

problems exist in speech processing; for example, where, when hearing streams of words, our brain needs to represent the syntactic and semantic structure of the sentence on the fly, anticipating future words. Cognitive flexibility may also be related to how fluidly the brain can represent likely future actions, contexts, or thoughts.

Ultimately, looking at individual differences in the flexibility of this representation could have implications in the clinical domain. It is often thought that mental disorder, in particular autism and schizophrenia, could be described as a failure mode of the predictive system [8,9], related either to the brain using wrong or incompletely learned beliefs or to failures in how neural networks implement approximate ‘Bayesian’ computations [10]. The neural substrate underlying this prediction system and the factors involved in its fluidity or its possible impairments, as well as the precise nature of the ‘code’, are still largely to be discovered.

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#### References

1. Glaser, J.I. et al. (2018) Population coding of conditional probability distributions in dorsal premotor cortex. *Nat. Commun.* 9, 1788
2. Pouget, A. et al. (2013) Probabilistic brains: knowns and unknowns. *Nat. Neurosci.* 16, 1170–1178
3. Fiser, J. et al. (2010) Statistically optimal perception and learning: from behavior to neural representations. *Trends Cogn. Sci.* 14, 119–130
4. Sanborn, A.N. and Chater, N. (2016) Bayesian brains without probabilities. *Trends Cogn. Sci.* 20, 12
5. Ma, W. and Jazayeri, M. (2014) Neural coding of uncertainty and probability. *Annu. Rev. Neurosci.* 37, 205–220
6. Ting, C. et al. (2015) Neural mechanisms for integrating prior knowledge and likelihood in value-based probabilistic inference. *J. Neurosci.* 35, 1792–1805
7. Rahnev, D. and Denison, R.N. (2018) Suboptimality in perceptual decision-making. *Behav. Brain Sci.* Published online February 27, 2018. <http://dx.doi.org/10.1017/S0140525X18000936>
8. Palmer, C.J. et al. (2017) Bayesian approaches to autism: towards volatility, action, and behavior. *J. Psychol. Bull.* 143, 521–542
9. Valton, V. et al. (2017) Comprehensive review: computational modelling of schizophrenia. *Neurosci. Biobehav. Rev.* 83, 631–646
10. Huys, Q. et al. (2015) Decision-theoretic psychiatry. *Clin. Psychol. Sci.* 3, 400–421

## Spotlight

### Shining Light on Social Learning Circuits

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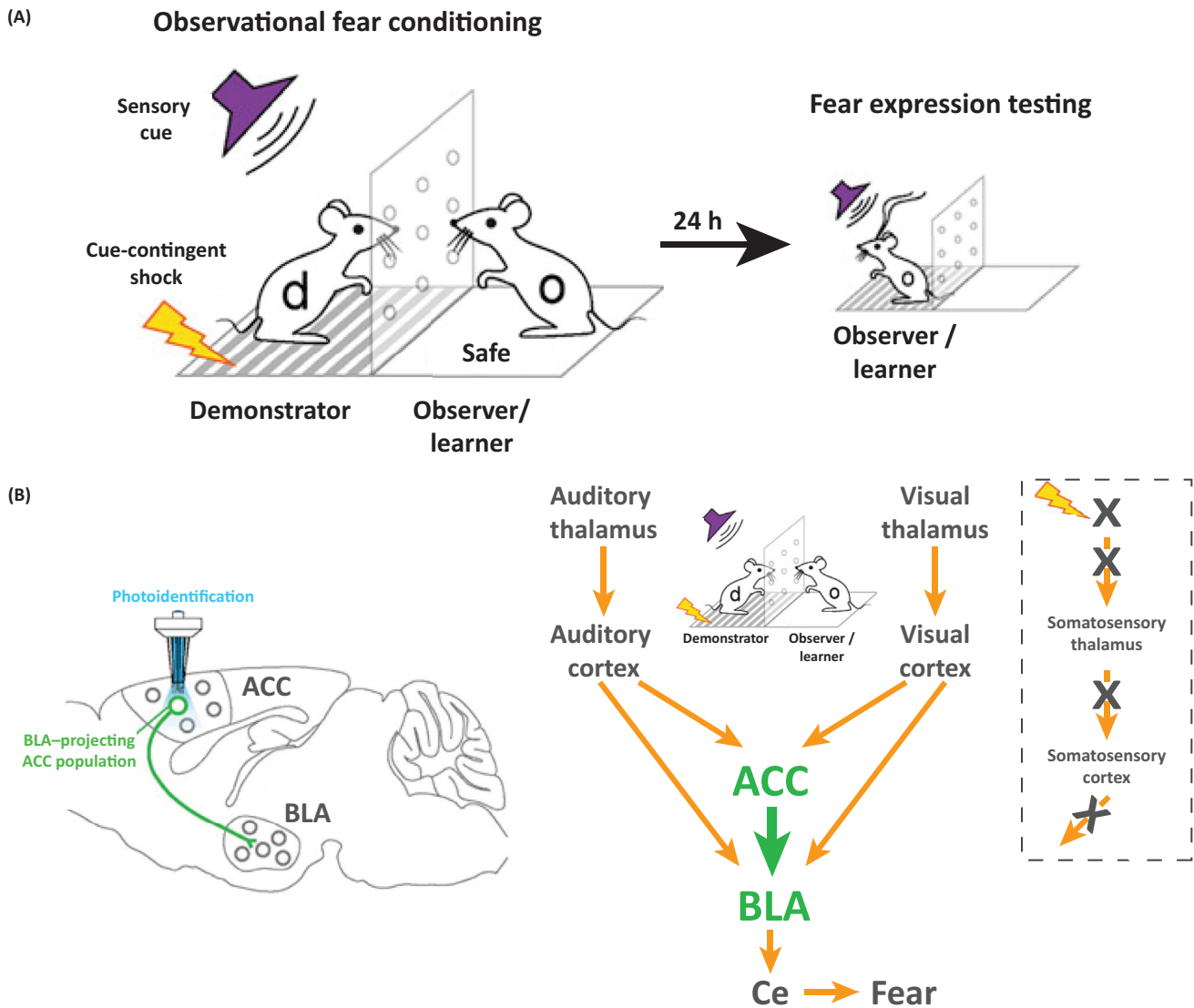
**Learning from others powerfully shapes our lives, yet the circuit-specific mechanisms underlying social learning in the brain remain unclear. A recent study in mice provides evidence that direct neuronal projections from the anterior cingulate cortex (ACC) to the basolateral amygdala (BLA) play a critical role in observational fear learning.**

