Neuroscience and Biobehavioral Reviews 107 (2019) 215–228

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review article

Conserved features of anterior cingulate networks support observational learning across species

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ARTICLE INFO

Keywords:
Social learning
Vicarious learning
Empathy
Social cues
Social transmission
Social dominance
Fear learning
Fear conditioning by proxy
Amygdala
Anterior cingulate cortex
Prefrontal cortex
Rodents
Primates
Facial expression

ABSTRACT

The ability to observe, interpret, and learn behaviors and emotions from conspecifics is crucial for survival, as it bypasses direct experience to avoid potential dangers and maximize rewards and benefits. The anterior cingulate cortex (ACC) and its extended neural connections are emerging as important networks for the detection, encoding, and interpretation of social signals during observational learning. Evidence from rodents and primates (including humans) suggests that the social interactions that occur while individuals are exposed to important information in their environment lead to transfer of information across individuals that promotes adaptive behaviors in the form of either social affiliation, alertness, or avoidance. In this review, we first showcase anatomical and functional connections of the ACC in primates and rodents that contribute to the perception of social signals. We then discuss species-specific cognitive and social functions of the ACC and differentiate between neural activity related to 'self' and 'other', extending into the difference between social signals received and processed by the self, versus observing social interactions among others. We next describe behavioral and neural events that contribute to social learning via observation. Finally, we discuss some of the neural mechanisms underlying observational learning within the ACC and its extended network.

1. Introduction

The ability to monitor behaviors in others and to learn by observation to maximize rewards and avoid dangers is a fundamental higher-level cognitive function shared by multiple species (Bastiaansen et al., 2009; Panksepp and Lahvis, 2011; Preston and de Waal, 2002). Findings from rodents, non-human primates, and humans provide evidence that exposure to behavioral cues during natural social interactions (e.g., witnessing aggression towards a social partner and responding with protective behaviors), initiates a learning process that connects the observed behaviors to outcomes (e.g., social bonding). During this process, the perceived social signals are integrated to produce adaptive behaviors. This phenomenon has been referred in the literature as social or observational learning. For example, during observational fear learning, exposure of a mouse or rat to cues that signal threat to others, including the smell, sight, and sound of a distressed conspecific, induces fear responses (Allsop et al., 2018; Carrillo et al., 2015; Jeon and Shin, 2011). Likewise, fear to snakes in demonstrator monkeys induces fear of snakes in laboratory-reared monkeys (Cook and Mineka, 1989; Mineka et al., 1984), and fear of a "visual cliff" (a graphical illusion painted on a flat floor) in mothers inhibits human babies from crawling over it (Gibson and Walk, 1960). These findings highlight that the ability of learning through observation is highly conserved across species.

Social cues can also modulate behavior via a non-associative process. Fear learning, for example, can be either attenuated or enhanced by the presence of social cues. The presence of a social partner or a familiar conspecific signals safety and can attenuate the acquisition,

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https://doi.org/10.1016/j.neubiorev.2019.09.009
Received 14 February 2019; Received in revised form 27 August 2019; Accepted 6 September 2019
Available online 08 September 2019
0149-7634/

consolidation, and expression of fear memories, a phenomenon known as social buffering of aversive responses (Beauchamp, 2008; Davitz and Mason, 1955; Guzmán et al., 2009; Harb and Taylor, 2015; Hennessy et al., 2009; Howell et al., 2017; Kikusui et al., 2006; Kiyokawa, 2017; Morrison and Hill, 1967). Social cues can also sensitize the brain and enhance fear learning reinforced by non-social unconditional stimuli at a later moment (Ito et al., 2015; Knapska et al., 2010). Likewise, vicarious social defeat can cause chronic anhedonia by altering the affective state of the observer (Iñiguez et al., 2018; Warren et al., 2013). The mechanisms by which the brain perceives, processes, and learns social cues to translate the learned information into adaptive behaviors are not well understood, although multiple processes have been implicated. These processes include the recognition of emotional facial cues in others (*reviewed by* Niedenthal and Brauer, 2012), mimicry or imitation (*reviewed by* Kavanagh and Winkielman, 2016), heightened attention to others (*reviewed by* Miklósi, 1999; Oláh et al., 2016), theory of mind (*reviewed by* Emery and Clayton, 2009), and the vicarious motivational state when observing the actions of others (*reviewed by* Apps et al., 2016).

Recent work in observational learning has started to home in on its neurobiological underpinning. For instance, studies in non-human primates (Apps et al., 2013; Chang et al., 2013), rodents (Allsop et al., 2018; Jeon et al., 2010; Kim et al., 2012), and humans (Lockwood et al., 2015; Olsson and Phelps, 2007) ascribe the anterior cingulate cortex (ACC) an important role in observational learning. Such attribution to the ACC comes by virtue of distinct neural specialization for processing social information that is supported by a vast network of connections to other structures with known social-cognitive functions.

Although many findings implicate the ACC-centered circuits in an organism's ability to learn socially transmitted information, the mechanisms by which neurons in these circuits compute information about others to guide learning and produce adaptive behavior are not completely understood. Likewise, little is known about the behavioral factors that promote social transmission of information, and the cellular and synaptic mechanisms involved. By bringing together insights from anatomical, neurophysiological, and behavioral studies across species, in this review we aim to examine the critical components of a larger ACC network to help formulate new mechanistic hypotheses regarding behavioral factors and synaptic processes by which evaluating and computing socially salient information about others can be tied to ACC circuits.

2. Brain regions constituting the ACC

The cortical areas of the ACC are divided in phylogenetically older agranular or dysgranular areas, that lack or contain a rather faint internal granular cortical layer 4 and granular areas that are present only in humans and non-human primates (Barbas and García-Cabezas, 2016; Carlén, 2017; Fuster, 2015). Despite the lack of full homology between the ACC of primates and other mammalian species including rodents, this area performs, in multiple species, overlapping cognitive functions, such as emotional regulation, motivational drives, and social cognition (Apps et al., 2016; Bicks et al., 2015; Fuster, 2001; Paus, 2001; Watanabe, 2017; Laubach et al., 2018). ACC regions form an arc around the genu of the corpus callosum and face towards the medial wall of the frontal lobes. In primates, ACC regions generally include Brodmann area 32 (often referred to as the dorsal anterior cingulate cortex, dACC), area 24 (often referred to as the ventral anterior cingulate cortex, vACC), and area 25 (often referred to as the subgenual anterior cingulate cortex, sACC). In addition, these ACC areas have been further subdivided into 32′, 24a, 24b, and 24c, based on relative location and cytoarchitectonic features (i.e., cell composition, size, spacing, density, and lamination). Fig. 1 illustrates the relative location of these ACC subdivisions.

Frontal cortices in rodents are evolutionarily less developed than in primates. However, despite much debate (Carlén, 2017; Laubach et al., 2018), distinct regions of the medial prefrontal cortex in rodents exhibit anatomical and functional features that resemble those observed in the primate ACC, and have been therefore recently redefined using the Brodmann nomenclature scheme (i.e., areas 32, 24, and 25; Vogt and Paxinos, 2014). Such rodent ACC areas substitute the areas previously known as the cingulate area 1 (Cg1, redefined to area 24b), cingulate area 2 (Cg2, redefined to area 24a), prelimbic cortex (PL, redefined to area 32), and infralimbic cortex (IL, redefined to area 25) (Paxinos and Franklin, 2019, 2004; Paxinos and Watson, 2014, 1998). This alternative Brodmann-based naming scheme provides great opportunities for neuroscientists to become more consistent with nomenclature, as well as with comparisons of ACC function across species.

