying a different discipline (i.e., outgroup members). Other work has shown that when people make eye contact, they are more likely to mimic each other's expressions, particularly if the expressions convey affiliative intent (Mauersberger, Kastendieck, & Hess, 2022). Together, these findings are consistent with an implicit socialization account of mimicry according to which mimicry contributes to the process of observational learning about social and cultural norms (Kavanagh & Winkielman, 2016).

That mimicry participates in generating a simulation of the corresponding emotion has been documented as well. The hypothesis is a functional application of the facial feedback hypothesis, according to which afferent feedback from facial muscles to the brain participates in the generation of corresponding feelings. A study by Strack and colleagues became instantly influential because the researchers documented the facial feedback effect using a technique that avoided concerns of experimental demand (Strack, Martin, & Stepper, 1988). In the study, participants holding pencils in the mouth in such a way to activate their smile muscles found mildly amusing cartoons to be funnier than participants who were holding pencils in such a way to minimize the activation of smile muscles. The work suffered from reports of non-replication (Acosta et al., 2016), which might have been due to failures to implement the original methods, or a lack of motivation to find the effect in the first place (Marsh, Rhoads, & Ryan, 2018; Noah, Schul, & Mayo, 2018). Meanwhile, research mapping the neural basis of facial feedback effects (Davis, Senghas, & Ochsner, 2009) and meta-analyses of the behavioral findings (Coles, Larsen, & Lench, 2019) continue to support the conclusion that the effect is small but real. Specifically, when people spontaneously or intentionally contract their facial muscles in ways that correspond to specific facial expressions, their emotions change accordingly (Coles et al., 2020; Critchley, & Nagai, 2012; Kraft & Pressman, 2012). The feedback effect also occurs for vocal signals of emotion (Aucoutu et al., 2016) such that covertly manipulating people's prosody feeds back to affect their emotional state in an emotion-congruent manner. A similar effect is found for mimicking bodily expression of emotion as well (Price, Dieckman, & Harmon-Jones, 2012). Conversely, preventing mimicry is associated with a reduction in the activation of components of the neural bases of emotion (Price & Harmon-Jones, 2015).

Finally, the use of the experienced emotion in processes of emotion understanding also receives support in an accumulating body of work (Keysers & Gazzola, 2009; Keysers, Kaas, & Gazzola, 2010). In a classic study of this question, patients with lesions in the right somatosensory cortex, which supports bodily sensation, showed deficits in their categorization of another person's facially expressed emotion (Adolphs et al., 2000). Other studies support this conclusion (Hennenlotter et al., 2009), and extend it to the categorization of vocal and bodily emotion as well (Kragel & LaBar, 2016; Reed et al., 2020).

There is accumulating and convincing evidence suggesting that in many cases the visual or auditory perception of emotion signals evokes spontaneous mimicry, which participates in the elicitation of a corresponding emotional state in the observer. The emotional state in turn is an input into emotion understanding including processes of perception and categorization. Mimicry is thus an area ripe for further investigation, as theorists make links also to the function of mimicry in non-human primates (Palagi et al., 2020).

Context Effects: Information From The Social And Physical Situation

When people try to understand the emotions of others, they typically look not only to the person sending signals of an emotional state, but also to the context, which can explain why the person's emotions came about in the first place (Houlihan et al., 2022; Barrett & Kensinger, 2010). Consistent with this claim, the neuroscience of emotion understanding points to the importance of neural regions involved in processing semantic knowledge (i.e., the anterior temporal lobe) and in computing causal attribution (i.e., the dorso-medial and ventrolateral prefrontal cortices) for the understanding of emotion (Sprunt & Adolphs, 2017).

A review of studies of the use of "context" in emotion understanding requires a definition of context. In some cases, theorists define context very broadly, including the body and posture of the emotional person, the social and physical environments in which the emotional person is embedded, and states internal to the observer themself. That is, in some accounts of emotion understanding, context includes all non-facial cues, and the emotional signal to be understood is a facial expression (Barrett, Mesquita, & Gendron, 2011; Lecker et al., 2020; see Matsumoto & Hwang, 2010 for principled distinctions among different types of contexts). However, emotions signaled by the face, voice, and body are integrated very early in the perception of facial expression (de Gelder, de Borst, & Watson, 2015). And the signals are all coming from the emotional person. Thus, rather than treating non-face, bodily expressions of emotion as context for understanding facial expressions, we assume that signals from the expresser are integrated into an overall understanding of what the emotion is (Campanella & Belin, 2007; Poyo Solanas et al., 2018; Reschke & Walle, 2021).

In accounting for how an observer arrives at an understanding of what emotion a person is experiencing, theorists also sometimes include in a definition of context features of the observer, such as their access to linguistic labels (e.g., Level 1 of the contextual model of Greenaway, Kalokerinos, & Williams, 2018). We reviewed the effects of labeling on emotion understanding earlier, again distinguishing the application of labels from the concept of context. Here, we define context more narrowly as the local social and physical situation (sometimes called the "scene") as well as the broader culture in which the emotion understanding occurs (e.g., Levels 2 and 3 of the contextual model of Greenaway et al., 2018). These inputs into emotion understanding go beyond informing an observer about what emotion is being experienced to also informing the observer about why the emotion is being experienced (i.e., its cause).