Social learning is arguably one of the most important and powerful learning strategies available to us. We learn about the world from our parents, family members, and close others, a process that starts at birth and continues throughout our lifespan. Our schools and universities are designed for social learning; we gain new skills and shape our worldview from knowledge gleaned from our teachers, friends, and peers. This universal human characteristic of social learning is also found in several other animals.

So, how do we learn from others? A large amount of research – encompassing behavioral and neuroscientific work done in humans and other animals – has been asking this question for long enough [1,2] that the breadth of social learning research has become too wide and complex to be easily summarized in a few sentences. We will therefore narrow our scope to focus on

one particular aspect of social learning: observational learning. Observational learning, or vicarious learning, is the learning that occurs through the observation of a model. It has been suggested that vicarious reinforcement plays a critical role in observational learning. Observing the reinforcement (either positive or negative in valence) of certain actions and outcomes in another individual results in changes in our own behavior [3,4]. Consistent with the role of reinforcement in social learning, vicariously rewarding events (e.g., seeing another individual consuming a reward) drive neuronal activity in brain regions involved in value-guided decision-making, including the ACC and the BLA [5,6]. However, the central question of how such brain regions acquire reinforcing information during vicarious learning remains unanswered.

A recent study by Allsop and colleagues [7] sheds light on this central question. This *tour de force* investigation spanning behavioral, electrophysiological, and optogenetic techniques helps delineate the circuit-specific mechanisms of observational learning. Capitalizing on the observational fear conditioning paradigm in mice (Figure 1A) – incidentally, also an effective method for studying social learning in humans [8] – the researchers uncover a direction-specific interaction between the ACC and the BLA. In the study, an observer mouse vicariously experiences a shock delivered to a demonstrator mouse paired with a predictive sensory cue. To better understand the behavioral contingencies necessary for observational fear learning, several distinct types of observer mice were tested to confirm that (i) prior experience of the shock, (ii) observation of the demonstrator mouse receiving a shock, and (iii) the vicarious shock being paired with a cue are all necessary components for observational fear learning. Next, based on electrophysiological recordings, the authors found that both ACC and BLA



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**Figure 1. Observational Fear Learning in the Anterior Cingulate Cortex (ACC)–Basolateral Amygdala (BLA) Circuit.** Observational fear learning requires input from the ACC into the BLA. (A) The observational fear learning paradigm used by Allsop and colleagues. Left: Observational fear conditioning phase. Right: Fear expression testing phase. (B) Left: Identification of the BLA-projecting ACC neurons set the stage for the discovery of the necessary function of this population in the acquisition of observational fear. Right: A simplified diagram of neural pathways involved in observational fear learning. Ce, central amygdala. Allsop and colleagues demonstrate that the ACC input to the BLA has a critical function in observational fear learning (green). Adapted, with permission, from [7].