While areas 24/Cg and 32/PL share many similarities in their pattern of anatomical connectivity with other brain regions, area 25/IL exhibits input and output patterns that are particularly distinct when compared to areas 24/Cg and 32/PL (Gabbott et al., 2005; Heilbronner et al., 2016; Hoover and Vertes, 2007; Morecraft et al., 2012; Vertes, 2004). Furthermore, area 25/IL exhibits functional roles that are quite distinct from the functional roles of areas 24/Cg and 32/PL (e.g., Balleine and O'Doherty, 2010; Burgos-Robles et al., 2013, 2009, Burgos-Robles et al., 2007; Peters et al., 2009; Wallis et al., 2017). For these reasons, in this review we do not intend to highlight the differences across these regions, but rather we intend to discuss a set of studies that have highlighted social functions in ACC areas, and intend to establish some ideas pertaining to how the ACC in general perceives and integrates social signals to facilitate observational learning. Yet, we recognize that the larger majority of the studies we discuss mostly examined areas 24/Cg and 32/PL, unless otherwise indicated.

Fig. 2 reviews some of the anatomical connections of areas 24/Cg and 32/PL in rodents, with layer specificity, and categorizes them into broad functional groups. Their specialized function and contribution to the processing of complex social signals are discussed elsewhere in this review.

3. The anatomical and functional connections of the rodent and primate ACC; homologies and unique features

Different subdivisions of the ACC are bidirectionally connected to distinct nuclear groups of the amygdala (Amaral and Insausti, 1992; Morecraft et al., 2012), whose function in mediating defensive behaviors is highly conserved among species including rodents and humans (Terburg et al., 2018). In primates, projections originating from basolateral nuclei of the amygdala target both the superficial layers and the deep layers of areas 24a and 24b (Morecraft et al., 2007; Morecraft and Van Hoesen, 1998). To clarify the amygdala nomenclature, the basolateral nuclei refer to the cortical nuclei of the amygdala that include the lateral, basal, and accessory basal nuclei in primates, or the lateral, basolateral, and basomedial counterparts in rodents, respectively (LeDoux, 2007). The pattern of connectivity from the amygdala to the cingulate cortex is truly exceptional as cortical projections originating in the amygdala typically terminate in the superficial layers of the cortex (Freese and Amaral, 2006). The amygdalo-cingulate projections that terminate in the deep layers of cingulate cortex where the motor neurons reside, create a direct pathway for limbic inputs from the amygdala to be translated into motor behaviors (Morecraft et al., 2007). In rodents, the amygdalo-cingulate projections also originate from the basal (basolateral) and accessory basal (basomedial) nuclei and to a small extent in the lateral nucleus (Reppucci and Petrovich, 2016). The rich, and relatively punctate connectivity of the ACC with the basolateral nuclei of the amygdala allows, in principle, the presence of multiple parallel loops that may carry out different functions.

The ACC receives other inputs from numerous areas that respond to social signals. Social signals including faces and bodies, certain types of touch, vocalization, certain odors, gestures and postures, biological motion, etc., arrive to the ACC from multisensory association areas, such as the superior temporal sulcus and the temporo-parietal area

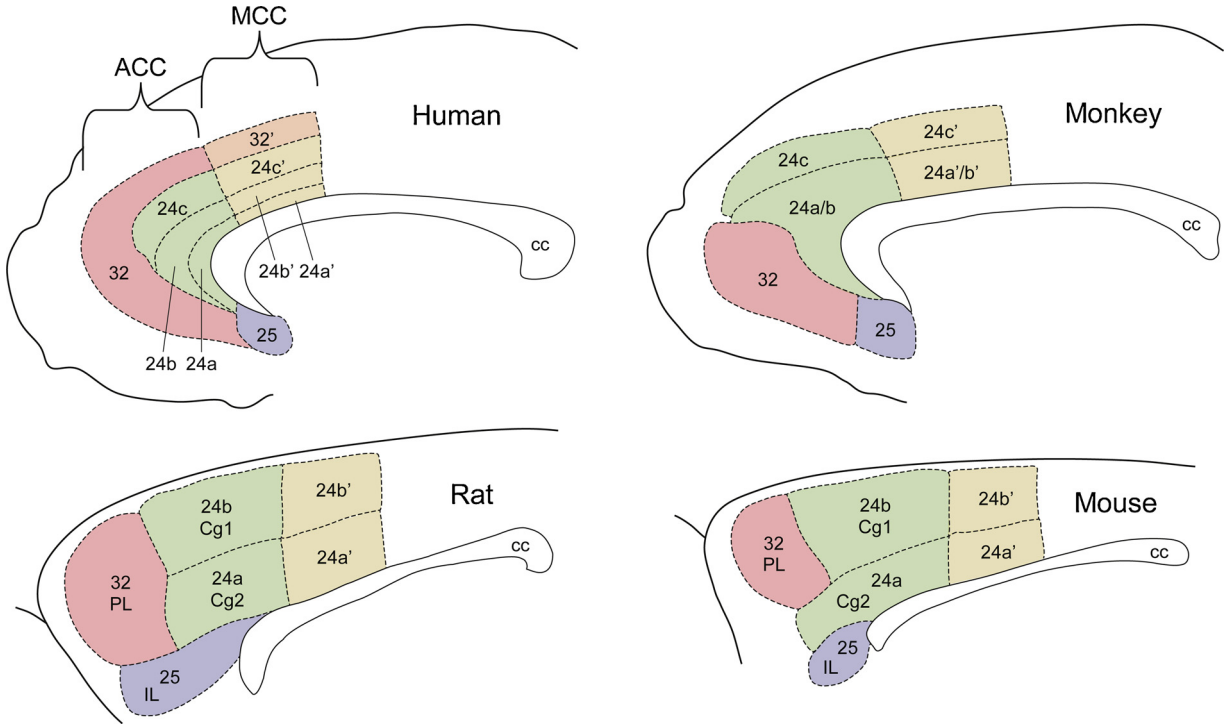

Fig. 1. Brain regions constituting the ACC in primates and rodents. Diagrams represent midsagittal sections of the human, monkey, rat, and mouse brains, and illustrate distinct brain regions that form part of the anterior cingulate cortex. While the construction of these diagrams considered various previous studies and brain atlases (Bush et al., 2000; Paxinos and Franklin, 2019; Paxinos and Watson, 2014; Rushworth et al., 2004; Vogt and Paxinos, 2014), the sizes and boundaries illustrated for each brain region are not precise. Numerical labels represent Brodmann nomenclature, whereas alphabetical labels represent other definitions given to some of the regions in rodents. ACC, anterior cingulate cortex; MCC, mid anterior cingulate cortex; Cg1, cingulate area 1; Cg2, cingulate area 2; PL, prelimbic cortex; IL, infralimbic cortex; CC, corpus callosum.

(Carmichael and Price, 1995; Heimer and Van Hoesen, 2006; Li et al., 2013; Vogt, 2016). The ACC is mostly agranular or dysgranular limbic cortex, therefore it is unlikely to participate in serial reprocessing of sensory thalamic inputs (Shipp, 2005), i.e., this area does not function as a quintessential sensory processor, but as a receiver of highly processed multi-sensory information that contributes to the sensory, decision-making, and motor dimensions of the ongoing behavior. Likewise, early sensory areas in primates are not known to project to the ACC.