Local Social And Physical Situations

Observers extract the gist of an emotional situation rapidly (Aviezer et al., 2011; Mumenthaler & Sander, 2015; Ngo & Isaacowitz, 2015), sometimes based on low spatial frequency information (Oliva & Schyns, 1997). Indeed, in studies using methods of electroencephalography (EEG), de Gelder and colleagues found that a fearful face presented in a fear context was associated with increased N170 amplitude as compared to a fearful face in a neutral context. The same differences in N170 amplitude were not observed when contexts were presented alone (Righart & de Gelder, 2006), and the findings were replicated using fear and happy contexts (Righart & de Gelder, 2008).

Some classic research on the use of social and physical situation information in emotion understanding concluded that context was an important determinant of attributions for the emotion (Munn, 1940; Goodenough & Tinker, 1931). But subsequent research found that observers largely base emotion understanding on facial expression, ignoring information from the context (e.g., Fernandez-Dols, Sierra, & Ruiz-Belda, 1993; Nakamura et al., 1990). Various methodological features of the early research could explain the inconsistent findings. These features include how context was instantiated (i.e., sometimes by written scenarios, others by visual scenes) and the prototypicality versus ambiguity of the facial expressions (Carroll & Russell, 1996). Just how situational information informs this process has received more research attention in the past decade.

Generally, findings in the burgeoning area of context effects in emotion understanding indicate that the accuracy and speed of facial expression recognition is enhanced when the expression is presented in an emotion-congruent context (Wieser & Brosch, 2012, for review). In contrast, emotion-incongruent contexts can reduce accuracy of the decoding of an emotion expression, even shifting the classification of the expression from one category to another (de Gelder & Van den Stock, 2011, for review). The effect of context on emotion understanding, however, depends on the relative informativeness of the situation and the expression displayed by the emotional person. Ambiguous facial expressions, for example, may require more reference to the situation, and certain prototypical expressions may be informative enough to be understood with little reference to the situation (Hess & Hareli, 2015).

Aviezer and colleagues' "Emotion Seeds" model holds further that context effects in the recognition of facial expression depend on the physical similarity between the observed expression and the expression that would normally be associated with the emotional context (i.e., the "emotional seeds"; Aviezer et al., 2008). For example, because anger and disgust expressions share many morphological features, an anger expression displayed in a disgust situation may be more likely to be perceived as signaling disgust than in an ambiguous situation or one typically associated with anger. Aviezer and colleagues (2008) hold that such effects obtain because context guides the observer's attention to features of an expression that corresponds to the emotion implied by the context.

Cultural Context

As mentioned previously in the chapter, in the discussion of emotion theories, there is ample evidence for cultural relativity in emotion understanding (Crivelli et al., 2016; Cordaro et al., 2018; Gendron et al., 2014a; Jack, Garrod, Yu, Caldara, & Schyns, 2012). And the influences of cultural context have been considered at different levels of processing and with different instantiations of culture.

The way that attention is allocated to facial features varies by the cultural background of the observer (Jack, 2013). Some research suggests that members of Western cultures weigh facial features differently when interpreting facial expressions (Blais et al., 2008; Yuki, Maddux, & Masuda, 2007). Research by Caldara and colleagues shows that whereas people of European descent and East Asians generally rely on the same features to classify facial expressions (particularly the eyes and mouth), and achieve similar levels of recognition accuracy, they use different gaze patterns (Caldara et al., 2010; Millet et al., 2012). Specifically, Westerners of European descent attend to local features while scanning facial expressions. In contrast, East Asians use their attention in a more global information sampling strategy.

The concept of local versus global processing also has been used to interpret findings suggesting that East Asians rely more on the social context relative to facial expressions in understanding the emotions of an expresser than do Westerners. Specifically, some studies show that the facial expressions of people surrounding a target person affect the emotion perceived in the target by East Asians more than they affect the emotion pereiceved by Westerners (Masuda et al., 2008; Masuda et al., 2012). Recent studies using EEG have drawn a similar conclusion. In one demonstration, the brain activity of mainland Chinese participants revealed that they prioritized a scene's social context in processing a facial expression more than did participants from the United States (Pugh, Choo, Leshin, Lindquist, & Nam, 2022).

While many studies of the role of cultural context in emotion understanding instantiate culture in terms of the nationality of the observer, others focus on culture as defined by broader, socioecological factors (Kashima et al., 2020; Oishi, 2014). These factors refer to aspects of the long-term physical and social environments that produce adaptations that were sustained by cultural evolution (Sng et al., 2018). A socioecological factor that is a robust predictor of emotional expression, experience, and regulation has been termed "historical heterogeneity" or "ancestral diversity" (Niedenthal, Rychlowska & Wood, 2017; Niedenthal et al., 2018). These synonymous terms refer to the extent to which a present-day country's population derived from many different countries (termed source countries) versus very few countries over migratory history. Canada and Argentina, for instance, host populations that derived from many source countries, while Finland and China host populations that have derived from far fewer other countries of the world.

