



Social regulation of survival circuits through learning

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In social species such as our own, learning about the value of things, people and situations often takes place in social situations. Here, we review new cross-species research on the social regulation of basic survival functions, such as defensive responses that are linked to basic learning processes. We show that domain-general learning brain circuits, specifically those involved in Pavlovian and instrumental conditioning, integrate information from the social domain to aid a variety of phenomena, ranging from social avoidance to the learning of moral values. We review behavioral and neural evidence highlighting both similarities and differences between social and non-social forms of learning, and suggest an integrative framework of social learning of value with the aim to further our mechanistic understanding of the interaction between survival circuits and social learning.

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Introduction

Surviving in a challenging world requires the orchestration of a symphony of defensive, ingestive, thermoregulatory, and reproductive behaviors [1]. In social species, such as our own, conspecifics are both part of the challenge and the solution for our survival. For humans, people can constitute a deadly threat, such as a friend turning into a foe. At the same time, the presence of others is fundamental to our survival because they provide protection, nurturance, and reproductive opportunities. But other individuals are not only the targets of our fears and desires, they also transmit valuable information about the social world. From early on

in the developmental trajectory, we learn from others—about what and whom should be approached and avoided, and what behaviors reap valuable or damaging outcomes. Information about the value of people, objects, and outcomes spreads during social exchanges, and can therefore rapidly propagate through large networks of interconnected individuals (e.g. social communities). Thus, social information, and the process by which it is transmitted, plays a critical role in regulating survival functions and their underlying neural circuitry.

Here, we focus on the relationship between survival functions related to basic learning and a network of brain regions responsible for processing social information. We review new research on the social regulation of basic survival systems, which illustrate that domain-general learning circuits, specifically those involved in Pavlovian and instrumental conditioning, integrate information from the social domain to aid a variety of phenomena, ranging from social avoidance to the learning of moral values. In spite of the growing body of research examining social learning in both the reward and aversive learning domain, here we will focus on the latter due to space limitations.

Although the social ecology (and thus the way social influences are expressed) varies greatly between species [2], basic learning mechanisms are conserved across taxa. The ability to reference animal models provides an advantage when trying to understand more complex learning systems, such as those observed in humans, and can be especially helpful in social environments that are evolving and dynamic, because the elements of the learning space explode exponentially. Despite the complexity of social environments, traditional approaches to investigating learning processes have been carried out in a relative social vacuum. However, a combination of new methodologies and paradigm shifts have begun to successfully elucidate social learning processes. For example, recent research in rodents and primates illustrates how Pavlovian and instrumental learning unfolds in increasingly complex social environments [3]. Parallel work in humans has also begun to fruitfully identify the cognitive and neural architecture of learning through vicarious experiences of threat [4–6], safety [7], reward [8,9], social hierarchies [10], trust [11], ostracism [12], and moral value [13,14].

Basic Pavlovian and instrumental learning processes

Learning to predict the future based on past events is critical for survival. In traditional Pavlovian learning

paradigms, an animal learns to predict future rewards and dangers through direct experiences. In this way, predictive stimuli come to control basic reflexive behaviors supporting various survival functions. For example, in direct Pavlovian threat conditioning, a conditioned stimulus (CS) is paired with a naturally aversive unconditioned stimulus (US), such as an electric shock, which can in turn elicit a range of defensive conditioned responses in the animal.

The amygdala provides some of the basic neural machinery needed during Pavlovian learning. In rodents, associative learning within amygdala circuits is mirrored by plasticity in the lateral nucleus of the amygdala (LA), where neuronal activity representing information about the tone (CS) and shock (US) coincide [15,16]. Information from the LA is relayed to the central nucleus of the amygdala that projects to different brain regions that regulate defensive responses, such as the Periaqueductal Grey (PAG), which mediates freezing and flight responses, and other brainstem and hypothalamic sites. Projections from the ventral tegmental area (VTA) via the ventral striatum to the prefrontal cortex, further tailor the learning process so that animal can seamlessly update their behaviors in line with feedback from the environment.