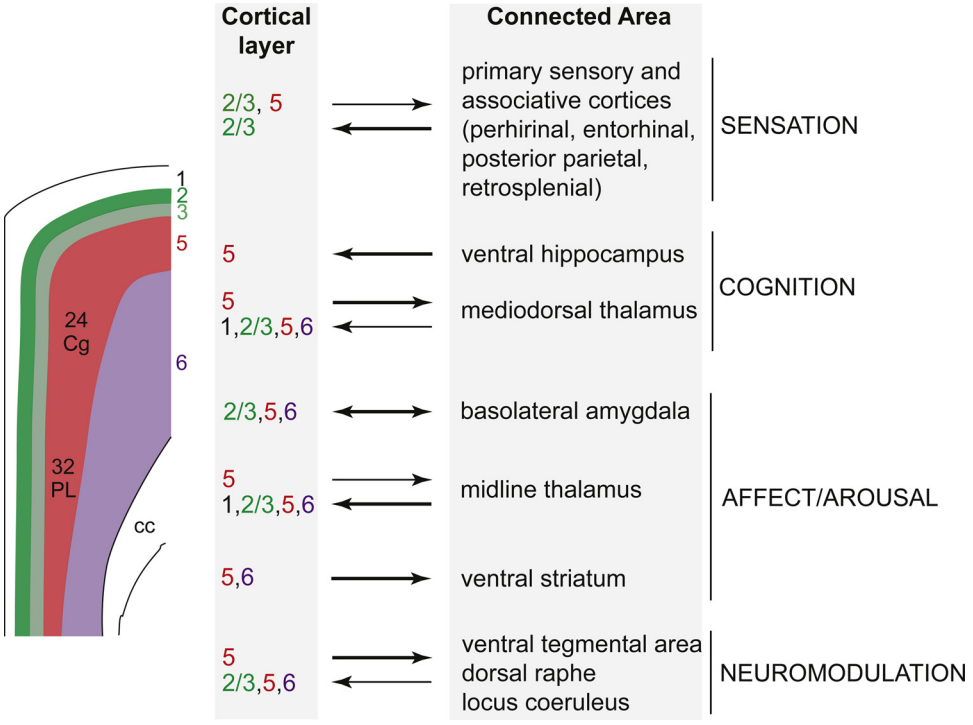

Fig. 2. ACC connectivity in rodents is organized to integrate complex sensory, cognitive, and emotional information. *Left*, Schematic of cortical layers in the rodent ACC. Cortical layers are color-coded. CC stands for corpus callosum. *Right*, Summary of connections of individual ACC layers with other brain areas involved in sensation, cognition, affect/arousal, and neuromodulation, based on anatomical tracing and electrophysiology studies (Aston-Jones and Waterhouse, 2016; Bissière et al., 2008; Cruikshank et al., 2012; Gabbott et al., 2005; Hoover and Vertes, 2007; Kamigaki, 2018; Lee et al., 2005; Little and Carter, 2012; Sara and Hervé-Minvielle, 1995; Vertes, 2004). Thicker and thinner arrows represent stronger and weaker connections, respectively. While stronger sensory inputs to the ACC tend to arrive through the supragranular layers 2/3, and stronger outputs originate in the infragranular layer 5, cells in both supragranular and infragranular layers also form extensive reciprocal connections with many brain areas involved in sensation, cognition, affect/arousal, and neuromodulation. The strong reciprocal connectivity of the ACC with this extended network may be optimal for integrating different types of information, including social and environmental cues, to facilitate observational learning.

The ACC, like the amygdala, and the limbic areas of the insula, receives highly processed sensory signals, i.e., signals of high stimulus dimensions, such as faces. It may be therefore, that a highly salient social feature such the eyes, are not sufficient by themselves as a high-contrast visual feature, to activate neurons in these areas, but the eyes that are socially engaged (e.g., in eye contact) may activate strongly the ACC. Indeed, neurons in the amygdala that project to the ACC signal that the subject is seeking and is engaged in eye contact (Mosher et al., 2014).

The ACC of rodents follows the same connectivity scheme, with few exceptions (*reviewed by* Laubach et al., 2018). Based on these inputs, the ACC of rodents and primates alike integrates socially salient information about others into a coherent social percept, and generates, based on this percept, outcome estimates for the actions of others and self. Support for these functions of the cingulate come from its activation during tasks that require the subjects to predict the (social) behaviors of others (Apps et al., 2013; Apps and Ramnani, 2014; Chang et al., 2013; de Araujo et al., 2012; Haroush and Williams, 2015). The ACC is also activated when animals witness a conspecific receiving rewards or aversive stimuli (Hillman and Bilkey, 2012; Jeon et al., 2010; Jones and Monfils, 2016; Kavaliers et al., 2005), or when humans observe the facial expressions (e.g., Simon et al., 2006; Vrticka et al., 2009) and vocalizations (e.g., Johnstone et al., 2006) of others. The same types of stimuli also activate the primate amygdala (Chang et al., 2015; Gothard et al., 2007; Livneh et al., 2012; Sliwa and Freiwald, 2017). Coactivation of the ACC and the amygdala supports processing vicarious rewards and emotional resonance in rats (Amemiya et al., 2016), monkeys (Livneh and Paz, 2012), and humans (Seara-Cardoso et al., 2016). Indeed, the neural activity recorded simultaneously from these two brain areas show overlap and complementarity (Klavir et al., 2013) but also remarkable differences. A recent report showed that information coding in the human ACC is more efficient, while coding in the non-human primates is more robust (Pryluk et al., 2019). Furthermore, neural activity in the ACC and the amygdala increases with the acute administration of the pro-social peptide oxytocin (Pisansky et al., 2017), further supporting a notion that signaling mechanisms within the ACC-amygdala circuit are important for emphatic behaviors.

3.1. ACC networks for cognitive functions during social learning

The ACC is one of the most interconnected areas of the mammalian brain. An excellent recent review by Apps et al. (2016) regarding the role of the ACC in social behavior organized the connectivity of the cingulate cortex into three main networks. The delineation of these networks is based on (1) the known anatomical connections of each subdivision of the cingulate cortex, (2) dissociable activation networks revealed by neuroimaging in humans, and (3) lesion studies and single unit recordings from cingulate area in multiple species. The three networks support (a) mentalizing, (b) action observation, and (c) value-based, affective-cognitive processing.

The mentalizing network processes abstract features of other-oriented information such as shame and guilt, attributing agency to perceived actions (Yoshida and Burling, 2011), or adjusting subjective rewards to social norms (Rizzolatti and Craighero, 2004). This network connects portions of the anterior cingulate (areas 24*a* and 24*b*) to the temporo-parietal junction and to the dorsomedial prefrontal cortex. In light of a recent review of the homologies between the rodent and the primate prefrontal cortex (Laubach et al., 2018), this network may be less prominent in rodents because the granular dorsomedial prefrontal cortex of primates may not have a rodent homologue (all prefrontal areas in rodents are agranular cingulate cortex).

The action observation network connects the anterior cingulate to ventral premotor and parietal sensory-motor areas. These areas become active when organisms observe the actions of others. The connections of the cingulate with premotor and sensory-motor areas may mediate imitation and mirroring the actions of others (Rizzolatti and Craighero, 2004). Anatomical evidence suggests that hand movements in humans and monkeys are coordinated by cortical action execution/recognition circuit that includes the insula (Di Cesare et al., 2018). Interestingly, neurons in this network, specifically in the ventral premotor area, respond not only when the self and others perform an action but also when a forbidden action is *not* performed, either by the self or by others (Bonini et al., 2014).

The third, *value processing network*, connects the anterior cingulate to the amygdala, the insula, and ventromedial, ventrolateral and orbitofrontal prefrontal areas (in primates, Broadman areas, 10, 11, 12, 13, 14, 25 and 32). This network incorporates an embodied, emotion-mirroring system (complementary but different from action mirroring included in the action observation network), which includes the insula, the amygdala, and the anterior cingulate. These areas meet the criteria for mirror mechanisms of emotion, namely they produce a specific emotion when artificially stimulated, contain neurons that respond to displays of that emotion, and lesions cause behavioral impairments in experience that emotion (Rizzolatti and Caruana, 2017). Given that little is known about the mirroring system in rodents, the conserved core of this network, namely the amygdala - orbitofrontal cortex -cingulate loop, may be the common denominator of observational learning across species. The amygdalo-cingulate limbic-motor loop (Gothard, 2014; Morecraft et al., 2012, 2007) coordinates reward and affect-motivated movements. Limbic-motor circuits set in register the motivation state, or value representation (of the self and of other) with actions (of self or of others). Indeed, neurons in the cingulate respond to the subjective value of rewards (ventral bank in primates) and to the actions required to obtain rewards (dorsal bank) (Cai and Padoa-Schioppa, 2012). Likewise, neurons in the primate amygdala respond to the facial expressions of others (Gothard et al., 2007) and to the facial expressions of self (Mosher et al., 2016). The value signals that motivate actions elaborated in the ACC appear to come from the amygdala via the OFC, as lesions of the amygdala alter more profoundly value encoding in OFC than in the ACC (Rudebeck et al., 2013).