Niedenthal and colleagues propose that in ancestrally diverse countries, people needed to rely on perceived facial expressions and other nonverbal signals of emotion to predict the behavior of an acquaintance or stranger because the social norms are more varied in such countries, and common language was initially not shared (Niedenthal et al., 2018; Niedenthal et al., 2019). The strategy would then be preserved in cultural display rules favoring emotional expressiveness. The same pressure to use nonverbal signals of emotion to communicate would be far less in countries low in ancestral diversity, and findings support this hypothesis (Rychlowska et al., 2015). By the same reasoning, the need to communicate nonverbally also would be reflected in the clarity of produced facial expressions such that individuals from ancestrally diverse countries might make expressions that result in higher recognition accuracy across cultures (Wood, Rychlowska, & Niedenthal, 2016b).

Ancestral diversity is related to the construct of normative tightness, or the extent to which social norms are prescriptive and consensual, such that social norms tend to be looser in ancestrally diverse countries (Niedenthal et al., 2019; Gelfand, 20253). If there is high variability of norms across and within situations (i.e., norms are loose), it is likely that ancestral diversity is associated with less attention to context in interpreting facial expressions. That is, in such cultures, the context does not provide a robust basis for predictions about another person's emotions because consensus about which emotions occur in which situations is relatively low. In a study by Zhao and colleagues, participants who were prevented from communicating with spoken language tended to synchronize their facial expressions during emotionally evocative interactions more than those who were allowed to communicate with spoken language (Zhao, Wood, Mutlu, & Niedenthal, 2022). In other words, synchronizing emotional expressions—an an efficient way to understand and predict another's emotions (see later section on affective synchrony)—may substitute for the use of contextual cues to determine a likely emotional response in some cases or in some cultures.

Emotion Labels: Influences Of Concepts

In addition to a repertoire of non-verbal signals of emotion, people also have an extensive vocabulary of words for emotions. The use of verbal labels for emotions has important effects on all stages of understanding the emotions of others, in addition to the understanding and regulation of one's own states as we discussed in the previous section. The effects of verbal labeling on understanding the emotions of other people include 1) effects on processing accuracy, and 2) assimilative biases toward an emotion category or affective dimension.

Studies addressing accuracy have harnessed an effect called "semantic satiation" in documenting a role for concept labels in accurate emotion understanding. Semantic satiation refers to the fact that when a word is repeatedly named aloud, access to the word's meaning is temporarily inhibited (Smith & Klein, 1990). Inhibiting access to emotion word meaning has been shown to cause reductions in facial expression recognition accuracy. In one study, Lindquist and colleagues found that semantic satiation was associated with worse performance on a task in which participants indicated whether two faces were the same or different (Lindquist et al., 2006). And Gendron and colleagues showed that when access to the word *anger* was inhibited during the encoding of a scowling face, that expression no longer served as an effective prime to the same expression encoded with uninhibited access to the word (Gendron et al., 2012). In other words, scowls were perceived differently depending on whether the observer could or could not apply a concept label to the expression. These findings are consistent with others showing that people with semantic deficits due to neurodegeneration in language processing areas of the brain, such as the anterior temporal lobe, also have deficits in emotion understanding (e.g., Calabria et al., 2009) and that people with alexithymia (i.e., compromised emotion labeling) have poorer emotion recognition when not provided with appropriate labels (Ihme et al., 2014; Nook, Lindquist, & Zaki, 2015). Other recent studies have examined the effects of access to, rather than inhibition of, emotion labels. For instance, Nook and colleagues (2015) showed that providing participants with labels for the emotion displayed in a facial expression increased efficiency and sensitivity in recognizing the emotion.

The influence of labels on the perception of facial expression is particularly evident when expressions are ambiguous. Halberstadt and Niedenthal (2001) showed participants computer-presented facial expressions that were approximately equal blends of anger and happiness. The images were accompanied by a disambiguating emotion label—either "angry" or "happy." Later, participants saw morph videos in which the initially seen faces changed gradually from clear anger to clear happiness and were instructed to find the exact image of each face they had seen previously. Faces that had been paired with angry labels were remembered as angrier than faces paired with happy labels. Subsequent research showed that memory for the labels was unrelated to the magnitude of the biasing effect, suggesting that the effect of the label occurred at the time of encoding and was not based on later memory for the label, per se. Consistent with this interpretation, Halberstadt and colleagues (2009) demonstrated that when participants saw ambiguous expressions with specific emotion labels they later mimicked the same ambiguous expressions using muscles corresponding to the expression named by the label. That is, participants who had seen an ambiguous face called "angry" contracted their corrugator muscles more than did participants who had seen the same face called "happy" (Halberstadt et al., 2009).

Generally, it appears that using a label for a facial expression provides the observer with semantic and perceptual information that is specific and categorical and therefore useful for drawing inferences about the cause of the denoted internal state (Lupyan & Clark, 2015). Labels refer to concepts that guide attention, judgment, and attribution and thus serve to influence not only the perceptual representation of the facial expression but subsequent cognition and behavior (Halberstadt et al., 2009; Nook et al., 2015). Indeed, merely having a label—even a nonsense one—can influence emotion perception because a categorical structure is applied to the percept (e.g., Ruba, Meltzoff, & Repacholi, 2020).