Apart from its rich subcortical connectivity, the amygdala is directly connected to cortical regions, such as the anterior cingulate cortex (ACC) and anterior Insula (AI) that together help to orchestrate behavioral output (e.g. adaptive learning). The ACC is a part of the affective pain processing system and receives projections from various sites, including the midline and intralaminar thalamic nuclei that are part of the medial pain system [17[•],18]. In humans, this network has been implicated in, among other things, the aversive experiences of receiving, anticipating, and controlling painful stimulation [19–21]. For example, a recent meta-analysis [22] showed that the ACC and AI are robustly involved during human fear conditioning, providing evidence that they play a supporting role in homeostatic autonomic and behavioral regulation. The specific functions of different subregions of the ACC remain contentious [23], which may be attributed in part to task specificity.

Learning critically modifies behavior, which can be studied through instrumental learning. In traditional instrumental learning paradigms, the organism learns to associate a behavioral expression with a directly experienced desirable or aversive outcome. For example, an individual might learn that a specific behavior leads to the successful avoidance of a punishment or to the attainment of a reward. Research in rodents illustrates that dopaminergic projections from the VTA to the ventral striatum and the prefrontal cortex (PFC) are central to instrumental learning [24]. These processes have been linked to

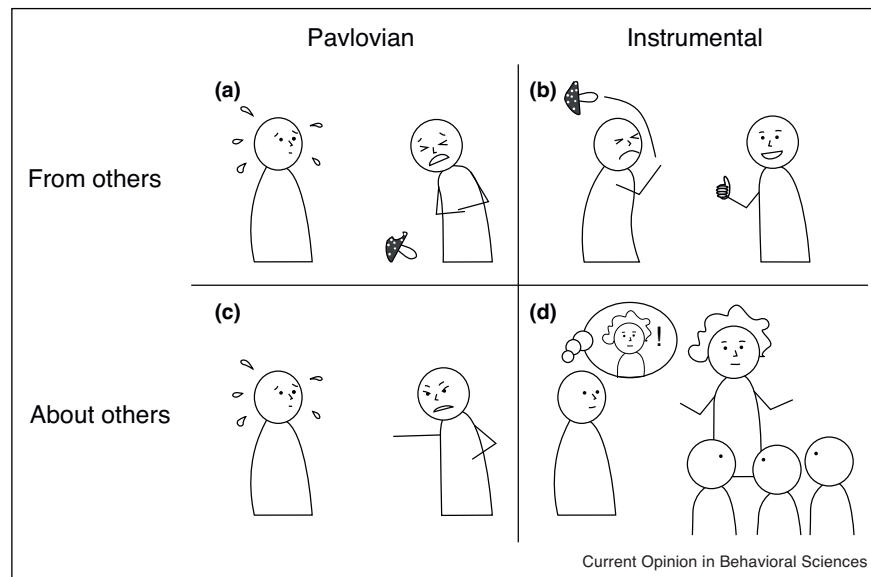
computational features of updating one's behavior through positive or negative reinforcement (known as Reinforcement Learning; RL). A key feature of RL, which has been related to the dopaminergic system, are error predictions. Although the lion share of RL research has targeted reward learning, a growing number of studies examine instrumental avoidance learning [25]. These studies demonstrate that the amygdala–striatal interactions underlie the acquisition of an avoidance response, such as choosing the cue that terminates an imminent shock [26,27]. Next, we aim to delineate how these basic learning networks interact with brain regions that are involved in processing social information, in order to mediate integration of social information onto survival circuits.