3.2. ACC networks for autonomic regulation during social learning

The rich connectivity of the cingulate cortex to subcortical areas involved in autonomic regulation also contributes to socio-emotional behavior, and implicitly to observational learning. These pathways ensure that the energetic state of the organism (e.g., arousal or depressed mood) meets its behavioral agenda (e.g., exploratory drive, hide for safety). Specifically, area 25, or the subgenual cingulate in primates and the homologous region in rodents, is tightly connected to monoaminergic brainstem nuclei such as the ventral tegmental area, raphe nuclei, and locus coeruleus (Chiba et al., 2001; Freedman et al., 2000; Gabbott et al., 2005; Lee et al., 2005; Sara and Hervé-Minvielle, 1995; Vertes, 2004), and to visceral afferents such as nucleus of the solitary tract and the parabrachial nuclei (Showers and Crosby, 1958). Although the connections between the parabrachial nuclei, solitary tract and the amygdala have been analyzed in more detail in the context of pain (Neugebauer, 2015; Palmiter, 2018), the same pathways appear to carry non-painful visceral stimuli that contribute to socio-cognitive states (Fulwiler and Saper, 1984). These connections may set the “tone” and the reactivity level in the cingulate. It has been proposed that these inputs to the subgenual cingulate sustain arousal during anticipation of positive outcomes thereby contributing to positive emotional states (Rudebeck et al., 2014). Failure to maintain positive anticipatory states reduces motivation to act and causes depression (Drevets et al., 1997; Keedwell et al., 2005). This might explain why in select patients stimulation of this area relieves treatment-resistant depression (Mayberg et al., 2005).

4. Other cognitive and social functions of the ACC shared by rodents and primates

Despite species-specific differences in cytoarchitectonics,

arealization, and connectivity of the medial frontal/prefrontal cortex (Heilbronner et al., 2016; Laubach et al., 2018; Morecraft and Van Hoesen, 1993; Neubert et al., 2015; Vogt and Paxinos, 2014), the anterior cingulate of rodents and primates (human and non-human alike) carries out an overlapping list of computations, relying on somewhat different algorithms and neural implementation. These functions include but are not restricted to processing rewards and punishment (Chudasama et al., 2013; Rudebeck et al., 2013, 2008), cost-benefit estimations (Kennerley et al., 2006; Kennerley and Wallis, 2009; Kolling and Rushworth, 2015) including the estimation of effort (Cowen et al., 2012; Hillman and Bilkey, 2012), error monitoring and error prediction (Behrens et al., 2007; Fu et al., 2019; Kerns et al., 2004; Kolling et al., 2016; Shenhav et al., 2013; Sheth et al., 2012), and the elaboration of motor behaviors (e.g., Procyk et al., 2016). Some of these functions are useful in non-social contexts, yet the role of the anterior cingulate in social behavior does not emerge from adopting these general functions to social behavior. A recent review by Apps et al. (2016) argues that the cingulate cortex contains specialization for social behavior. A key specialization for observational learning is the presence in the ACC of neurons that respond selectively to information that pertains to the subjective experience and to the actions of others. These neurons are intermingled, and most likely interconnected with other neurons involved in cognitive control and error monitoring (Fu et al., 2019).

Through error monitoring an organism can compare, at both short and long-time scales, the outcome resulting from an action to the expected outcome. When errors are detected, new strategies are elaborated to avoid in the future similar errors (cognitive control). Although the neural events causal to and correlated with cognitive control have been studied primarily in behavioral paradigms motivated by primary reinforcers (e.g., food or juice), it is highly likely that the cognitive control of social behaviors exploits the same error monitoring and corrective system (Platt et al., 2016). Indeed, observational learning maximizes rewards or desired outcomes based on monitoring the action-outcomes experienced by others. By observing the actions of others and the subsequent errors, the observer is able to estimate the outcome of new strategies or behaviors. This is persuasively illustrated by neurons in the anterior cingulate of non-human primates that encode plans to switch to alternative actions based on outcome estimation (Kennerley et al., 2006; Sheth et al., 2012; Shima and Tanji, 1998). A recent report on neural correlates of error-monitoring and post-error adjustments in the human cingulate and the adjacent pre-supplementary motor area, indicate that cognitive control is instantiated by the coactivity of subpopulations of neurons that signal error, error history, conflict, and cognitive control state (Fu et al., 2019).

The most prominent physiological marker of error monitoring in the ACC is the Error-Related-Negativity (ERN), an evoked potential coinciding with errors that is large enough to be measurable with scalp electrodes in humans. The typical behavioral consequence of an error is the Post Error Slowing (PES), a delay in motor behavior in trials immediately following an error. This might be due to the inhibition of the motor loops originating in the ACC and other motor areas. Indeed, stimulation of these motor areas in the context of error-prone tasks, delays behaviors in order to avoid errors (Stuphorn and Schall, 2006). Although in rodents the ERN is less obvious, inactivation of the rodent cingulate cortex eliminates post-error slowing (Narayanan et al., 2013). In non-human primates, disruption of the cingulate cortex and of adjacent areas of the medial prefrontal cortex prevents suboptimal reward history to promote the elaboration of new behavioral strategies (Kennerley et al., 2006; Shima and Tanji, 1998).

In most species studied, observational learning requires the direct adjustment of actions of self to the observed actions of others. Reviewing the similarities between the rodent and primate cingulate Laubach and colleagues concluded that the rat and monkey ACC performs similar computations when organisms sequence (and plan) actions and outcomes (monkey: Procyk et al., 2000) (rat: Lapish et al., 2008), and when they monitor and adjust their performance (monkey: Ito et al., 2003) (rat: Narayanan and Laubach, 2008). The motor functions of cingulate cortex emerge from the anterior part of the midcingulate or dorsal cingulate in primates that is homologous to the Cg1 and Cg2 in the rodent ACC (Laubach et al., 2018; Vogt, 2016). These areas of the cingulate coordinate motor behaviors incentivized by rewards (e.g., obtaining juice reward) and by social imperatives (e.g., reassurance through facial expressions) that are strongly driven by limbic inputs (Gothard, 2014). The limbic-motor function is illustrated by the observation that motor actions coordinated by the cingulate cortex are selected based on the expected reward (Shima and Tanji, 1998). In the same vein, the activation of the orofacial motor representation in anterior midcingulate in humans depends on the amount of juice reward delivered as feedback during an exploration task (Amiez et al., 2013).

5. Social signals versus interactive social signals in the ACC

Many areas of the social brain respond to *social cues*, but few respond to *social interactions*. Sliwa and Freiwald (2017) used whole brain functional magnetic resonance imaging (fMRI) in monkeys to compare brain activity elicited by (1) interacting objects, (2) inactive monkeys, (3) active but not interacting monkeys, and (4) interactive monkeys. The videos that depicted active but not interactive monkeys enhanced neural responses in the action observation/mirror neuron system localized to ventral premotor and parietal areas. Watching videos of social interactions, one can observe the activation of multiple subdivision of cingulate cortex (areas 32, 24) along with dorsomedial prefrontal areas, premotor and polysensory areas of the frontal and temporal lobe, and areas that process reward and valence, including the amygdala. The strongest indication that the cingulate cortex and other medial prefrontal areas such as pre-supplementary motor area (Broadman area 6) are specialized to support social interactions comes from the differential and simultaneous representations of self and other (e.g., Decety and Sommerville, 2003; Rizzolatti and Sinigaglia, 2010; Tomlin et al., 2006; Yoshida et al., 2011). For example, when the monkeys have to use the actions of their social partner to inform their own behavior, neurons in medial prefrontal cortex respond differentially to the same action when perform by self and by the social partner (Yoshida et al., 2011). These neurons signal agency, an obligatory ingredient for separating the perceived outcomes into those caused by the self and by others (Frith and Frith, 2006). This differentiates the ACC and the dorsomedial prefrontal cortex from other components of the social brain (e.g., the face patches) that respond selectively to social signals but not social interactions. While selective responses to social signals serve *social perception*, selective, and simultaneously active responses to self and other serve *social interactions*. Social interactions recruit the motor system, even synchronizing motor cortical activity in social partners (Tseng et al., 2018).