In summary, people perceive emotional signals via many channels including the face, voice, and body, and in specific dynamic features of all three. With their faces, voices, and bodies, observers can mirror the displays of others and use feedback from their bodies as input for emotion understanding. From the situation and cultural context, observers of emotional displays can arrive at understandings not only of what emotion is being experienced but also why. Finally, language can be used to apply concepts to percepts such that the structure and meaning of other's emotional displays become represented for verbal communication.

Affective Synchrony

Because humans are social beings, many of their goals—and therefore, emotions—are interdependent (Elfenbein, 2014; Goldenberg et al., 2017). People often find themselves in emotion-eliciting situations with other people: A threat to one person is a threat to another, and an opportunity for others is an opportunity for the person. People experience vicarious emotions on behalf of people to whom they are close (López-Solà et al., 2020) and on behalf of the groups to which they belong (Smith & Mackie, 2015). This tendency to experience the emotions of close others is a part of empathy (Zaki, 2014).

People also match others' emotions even if they are not in interdependent relationships with them. Other people are useful sources of information, so when one person is uncertain about how to appraise a situation or how to respond, they can reference and adopt the emotions of people around them (Clément & Dukes, 2017); this is sometimes known as "emotion contagion" (Hatfield et al., 2014). Contagion can be direct—one person's emotion directly induces a similar emotion in another—and sometimes contagion occurs because one person adopts the emotion appraisal of the other (Parkinson, 2011).

The ways in which one's emotions covary with the emotions of people around them are collectively known as "affective synchrony," a topic that has exploded in popularity in the last few decades (for a review, see Wood et al., 2021; West & Mendes, 2023). In this section, we sample from studies demonstrating affective synchrony. We then put our functionalist hats back on and discuss why affective synchrony is (sometimes) adaptive.

When two or more people's emotions synchronize, there are three possible explanations: they are responding to a shared situation, they are experiencing emotion contagion, or they are using each other as references for how to feel about the situation. First, two or more people's emotions may synchronize simply because they are experiencing a shared emotion-eliciting context (Elfenbein, 2014). But even though two people's emotions may be similar because of a third variable—the situation—their mutual presence and relationship to each other can still moderate their levels of affective synchrony. Partners are more likely to synchronize their feelings during a shared experience when they are friends (versus strangers), when they are visible to each other, and when they can socially reference each other (Bruder et al., 2012).

Awareness of emotion synchrony, in turn, can increase feelings of social connection. For instance, when previously unacquainted dyads watched four hours of a TV show together, the partners who had synchronized emotional responses to the TV characters felt more socially connected (Cheong et al., 2020). Although emotional synchrony was not manipulated in this study—meaning the relationship between social connection and synchrony is only correlational—other work supports the claim that synchrony can cause increases in perceived social connection. When researchers manipulated the synchrony of virtual reality characters' movements and the movements of participants, the synchrony condition led participants to feel closer to the characters than in the non-synchrony condition (Tarr et al., 2018).

People are motivated to experience emotional events with others, as opposed to alone, even though it does not necessarily increase the hedonic value of the experience (Gump & Kulik, 1997; Jolly et al., 2019). Knowing that another person is experiencing the same emotions as oneself increases the subjective intensity of the emotion, be it fear, happiness, or sadness (Shteynberg et al., 2014). Sharing emotions with others also fosters a sense of togetherness, shared goals, and increased capacity—a single person does not have to handle the emotion-eliciting event by themselves (Gonzalez et al., 2021). Having a shared emotional response also reduces stress: When participants who were engaging in a threatening task knew that another person felt similarly threatened, it reduced their cortisol levels (Townsend et al., 2014). Experiencing the same emotion as an entire group of people—for instance, during a protest march—strengthens participants' sense of collective identity, social integration, and sense of self-efficacy (Páez et al., 2015).

The second reason people's emotions synchronize is direct emotion contagion: An emotion in one person triggers a similar emotional state in the other (Elfenbein, 2014). Through this mechanism, perceiving an emotion in another person elicits a similar emotion in oneself. For instance, some forms of laughter are contagious, spreading not only the behavior of laughing but also the underlying positive affect (Bachorowski & Owren, 2001). One person can catch another's laughter even if they do not know what caused the first person's laughter. More generally, extensive evidence reveals how frequently people mimic each other's nonverbal emotion displays, as we discussed in our earlier section on emotion understanding (e.g., Arnold & Winkielman, 2020; Chartrand & Lakin, 2013; Salazar Kämpf et al., 2017). It is not just nonverbal communication that can mediate emotion contagion; conversation also aligns emotions. During storytelling, listeners' and speakers' feeling states often synchronize, which is reflected in the alignment of their neural activity (Kang & Wheatley, 2017; Smirnov et al., 2019).