neurons encode the fear-eliciting cue during the observational conditioning phase. Additionally, the team recorded neural activity from the ACC cells that directly project to the BLA. They reported that this population of cells, compared with other, ‘non-network’ ACC populations, shows particularly enhanced cue-evoked activity,

suggesting a possible functional role of the BLA-projecting ACC cells in observational fear learning.

Notably, recording from the BLA neurons while optogenetically inhibiting the ACC input to the BLA revealed that encoding of the observational fear cue in the BLA is critically dependent on the ACC input.

But is this input necessary for observational fear learning? Optogenetically inhibiting the ACC input to the BLA blocks cue acquisition from observational fear conditioning while leaving intact the ability to acquire fear in a classical nonsocial fear-conditioning context. Although it was known that the ACC is necessary for observational fear learning

[9], Allsop and colleagues demonstrated that the direct pathway from the ACC to the BLA is what causally underlies this process (Figure 1B). Furthermore, to probe the generalizability of this corticoamygdala mechanism in social interactions, the same optogenetic inhibition of the ACC input to the BLA was used to test the formation of social preferences from observing social interactions between a control mouse and an aggressive mouse. In a subsequent three-chamber task, the mice with inhibited ACC inputs to the BLA did not show the expected avoidance of the aggressive mouse. Intriguingly, despite the fact that these two brain regions are heavily reciprocally connected, optogenetic inhibition of the projection from the BLA to the ACC did not seem to affect observational fear conditioning. This raises a fascinating possibility that these reciprocal connections underlie different neural processes, and the information transmission from the BLA to the ACC may be involved in other types of social behaviors that might rely on the initial computations being performed in the BLA.

Social learning requires a broad spectrum of neural computations involving multiple

brain regions. This new study by Allsop and colleagues uncovers a previously unknown direction-specific corticoamygdala circuit underlying one key aspect of social learning; namely, learning from observing another's negative outcome. From here many other exciting questions remain to be answered. For instance, it would be interesting to test whether the same mechanism is in operation in the primate brain. Humans and monkeys show sulcus and gyrus divisions in the ACC, something that is absent in rodents, and in the primate brain the gyrus of the ACC is believed to process more socially oriented information compared with the sulcus [5,10]. Furthermore, understanding whether this direction-specific ACC–BLA coordination is essential for learning from others' positive outcomes and imitation learning, as well as for prosocial behavior and empathy, will further enrich our understanding of ACC–BLA coordination in social behavior. Undoubtedly, the study by Allsop and colleague will play a momentous role in guiding exciting future research into social cognition.

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#### References

- Rosenthal, T.L. and Zimmerman, B.J. (2014) *Social Learning and Cognition*, Academic Press
- Whiten, A. (2017) Social learning and culture in child and chimpanzee. *Annu. Rev. Psychol.* 68, 129–154
- Wittmann, M.K. et al. (2018) Neural mechanisms of social cognition in primates. *Annu. Rev. Neurosci.* Published online March 21, 2018. <http://dx.doi.org/10.1146/annurev-neuro-080317-061450>
- Joiner, J. et al. (2017) Social learning through prediction error in the brain. *NPJ Sci. Learn.* 2, 8
- Chang, S.W.C. et al. (2013) Neuronal reference frames for social decisions in primate frontal cortex. *Nat. Neurosci.* 16, 243–250
- Chang, S.W.C. et al. (2015) Neural mechanisms of social decision-making in the primate amygdala. *Proc. Natl. Acad. Sci. U. S. A.* 112, 16012–16017
- Allsop, S.A. et al. (2018) Corticoamygdala transfer of socially derived information gates observational learning. *Cell* Published online May 3, 2018. <http://dx.doi.org/10.1016/j.cell.2018.04.004>
- Olsson, A. and Phelps, E.A. (2007) Social learning of fear. *Nat. Neurosci.* 10, 1095–1102
- Jeon, D. et al. (2010) Observational fear learning involves affective pain system and Cav1.2 Ca<sup>2+</sup> channels in ACC. *Nat. Neurosci.* 13, 482–488
- Rudebeck, P.H. (2006) A role for the macaque anterior cingulate gyrus in social valuation. *Science* 313, 1310–1312