As rank in a hierarchically structured primate society is defined relative to others and relative to the size of the social group, the covariation of neural activity in the ACC with social status also supports the role of the ACC in processing interactive social signals (Noonan et al., 2011; Sallet et al., 2011). Dominance and social ranking within mouse colonies also implicate the ACC. Rodent models allow meaningful manipulations to further explore this role, such as altering social status by altering plasticity in ACC neurons. Specifically, increasing synaptic strength by viral expression of the GluA4 subunit of AMPA receptor or Ras in the ACC neurons increased dominance rank measured by the tube test. In the tube test two mice are placed at the two ends of the tube and the subordinate mouse will retreat to allow the dominant mouse advance through the tube. Conversely, artificial decreases in synaptic strength by overexpression of the GluA4 C-tail or Rap1, decreased the dominance rank (Wang et al., 2011). Furthermore, sociability is decreased by shifting the excitation/inhibition balance in the medial prefrontal cortex towards inhibition (Yizhar et al., 2011).

Decisions to conform to social rules and norms also activate the ACC, so that the subjective value of rewards is defined in relations to valuation of the same reward by others (Apps and Ramnani, 2017; Izuma, 2013). From these studies it is clear that beyond processing social cues and rewards (whether to self and other), the ACC is processing social *interactive cues*, where rewards (or status) and actions are defined and evaluated in relation to the rewards and actions of others. Neurons in the ACC seem to encode separately but keep track simultaneously of self-and other, which indicates a higher-level, multidimensional representation of social information.

6. Interaction and communication in observational learning

How do individuals select information they should attend to and retain from their environment? To date, the majority of non-human animal models of learning focus on creating an association between a conditioned stimulus and an unconditioned stimulus through direct experience (e.g., classical fear conditioning). Direct exposure to an event, however, is not the only way that individuals acquire memories or form associations. Information can also be acquired indirectly, via social transmission between conspecifics. This form of learning may, in some contexts, prove to be a more effective and safer means of acquiring information, since it enables the learner to acquire knowledge while minimizing risks. Much research has been devoted to understanding how human and non-human primates acquire information through observation (Cook et al., 1985; Cook and Mineka, 1987; Hygge and Ohman, 1978; Mineka et al., 1984; Mineka and Cook, 1988; Olsson and Phelps, 2004); yet, research on the social transmission of fear in non-primate mammals has only more recently emerged (Allsop et al., 2018; Atsak et al., 2011; Ben-Ami Bartal et al., 2011; Bredy and Barad, 2009; Bruchey et al., 2010; Carrillo et al., 2015; Chen et al., 2009; Guzmán et al., 2009; Jeon et al., 2010; Jones et al., 2014; Jones and Monfils, 2016; Kavaliers et al., 2005; Kim et al., 2010; Knapska et al., 2010; Langford et al., 2006; Masuda and Aou, 2009; Pereira et al., 2012).

6.1. Observational fear learning paradigms

Observational learning can be broadly defined as the acquisition of new information through observation of a conspecific's response to stimuli. Through this form of learning, a naïve animal may identify an associative relationship between two stimuli (*observational **associative** learning*) or learn to associate a behavioral response with the presentation of a stimulus (*observational **operant** learning)*. In this section, we focus on the former. In a typical observational fear learning paradigm, rats (or mice) are placed on either side of a divider. For a brief overview of observational operant learning, please refer to a recently published review by Monfils and Agee (2019). The "demonstrator" is directly exposed to an aversive US (usually a footshock), and the "observer" witnesses the event. The divider can be transparent or opaque, to allow (or not) visual access. As such, rather than being an "eye-witness", the observer may have access to visual and/or non-visual cues to process the information. Jeon et al. (2010; 2011) performed an elegant series of experiments using this paradigm, and found that a mouse that witnessed another mouse receiving shocks in a context showed fear to that same context when tested at a later time, suggesting that observational fear learning may be used to study long-lasting acquisition of socially-transferred emotional information. It is important to note that in a typical observational learning paradigm, the number, intensity, duration and frequency of shocks administered are typically quite high (e.g., in Jeon et al. [2010]: 24 shocks, 2 s in duration, 1 mA intensity, and an inter-trial interval of 10 s), and the observer and demonstrator do not have the opportunity to physically engage with one another during the demonstrator's experience with the US (and the associated behavioral display).

Bruchey et al. (Bruchey et al., 2010) developed a different paradigm in which rats can acquire fear responding to a neutral stimulus in the absence of an unconditioned stimulus. In this paradigm, termed fear conditioning by proxy, a subset of rats acquire fear to a stimulus simply by being allowed to freely interact with a previously conditioned conspecific while the latter re-experiences the conditioned stimulus and displays a conditioned response. This experimental design was developed to determine whether fear responding could be socially transmitted between conspecifics during retrieval of a discrete memory. Bruchey et al. (2010) found that during the fear conditioning by proxy session, in which the observer and demonstrator rats can freely interact, the fear conditioned rats shows significant freezing, while the fear conditioned by proxy rat does not. When tested at a long-term memory test the next day, the observer rats (those conditioned by proxy) show a broad range of variability, with some rats not freezing at all, and others freezing for as much as 80% of the conditioned stimulus (Jones and Monfils, 2016). The degree of pro-social interactions (e.g. grooming, paw to body contact, nose-to-nose contact) between the fear conditioned and fear conditioned by proxy rats during training is a significant predictor of freezing during the long-term memory test.

There are important differences between fear conditioning by-proxy and other social fear learning paradigms. Unlike other models of social transmission of fear, fear conditioning by proxy does not involve an unconditioned stimulus-demonstrator unconditioned response association. Rather, during the fear conditioning by proxy interaction, the response displayed by the demonstrator is a conditioned response. It is also important to emphasize that whereas most observers acquire fear in a typical "observer-demonstrator" paradigm, only a subset acquire fear in the fear conditioning by proxy paradigm. The precise reasons underlying why only a subset of individuals acquire fear conditioning by proxy remain to be determined, though we have some clues. It appears that one of the best predictors for freezing at the long-term memory test following fear conditioning by proxy training is the amount of social contact the fear conditioned by proxy rat displays toward the fear conditioned rat during the training session. This, in turn, appears to be, at least in part, by dominance status (Jones and Monfils, 2016), and familiarity/kinship (Jones et al., 2014).

How is fear acquired via social transmission in rodents? The answer to this question is, in part, paradigm-dependent, though there are elements that appear to be common across social transmission of fear experimental designs. Importantly, as this is an emerging and dynamically evolving field of research, it is likely that a number of factors contributing to this form of learning have yet to be uncovered. Here, we at least describe the role of ultrasonic vocalizations (USVs) and chemosensation as modes of communication that may enable the transfer of information between conspecific rats or mice. Next, we briefly discuss the phenomenon of emotional contagion that might play a role in social transmission of information in rodents.

6.2. Ultrasonic vocalizations in observational learning

Vocalizations in rats in the lower spectrum of the ultrasonic range around 22 kHz are associated with negative affect elicited in situations where the rat is experiencing a fear-inducing state, such as the presence of a predator (Blanchard et al., 1991), painful (Calvino et al., 1996; Han et al., 2005) or startling stimuli (Kaltwasser, 1991), or in aggressive encounters with other rats (Thomas et al., 1983). Higher frequency vocalizations (typically referred to as 50 kHz calls) generally occur with activities with a more positive affect such as play (Knutson et al., 1998), social exploration (Wöhr and Schwarting, 2007), and anticipation of reward (Burgdorf et al., 2000).