Emotions are more likely to spread within interdependent relationships (i.e., when people share, or believe they share identities or outcomes). A friend's happiness is cause for one's own happiness (Howell et al., 2017). This interdependence can be created rapidly in the lab. When strangers were told they were similar to each other and then one person was placed in a stressful situation, the other person experienced vicarious distress (Cwir et al., 2011; see also West et al., 2017). More recent work found that this dyadic coherence can come at a physiological cost: Greater physiological assimilation was associated with less within-person stability (Thorson & West, 2018), and stability, as we discussed earlier, is associated with greater well-being (Hardy & Segerstrom, 2017; Howell et al., 2017). Thus, individuals who are more vulnerable to social influence may pay for this putative improvement in social connection with their own physical health.

Interestingly, successful cooperation and interdependence demand that partners help regulate each other's emotions rather than simply mirroring them. Interpersonal regulation sometimes requires emotional divergence rather than synchrony: When one person is stressed, the other person must calmly regulate them (Butler, 2015; Corner et al., 2019). Thus, even among satisfied romantic partners, affective synchrony is not a stable attribute, and many couples reliably demonstrate emotional complementarity rather than synchrony (Hilpert et al., 2022; Sels et al., 2020). Probably the "best" dynamic is flexibility and the ability to match a partner's emotions only when it serves individual and dyadic goals rather than being yanked about by their emotional whims. Indeed, previously unacquainted dyads in one study synchronized their smiles but not their frowns (Riehle et al., 2017), and the success of newly formed teams in another study was positively correlated with smile synchrony and negatively with sympathetic nervous system activity (Mønster et al., 2016).

We have discussed how affective synchrony can arise from both a shared context and through direct emotion transmission. A third potential cause of affective synchrony is the transmission of emotion appraisals via social referencing (Parkinson, 2011). People learn how to feel about novel or ambiguous situations by referencing the emotional responses of others (Bruder et al., 2014; Walle et al., 2017). Social referencing is often studied in young children, but adults also learn how to feel about situations based on cues from others (Parkinson et al., 2012). In the short term, adopting the other person's emotional response leads to affective synchrony, but in the long run, it can alter one's emotional response tendencies as they learn how to appraise similar situations (Pärnamets et al., 2020). College roommates who were assigned by their college to live together had more similar emotional responses to movie clips than participants who were not roommates (Anderson et al., 2003). This suggests that, over the school year, they shaped each other's emotional response tendencies.

Learning others' emotional responses to events does not require a complex theory of mind: Rats demonstrate social referencing, becoming afraid of stimuli that cause other rats to freeze (Cruz et al., 2020). All that is required is that, on a previous occasion, they have experienced the fear-inducing stimulus alongside another rat to learn the association between another rat freezing and their own fear state.

Functions Of Affective Synchrony

It is apparent that people often match the emotions of those around them, and this is either because of a shared context, through direct contagion or social referencing. We have hinted at some of the functions of affective synchrony, but here we review them more explicitly. Affective synchrony makes interactions more predictable, can strengthen social bonds, and lays the groundwork for interpersonal emotion regulation.

First, synchrony, including observable forms of affective synchrony, makes an interaction more predictable and reduces the degrees of freedom—the number of uncorrelated dimensions—within the dyad (Koban et al., 2019; Wood et al., 2021). This facilitates mutual understanding, cooperation, and joint action (Mitkidis et al., 2015; Valdesolo et al., 2010). Knowing that one's emotional response to a situation aligns with another person's, as we have reviewed, provides convergent evidence that the response is warranted. When a person's emotional response conflicts with someone else's, the prediction error requires either a reappraisal of the eliciting stimulus or a reevaluation of whether the partners indeed share the same goals. So long as partners match in their emotional responses to stimuli, the interaction will be more fluent and predictable.

Second, and partly because of the first function, affective synchrony can increase feelings of interpersonal closeness and similarity. By making the interaction predictable and fluent, affective synchrony makes an interaction enjoyable. In a series of studies, consumers interacting with sales associates were more satisfied with the exchange if the sales associate matched their level of nonverbal expressivity because it made the interaction feel more effortless (Kidwell et al., 2020).

Further, shared emotional responses is a cue that people have shared goals, attitudes, and identities. Anything that enhances feelings of similarity has the potential to bring people together. Evidence supports the idea that behavioral and communicative synchrony, including nonverbal emotion displays, is correlated with, or even causes, positive social outcomes (e.g., Lang et al., 2017; Valdesolo et al., 2010). Interestingly, the impact of social relationships on well-being is stronger for people who are more susceptible to emotion contagion and physiological synchrony (Mayo et al., 2022).

However, the story is more complicated than synchrony always increasing social connection. As we have already suggested, the benefits of synchrony depend on the relationship and the context. A comparison of relationship types found suggestive evidence for greater physiological synchrony among strangers compared to friends and romantic partners (Bizzego et al., 2020). Another study tracked contagion of self-reported emotions between strangers across six interactions (Tsang et al., under review). As the partners grew closer over time, they showed less emotion contagion. Thus, it may be that dyads effortfully cultivate affective synchrony to reach the desired level of interpersonal closeness—a task that is more imperative early in a relationship.