USVs in mice have been found to emit a wide range of frequency-modulated ultrasonic vocalizations (typically within the 30–110 kHz range) that can be divided into predictable syllables (Ferhat et al., 2016; Gourbal et al., 2004; Holy and Guo, 2005; Portfors, 2007). These vocalizations have traditionally thought to be primarily linked to male courtship behavior (Chabout et al., 2015; Holy and Guo, 2005), though

more recent research indicates that male and female mice alike may also emit these calls as a territorial response to intruders (Hammerschmidt et al., 2012; Scattoni et al., 2011) (*for review, see* Portfors and Perkel, 2014). Research into how USVs in mice might communicate affective states is more limited, though USV emission has been observed to change following restraint stress, suggestive of production during an aversive experience (Chabout et al., 2012; Gaub et al., 2016; Grimsley et al., 2016) (*for review, see* Ehret, 2018). It is also important to note that Chen et al. (2009) have reported that squeaks produced by demonstrator mice are sufficient to enable social fear transmission. Outside of Chen et al.'s experiment, explicit research into whether USVs in mice influence social learning does not, to our knowledge, exist, though the aforementioned results do provide evidence that they could indeed possibly serve this function.

Auditory information appears to be an important component of social transmission of fear paradigms, with the presence of negative affect vocalizations (22 kHz range) (Kim et al., 2010), or the sudden onset of silence (Pereira et al., 2012) being important indicators of danger in a social setting. Jones and Monfils (2016) found that in fear conditioning by proxy, the majority of rats do not vocalize at all during the social transmission of fear, but this does not preclude a conspecific from learning about associative fear. In line with this findings, other groups have found evidence suggesting that 22 kHz vocalizations have little to no effect in naïve rats (Kisko et al., 2017; Wöhr et al., 2015). Still, for the rats that *do* vocalize in the 22 kHz range during fear conditioning by proxy, the duration of the vocalizations is positively correlated with the amount of fear acquired socially, as measured by freezing displayed by the observer the following day (Jones and Monfils, 2016).

6.3. Chemosensation in observational learning

Primates are considered microsmatic and most of them are lacking the vomeronasal organ and the accessory olfactory bulb (Smith et al., 2014) present in rodents. Nevertheless, olfaction plays a role in their social behaviors (McGann, 2017; Shepherd, 2004), as illustrated by chimpanzees recognizing group members and kin based on olfactory cues (Henkel and Setchell, 2018) and humans choosing mates based on olfactory signals (Jaworska et al., 2017).

In rodents, unlike in primates, chemosensory pathways transmit the largest proportion of social information (Arakawa et al., 2008; Camats Perna and Engelmann, 2017; Ferretti et al., 2019; Ishii and Touhara, 2019; Stowers and Kuo, 2015; Wesson, 2013). Secreted chemicals activate receptors in the main olfactory epithelium and Gruenberg ganglion, which transmit the information to the main olfactory bulb and then to the piriform cortex, medial amygdala and hypothalamus (Stowers and Kuo, 2015). They also activate receptors in the vomeronasal epithelium, which transmit the signal to the accessory olfactory bulb, and then to the medial amygdala, hypothalamus, and bed nucleus of the stria terminalis (Anderson, 2016; Matsuo et al., 2015; Stowers and Kuo, 2015). While the main and accessory olfactory bulbs do not project to ACC, their downstream targets send axons to ACC, although these are relatively sparse (Hoover and Vertes, 2007; Price et al., 1991). Loss of main olfactory system has been shown to produce deficits in a wide range of social behaviors (Matsuo et al., 2015). These findings suggest an important role of chemosensory pathways in social learning in rodents.

6.4. Emotional contagion in social learning

Emotional contagion refers to the process in which an observed behavioral change in one individual leads to the reflexive production of the same behavior by other individuals in close proximity, with the likely outcome of converging emotionally (Panksepp and Lahvis, 2011). One of the classic displays of contagion in primates is that of yawning—yawning on one individual's part appears to strongly correlate with yawning from others in the vicinity (Anderson et al., 2004). Dogs, as well as rats and mice, also appear to display yawning contagion (Joly-Mascheroni et al., 2008; Li et al., 2010; Moyaho et al., 2015). Blinking, in the context of highly engaged social interactions (e.g., eye contact during prosocial or angry encounters) also seems to be contagious: both humans and non-human primates synchronize their blinks (with a delay of approximately ½ s) to the blinks of their social partner (Ballesta et al., 2016; Nakano and Kitazawa, 2010). Observational fear learning can, in part, be explained by contagion. Effectively, in the typical "observer-demonstrator" paradigm, an immediate response (e.g., freezing, heart rate changes) to witnessing the event is generally observed in rats and mice (Atsak et al., 2011; Chen et al., 2009; Gonzalez-Liencres et al., 2014; Jeon et al., 2010).

7. Neural mechanisms for the learning of emotionally salient social cues

Studies in rodents have begun to elucidate the neural mechanisms associated to the encoding and integration of emotionally salient social signals during observational learning. Particularly, studies using the "observer-demonstrator" fear learning paradigm (Allsop et al., 2018; Jeon et al., 2010; Jeon and Shin, 2011) have become substantially successful to establish novel mechanistic explanations on how the ACC and its extended network promote observational learning. For instance, Allsop et al. (2018) recently validated a variation of the observational task used by Jeon and colleagues (detailed in Section 6.1; 2010; 2011) in which electrical shocks to demonstrators were signaled by an auditory cue (Fig. 3A). In contrast to the contextual-based observational paradigm used by Jeon and colleagues, the cue-based paradigm by Allsop et al. (2018) time-locked distress social signals to the cue, thereby transferring aversive properties to the auditory cue itself. This led to the formation of a cued fear memory in observer mice that elicited more prominent fear-related reactions during cue epochs than baseline epochs, even in the absence of demonstrator mice, and regardless of the contextual environment in which observer mice were tested (Allsop et al., 2018). Another advantage of the cue-based observational fear paradigm was that it allowed a multi-trial structure that was ideal to track the evolution of changes in neural firing across multiple stages of learning (i.e., habituation, conditioning, and test), while still maintaining high statistical power. Thus, the simplicity and high controllability of experimental conditions in this cue-based observational fear paradigm offers great opportunities to examine neural mechanisms and dynamics during multiple aspects of social learning, such as the perception and processing of socially transmitted distress signals, as well as their association with the environmental cues that predict them. Although Jeon and Allsop's observational learning paradigms have been focused on aversive forms of learning, similar principles could easily be implemented to examine neural computations and circuit dynamics during reward-related learning (Behrens et al., 2009, 2008), such as social transmission of food preference (Galef, 2003, 1992, Galef, 1990).

7.1. Integration of social and environmental signals in the ACC during observational fear learning

The ACC shows prominent neural correlates during observational fear learning. For instance, the ACC in mice develops potentiated neural oscillations in the theta frequency range during this type of learning (Jeon et al., 2010). Furthermore, large proportions of ACC neurons exhibit potentiated responses during observational fear learning (Allsop et al., 2018). Such ACC responses are mostly excitatory (i.e., increased activity compared to baseline) and occur while mice perceive the cues that predict electric shocks to demonstrators (Fig. 3**B-C**), as well as during the shock periods themselves when the demonstrators display the most prominent aversive reactions (Allsop et al., 2018). During similar observational tasks in rats, a recent study demonstrated that the

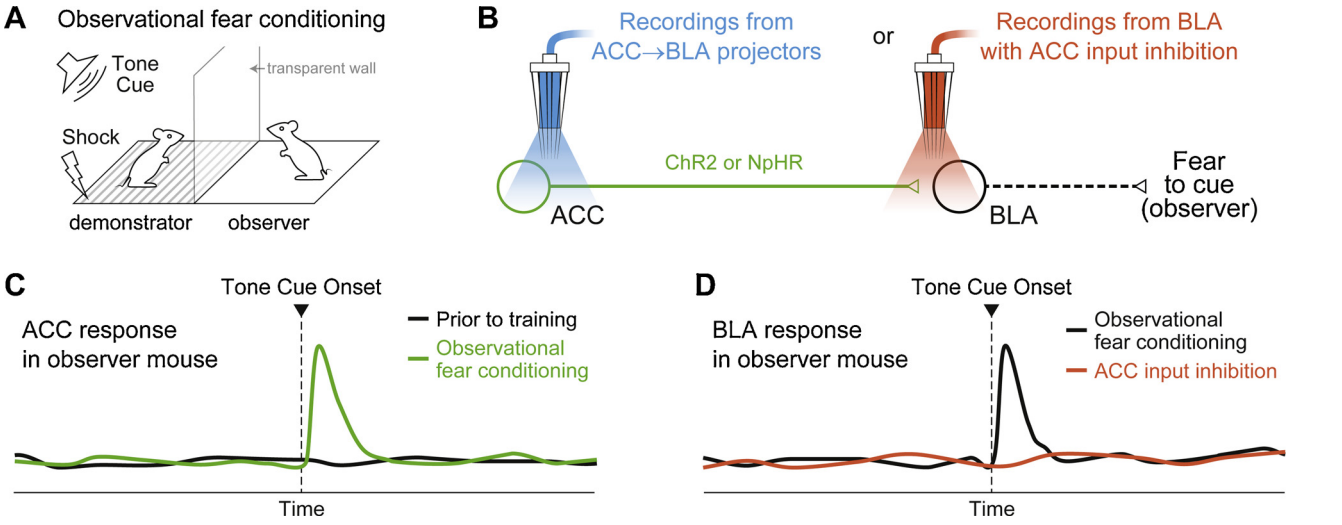

Fig. 3. Activity in the ACC-BLA pathway during observational fear conditioning. Illustrations summarize findings by Allsop et al. (2018)**. *A,*** Schematic of the observational fear paradigm. Demonstrator mice received tone-shock pairings, while observer mice witnessed these events through a transparent wall from the adjacent compartment. ***B,*** Schematic of *in vivo* neural recordings combined with optogenetic strategies to monitor the activity of either ACC-to-BLA projectors or BLA neurons during the task. ***C,*** ACC-to-BLA projectors acquired prominent responses to the shock-predicting cue. ***D,*** BLA neurons also acquired prominent responses to the cue, but such responses were abolished by photoinhibition of the ACC input.

ACC contains neurons that exhibit pronounced elevated activity when demonstrators receive electric shocks (Carrillo et al., 2019). Such elevation of neural activity in the ACC was attributed to a "mirror-like" emotional contagion effect (i.e., similar patterns of activity were observed when rats experienced pain themselves and when they witnessed pain in other rats) (Carrillo et al., 2019). These electrophysiological findings highlight strong ACC participation during observational fear learning in rodents and suggest that the ACC integrates social and environmental signals to promote this type of learning.

While electrophysiological findings could just have highlighted ACC participation, additional examination has revealed that ACC activity is vital for observational fear learning. It has been shown in mice that the acquisition of fear memory through observation is impaired by temporal inactivation of the ACC (Jeon et al., 2010; Kim et al., 2012). Similarly, fear in rats while witnessing others receiving shocks is impaired by ACC inactivation (Carrillo et al., 2019). Observational fear learning can also be disrupted by ACC-restricted deletion of $Ca_V1.2$ L-type calcium channels (Jeon et al., 2010), which have been shown to be highly expressed in the ACC (Day et al., 2002), mediate aversive experience-dependent gene expression (Bavley et al., 2017), and contribute to the excitability and plasticity of ACC neurons (Liauw et al., 2005). In addition, observational fear learning can be disrupted by local administration of either dopaminergic antagonists or serotonergic agonists into the ACC (Kim et al., 2014). Finally, to highlight bidirectional modulation, it has been reported that observational fear learning can be facilitated by electrical stimulation of the ACC (Kim et al., 2012).

Although ACC activity facilitates observational fear learning, ACC activity is trivial for the recall of this type of memory. It has been shown that pharmacological inactivation of the ACC during test sessions (e.g., 24 h after observational fear training) fails to disrupt the recall (Jeon et al., 2010). This suggests that the role of ACC activity during this type of learning is to promote memory formation in downstream regions, from which these memories can be later retrieve.

7.2. The amygdala as a crucial downstream region of the ACC during observational fear learning

The amygdala, especially the basolateral nuclei (including in rodents the lateral, basolateral, and basomedial regions; which from now on we will refer to as the "BLA") is unequivocally fundamental for learning fear associations through classical conditioning methods in which direct experience of punishment is required (*for review, see* Aggleton, 2000; Duvarci and Pare, 2014; Janak and Tye, 2015; LeDoux, 2007, 2000; Maren and Quirk, 2004). Growing evidence indicates that BLA is also fundamental for learning fear associations through observational methods (*for review, see* Debiec and Olsson, 2017; Ferretti and Papaleo, 2019; Olsson and Phelps, 2007). In this section we focus on some studies in rodents demonstrating that neural activity in the BLA and its interactions with the ACC support observational fear learning.

The BLA exhibits potentiated theta oscillations during observational fear learning that are highly synchronized with the theta oscillations observed in the ACC (Jeon et al., 2010). Similarly to the ACC, many neurons in BLA develop potentiated responses to social and environmental cues during observational fear learning (Fig. 3D; Allsop et al., 2018). However, compared to ACC neurons, BLA neurons require a relatively larger amount of training to develop potentiated responses during observational fear learning. This suggests an ACC-to-BLA directionality for the encoding of these memories. Supporting this hypothesis, Allsop et al. (2018) combined electrophysiology and optogenetic strategies to demonstrate that ACC neurons that directly project to the BLA exhibit stronger responses during the observational fear task than other ACC subpopulations. They also found that selective inhibition of ACC inputs to the BLA profoundly disrupts both, BLA responses and behavioral responses, during this task. In addition, they found that selective inhibition in the opposite direction (i.e., BLA-to-ACC) did not affect observational fear learning. These findings provide important evidence for the hypothesis that ACC-to-BLA communication promotes memory formation during observational fear learning.

Finally, BLA activity is necessary during the long-term recall of fear memories learned through observation. This was shown by Jeon et al. (2010) using pharmacological inactivation of the BLA, and contrasts the finding that ACC activity is trivial during memory recall in this task. Consistent with these findings, Allsop et al. (2018) demonstrated that selective optogenetic-mediated inhibition of ACC inputs to the BLA fails to disrupt fear recall after observational fear learning. Therefore, it seems that once fear memories learned through observation have been formed within the BLA, recalling these memories later on only requires BLA activity but not ACC involvement.

7.3. Working model for ACC-BLA interactions during observational fear learning

To summarize the findings on this section, network interactions between the ACC and BLA play a crucial role during observational fear learning. While neural activation in the ACC supports observational fear learning by signaling emotionally salient social cues, the ACC transmits this information to the BLA to further promote memory encoding. Observationally-learned fear memories can be subsequently accessed from the BLA to modulate behavior, even in the absence of ACC involvement (Allsop et al., 2018). This model is consistent with previously suggested models that also take into account findings from human studies (Debiec and Olsson, 2017; Olsson and Phelps, 2007).

8. Observational fear learning produces enduring reorganization of the ACC-BLA network

While the ACC-BLA network exhibits fast computations that promote memory formation during observational fear learning, this network also exhibits enduring synaptic adaptations that may affect other behaviors. Two types of neuronal adaptations identified so far include synaptic changes in ACC inputs to BLA principal neurons and in the local GABAergic inputs to the principal neurons in the ACC layer 5.