Atwood and colleagues (2020) have challenged the body of research supporting the claim that synchrony facilitates interpersonal closeness, providing compelling evidence that the effects are driven by participants' expectations that synchrony has such an effect. But this *is* the mechanism, not a flaw in the research. The rats described earlier only socially referenced other rats' freezing behavior if they had learned to associate others' freezing with their own fear (Cruz et al., 2020). Likewise, humans who feel closer to those with whom they synchronize may do so because they have learned that synchrony is a cue of interpersonal similarity, which is a good predictor of future closeness (McPherson et al., 2001).

Finally, synchrony between two or more people means that they each have a direct channel through which to influence each other's emotion states. Once the rats' freezing behavior becomes entrained through conditioning, one rat can upregulate (or downregulate) another's distress by freezing (or not freezing). Once friends discover they have a shared taste in books and movies, they may be compelled to like something they might not otherwise like because their friend's attitude has previously been such a strong predictor of their own. Part of this may be a desire to conform, but part of it is social referencing. Strategic use of synchrony to co-regulate is apparent in parent-infant interactions. Parents regularly increase or decrease infants' arousal levels with their voices, bodies, and faces, and such embodied expressivity predicts the child's future attachment style (Shai & Belsky, 2017). This only works if the infant is able to match the parent's expressed emotion state. Some—but not all—romantic couples show similar co-regulation patterns (Hilpert et al., 2022; Sels et al., 2020).

As work on affective synchrony continues to expand, thanks in part to advances in measurement and statistical estimation of synchrony, we will continue to learn about all the ways that emotions are an inherently shared and interpersonal process. To understand the complex dynamics between individual-level goals and emotions and dyad- and group-level goals and emotions, affective science will have to use tools such as dynamical systems to model the complexity and richness of social interactions (e.g., Butler, 2011).

FUTURE DIRECTIONS IN AFFECTIVE SCIENCE

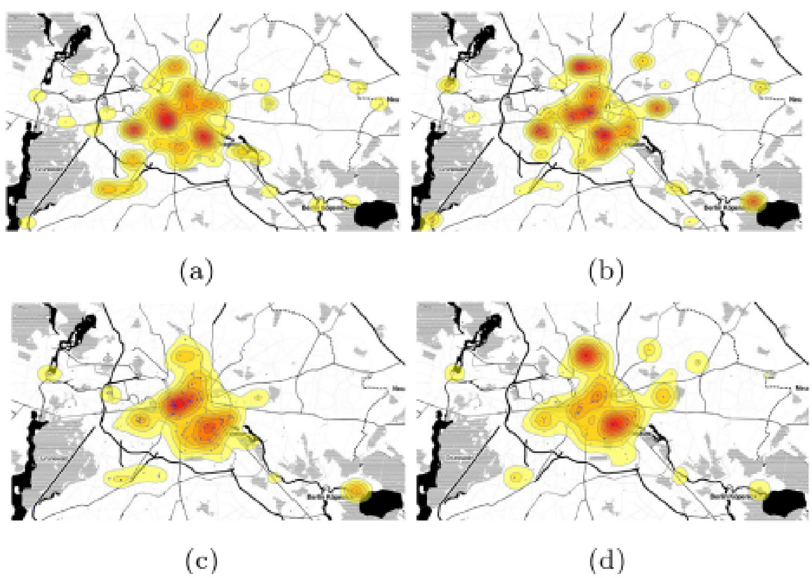
As is clear from the present synthesis and analysis, the future of affective science is bright. This is partly due to the availability of new tools for the assessment of emotions online, in the wild, and with high spatial and temporal precision. Just as novel technologies in affective science have advanced theory in affective science, in the coming decade we expect other new methods to drive novel contributions as well. Two general areas may be fruitful for future research, including methods in big data science, particularly the use of geo-locating data, and innovation in the design of robots and other artificial social agents (Gray & Waytz, 2025).

Big Data And Geo-Location

As our analysis of the influence of context on the perception of emotion suggests, emotions are not evenly distributed in space. Access to big data and the development and availability of information and communications technologies, especially the use of geographical information science (GIS), can be used to derive novel hypotheses about where and when people experience emotions (Huang et al., 2020; Liu et al., 2015; Ye, Huang, & Li, 2016; Janowicz et al., 2019; Li et al., 2021; Zhang, Zhu, & Wu, 2019).

The existence of millions of geo-tagged images uploaded to social networking websites has facilitated the mapping of emotions, as represented by facial expression or by natural language processing, within and across cities of the world. Fig 6 illustrates the dispersion of uploaded photographs expressing anger, disgust, happiness, and surprise across the city of Berlin (Ashkezari-Toussi et al., 2019). The same study compared emotions across the cities of Athens, Beijing, Berlin, Brussels, Buenos Aires, Copenhagen, Helsinki, Melbourn, New York, Ottawa, Paris, and Prague.

***Figure 6*: The Concentration of Different Emotions, as Represented by Facial Expression Images, in Berlin, Germany**



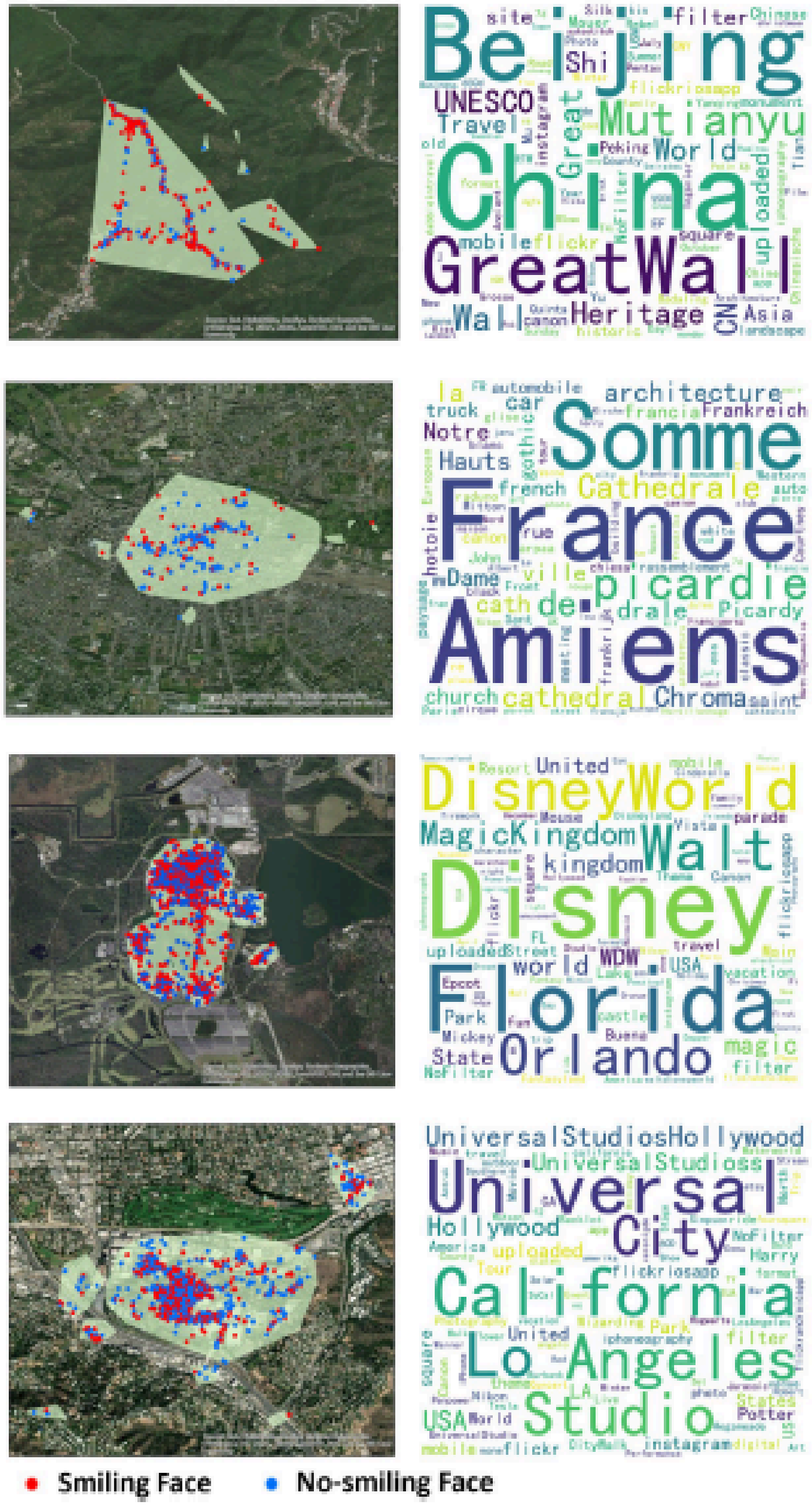
Note: a) anger, b) disgust, c) happiness and d) surprise (from Ashkezari-Toussi et al., 2019).

As another example, Kang and colleagues (2019) developed a novel method for extracting and characterizing happiness from facial expressions found on the photo management and sharing application called Flickr. The expressions were geo-tagged and were associated with 80 different tourist sites across the world (Fig 7 for illustration). Using these data, the researchers investigated the relationship between the expression of happiness in different environmental contexts such as the presence of water or natural landscapes and reported a ranking of the happiest tourist sites. Such findings and others have implications for business, development, and policy. But when paired with theory in affective science, such methods can be leveraged to study more basic processes, linking not only physical aspects of spaces to emotion, but also social, climatic, and historic ones.

These methods will also inspire new research on emotion in large groups (either virtual or in-person) (e.g., Del Vicario et al., 2016; Goldenberg & Gross, 2020). For instance, the spatial distribution, location, and contagion of response during exceptional events such as the COVID-19 pandemic and hurricanes, and even divisive and sometimes violent times in politics, can be modeled to suggest hypotheses about emotional responses among group members in time and space, and consequences for behavior (e.g., Brady, Crockett, & Van Bavel, 2020; Brady et al., 2017; Kryvasheyeu et al., 2015). This is particularly important when investigating large group behavior that requires coordination such as evacuation from natural and other disasters (e.g., Lwowski, Rad, & Choo, 2018).