The synaptic transmission from ACC to BLA was tested *ex vivo* by recording postsynaptic responses in BLA neurons during blue light stimulation of the ACC axons expressing channelrhodopsin (Ito et al., 2015). It was reported that observational fear training decreased the ratio between the AMPA and NMDA receptor-mediated responses. This effect was specific to the ACC-BLA pathway, as no changes were found in inputs from the TeA (temporal cortex, association area), which integrates multimodal sensory information (McDonald, 1998; Sheinberg and Logothetis, 1997). The decrease in AMPA/NMDA ratio was also social learning-specific, as no changes were found after non-social stressors, including two-hour immobilization or classical auditory fear conditioning reinforced by mild electrical footshock. The reduction in the AMPAR/NMDAR ratio resulted from increases in the NMDAR currents and coincided with the emergence of silent synapses, which contain NMDA receptors but lack AMPA receptors. There was no reduction in the AMPAR currents, which suggests that silent synapses were generated *de novo* and not by withdrawal of AMPAR from functional synapses. Because silent synapses can become functional after insertion of AMPAR, they provide a substrate for synaptic facilitation. The acquired propensity for increased facilitation in the ACC-BLA pathway has been confirmed both *ex vivo* and *in vivo* during inhibitory avoidance training (Ito and Morozov, 2019). It remains unknown how these synaptic changes contribute to observational fear memories per se, but they provide a potential mechanism for the enhanced inhibitory avoidance learning in mice that experienced observational fear training in the past (Ito et al., 2015).

9. Observational fear learning reorganizes GABAergic circuits in the rodent ACC

Following observational fear learning, GABA circuits in ACC may also undergo reorganization in the form of potentially switching the patterns of interactions between the ACC and other brain areas (Liu et al., 2017). In ACC, observational fear altered the short-term plasticity of GABAergic inputs to the layer 5 principal neurons (PNs). The presynaptic GABAb autoreceptors normally suppress these inputs, which causes the decline in the inhibitory postsynaptic currents in the principal cells during repeated stimulation of GABAergic neurons. Observational fear had opposing effects on GABAergic inputs from two classes of GABAergic neurons. It attenuated the GABAbR suppression of inputs from the somatostatin-expressing interneurons (Sst-INs), but enhanced the suppression of inputs from the parvalbumin-expressing cells (PV-INs) (Liu et al., 2017). Given that PV-INs target mostly the somas and proximal dendrites of PNs, whereas the Sst-INs target distal dendrites (Markram et al., 2004), observational fear likely shifts inhibitory drive along the somato-dendritic axis of PNs from the soma and proximal dendrites to the distal dendrites. The shift is expected to enhance connectivity among the layer 5 neurons, because they project mainly to the proximal basal dendrites of one another (Markram et al., 1997), and to attenuate connectivity from the layer 2/3 neurons to the layer 5 neurons, because the inputs target apical dendrites (Thomson and Bannister, 1998). At the same time, it is expected to weaken the remote connectivity from the thalamus, whose axons travel via the cortical layer 1 and target apical dendrites, and to enhance the connectivity with the BLA, whose axons are abundant in the layer 5 and target the basal proximal dendrites (Hoover and Vertes, 2007; Oh et al., 2014). Thus, the GABAergic adaptations to observational fear are likely to rearrange both local and remote connectivity of neurons in ACC and change its interactions with other areas of the brain. Based on these findings, it is possible that the formation of silent synapses in the ACC-BLA pathway and changes in GABAergic transmission are not cell-specific. Nevertheless, by altering remote connectivity or synchronization, they can facilitate plasticity in specific neuronal ensembles that store socially-reinforced memories.

10. Concluding remarks

We compiled evidence for well-conserved neural networks centered on the ACC that detect, interpret, and encode socially-derived signals during social learning across multiple species. As social learning is a highly dynamic and rapidly evolving field of research, our interpretation of the existing literature may soon require further revisions. Nevertheless, the ideas emerging from the evaluation of the current literature provide a framework for compartmentalizing the ACC networks in subdivisions that may support distinct yet related forms of social learning.

10.1. Future avenues

Studies in humans and non-human primates suggest that the cingulate cortex (including areas of the anterior cingulate, mid-cingulate, and posterior cingulate cortex) is activated by a multitude of functions, many of which serve social behaviors and observational learning. The diversity of functions attributed to the cingulate cortex, might be explained, by its rich connectivity with other cortical and subcortical areas, specifically with the components of the “social brain” (Dunbar, 1998). The amygdala is a prominent node of the social brain that is bidirectionally connected to multiple subregions of the cingulate cortex. It appears that neural ensembles in the ACC respond to particular social situations (Livneh et al., 2012; Mosher et al., 2014; Rutishauser et al., 2015; Wang et al., 2014) that are linked to neural events in the amygdala (Klavir et al., 2013). Recent studies in rodents showed that social learning elicits broad synaptic changes that influence functional connectivity between the ACC and the amygdala (Allsop et al., 2018; Ito et al., 2015; Liu et al., 2017). One challenge for future studies is to keep identifying highly selective social learning neural engrams to better understand how they map onto diverse functions of the ACC-amygdala circuits and how they enable behavioral adaptation in response to social cues. Future studies may determine whether learning through observation recruits the same or different neural ensembles that are typically recruited when learning through direct experience.

An emerging question in the field is how social factors such as dominance status affects the neural mechanisms controlling social transmission and learning. In case of fear learning by social transmission, dominance status plays an important role (Jones and Monfils, 2016). Whereas subordinate rats readily acquire fear by proxy when they interact with a previously fear-conditioned dominant conspecific, dominant rats do not reliably acquire fear via social transmission from

subordinates. In a similar vein, the decision making and anxiety level of human subjects (correlated with increased activity levels in the ACC) was negatively impacted by collaborating with a social partner of low reputation (Qi et al., 2018). Future studies examining differences in circuit mechanisms between dominant and subordinate animals should shed light on the neurobiological players by which dominance status influences social fear learning.

Gender specific mechanisms of social learning have been scarcely addressed. A few early studies suggest some differences in the neural mechanisms of social learning between males and females. For example, it has been reported that male but not female rats exhibit increased c-fos activation in the BLA and ACC areas during some forms of social transmission (Knapska et al., 2006; Mikosz et al., 2015). In humans, women, but not men, show correlations of right hemisphere activation and empathy (Rueckert and Naybar, 2008).

Finally, social learning is particularly important during development because it may form the bases for the development of emotion regulation and social-cognitive function. Recent studies in rodents have shown that a caregiver can impart fear learning in the offspring via a process called social referencing (Chang and Debiec, 2016; Debiec and Sullivan, 2017, 2014), while human studies suggest that infants are more sensitive to caregiver fear and anxiety (Aktar et al., 2018; Murray et al., 2008). In addition, developmental differences in social learning appeared to be linked to a developmental shift in the processing of experienced and observed feedback during learning (Rodriguez Buritica et al., 2018). Altogether, these findings indicate the importance of future studies to examine the neurobiological mechanisms underlying social learning during development, as well as other factors that influence developmental differences in the ability to use observed versus experienced feedback.

Competing interests

The authors declare no conflicts of interest.

Acknowledgements

The authors assembled this review article based on a recent scientific symposium held at the International Behavioral Neuroscience Society meeting (IBNS 2018) in which they presented work related to the topic. The symposium was titled *"Social transmission of information in mammals: Key insights from rodents and non-human primates"*. The authors thank Dr. Gregory *J*. Quirk for his helpful comments and suggestions on the manuscript. A.B.-R. acknowledges support by the Brain and Behavior Research Foundation (NARSAD Young Investigator Award) and 3 R01 MH102441-01 (Research Supplement to Promote Diversity in Health-Related Sciences). K.M.G. acknowledges support by the NIH/NIMH grant P50- MH100023. M.H.M. acknowledges support by the NSF grant NSF-1748911. A.M. acknowledges support by the NIH grants R01-MH 112093-01 and 5-R21 MH112093-02.

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