Of course, the initial studies just reviewed only hint at where emotions are felt in the world because they rely on highly curated photographs of facial expressions and suppose that the expressions provide good evidence for the experience of emotion. In future work, researchers will do well to associate momentary assessments of emotional states as well as physiological states assessed by ambulatory devices to further test hypotheses about the contexts that give rise to emotions such as happiness and fear, as well as feelings of belonging.

***Figure 7*: Locations of Photos of Smiling (Red) and Nonsmiling (Blue) People Taken at Four Tourist Destinations**



Note: From top to bottom: the Great Wall in China, Amiens Cathedral in France, Disneyworld Magic Kingdom Park in Florida, and Universal Studios Hollywood in California. From Kang and others (2019).

Emotional Robots And Artificial Social Agents

Artificial social agents—technologies that interact with users via human norms of communication such as Apple's Siri and Amazon's Echo voice assistants—offer the promise of significant societal benefits. They already assist people in day-to-day activities, from shopping to reviewing health plans, and can be used to promote independent living in healthy aging. The accelerating use of social agents in consumer technology also highlights the broad reach of future applications. Recent data on consumer electronics show that one in four people in the U.S. has a Siri personal assistant and one in four households has a home assistant manufactured by Amazon or Google. While these technologies are ubiquitous, their success and societal impact will be limited if they are not designed to engage with their users at an emotional level. How can an iPhone, an autonomous vehicle, a learning-companion robot, or an exercise coach engage emotionally with its user?

Successfully "emotional" robots and artificial social agents must be able to a) understand the emotion signals of humans, b) use information from those signals to update their own behavior (e.g., recognize a frustrated human and seek ways to remedy the situation), and c) produce believable and understandable signals of their own. The first task will not be truly solvable until affective scientists achieve high accuracy in categorizing the meaning of naturally occurring emotion signals. As implied in the section on emotion perception, this will likely require integrating information from the context and prior encounters with the human in question. Gratch (2008) argues that the idea that emotion signals are "readouts" of underlying emotion states, a claim made by basic emotions theory, will not serve this endeavor. Instead, emotion signals must be treated as communicative acts designed to influence social (in this case, robotic) partners. The second task requires an algorithmic understanding of how emotion signals map onto underlying goals and intentions. Not surprisingly, appraisal theory is playing a central role in this endeavor (e.g., Kim & Kwon, 2010).

With regard to the third task—having robots produce believable emotion signals–the past decade has witnessed advances in on how robots' facial-expressive features (e.g., eye aperture and shape, eyebrows), color, and head gestures (e.g., nodding) can communicate emotion successfully with humans (Cohen, Looije, & Neerincx, 2014; Lakatos et al., 2014; Lin et al., 2022; Löffler, Schmidt, & Tscharn, 2018; Rosenthal-von der Pütten, Krämer, & Herrmann, 2018; Song & Yamada, 2017; Tsiourti et al., 2017).

While robots with newly-developed emotion expression features manage to avoid the "uncanny valley" —the design space between cartoonishly unrealistic agents and agents that are *almost*, but not quite, human–they have a long way to go before interactions with them will feel as intuitive as they do with another human. The design of robots and other social agents still fails to implement affective synchrony, and thus experiences of successful prediction, emotional self-agency, and a state of effective communication and affiliation that are facilitated by the achievement of some forms of affective synchrony are not present in human-computer interaction. However, features that support affective synchrony can be imagined for social agent design in the coming years as well (Lorenz, Weiss, & Hirche, 2016).

The fact that humans perceive social agents as emotionally unresponsive severely limits the use and societal benefits of such technologies. Emotional engagement is most vital for individuals new to the technology, who often come from disadvantaged populations such as the elderly, children, and individuals with disabilities. The elderly, for instance, can find simple robots such as the Roomba floor cleaning assistant, to be frightening rather than helpful (e.g., Marchetti et al., 2022). When endowed with emotional responsiveness, smart devices could offer more rewarding interactions and thereby better achieve their potential.

CONCLUSION

Since a chapter on the topic was last published in *The Handbook of Social Psychology* (Keltner & Lerner, 2010) research on emotion has evolved in new and interdisciplinary ways. Some part of the progress is attributable to innovation in data access, measurement, and analytic methods. But theorizing has also advanced in exciting and synergistic ways. We now find more points of contact, or potential points of contact, between theoretical approaches, new ways of integrating insights from one topic within affective science to another, and reasons to expect interactions between emotion processes not previously imagined. Notably, emotions are social and involve the understanding and regulation of other's emotions (Beckes & Coan, 2011; Coan & Sbarra, 2015; Kappas, 2013; Mesquita & Albert, 2007; Reeck, Ames, & Ochsner, 2016). Thus, emotions attract an individual into a social interaction, engage the individual in an interaction of a particular tone or length, become intensified or inhibited during the interaction, and involve the co-regulation of elicited emotions. Our hope is that the insights conveyed in the present chapter fosters new approaches to studying dyadic and group emotion experience, and especially experiences of dyads and groups in real-world contexts. What happens "in-the-wild," emotionally speaking, will most certainly be revealed by research in affective science over the next decade.

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ENDNOTES

1. Barrett (2012) writes, “emotions would not exist in animals who do not possess ontologically subjective emotion categories” (p. 11). ↑