Survival through social regulation learning Learning about value from others

Learning from others ('demonstrators') allows individuals to circumvent needing to directly experience potentially noxious consequences. This speeds learning and allows an individual to utilize others' mistakes to optimize their own behavior. For example, watching a demonstrator become sick from a poisonous mushroom (Figure 1A) or actively avoid the mushroom (Figure 1B) can save an individual from directly experiencing a lethal event. Learning about threats from others constitutes an adaptive function documented across a range of species [2], but has also been implicated in the development of dysfunctional fears and phobias in humans [28–30]. Vicarious social learning depends, in part, on the same basic Pavlovian and instrumental learning mechanisms that serve as a defence towards threats recruited during direct learning [4,6,31[•]]. During social threat learning, the direct experiences of the threatening event are replaced by information transmitted through observation or instruction. For example, instead of directly experiencing a painful US, the demonstrator's expressions of pain can function as a social US. In this way, learning from others co-opts a basic Pavlovian learning network, which enables information to be integrated across additional regions that are associated with social value processing.

This conclusion that vicarious and direct forms of learning are partly dependent on the same Pavlovian mechanisms is supported by studies across species. For example, experiments in rodents reveal that the amygdala plays a critical role in vicarious threat learning, as pharmacological inactivation of the LA prevents acquisition of vicarious threat [32[•],33[•],34]. It has been further suggested that the synchronized activity between the amygdala and ACC, together with activity in thalamic nuclei in the medial/affective pain system (but not in the lateral thalamus, involved in sensory pain processing) mediates observational learning of threats [33[•]]. Recent work [17[•]] confirmed and extended these observations by showing that ACC neurons projecting to the basolateral amygdala

Figure 1



Examples of different forms of social learning. The learner learns *from* other another individual about (a) a dangerous object (Pavlovian) and (b) an adaptive behavior (instrumental), and learns *about* another individual whether s/he is (c) dangerous (Pavlovian) and (d) trustworthy, by observing others' reactions/behavior (instrumental).

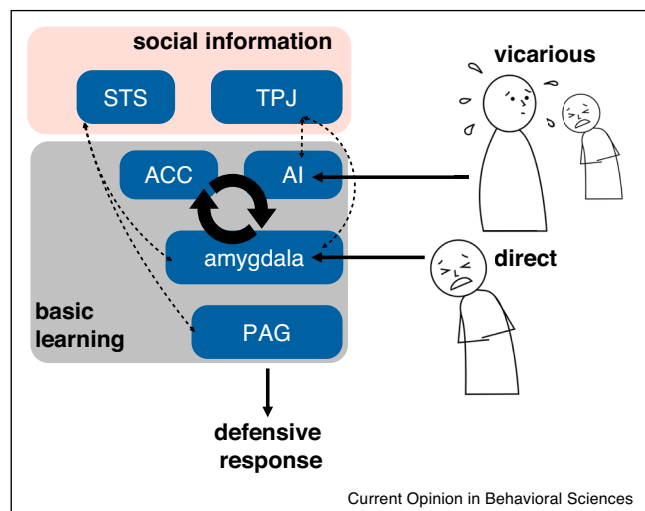
(BLA) preferentially encode socially aversive cue information (i.e. social US), and that selective inhibition of these projections impairs acquisition, but not expression, of observational threat learning. These findings demonstrate that vicarious information about the aversive value of a cue is transmitted from cortical areas (here, the ACC) to the amygdala, and that this pathway is critical for successful observational threat learning. Technical constraints preclude functional imaging of the human brain with similar spatial resolution, but an intriguing avenue forward would be to examine humans with selective lesions to homologous brain regions [35].

Brain imaging studies illustrate that, similar to non-human animals, complex social learning in humans also recruits basic learning networks. Indeed, vicarious social threat learning involves a set of neural regions that support Pavlovian learning: amygdala, AI, and ACC [10,31[•],36,37]. Moreover, vicarious threat learning engages activity in the midbrain PAG, including regulation via the endogenous opioid neuropeptide system [10], which is known to be central to defensive responses arising from direct aversive experiences [38]. These results support our idea that information is shared between basic learning circuits supporting defensive functions and higher-level social processing. Further support of such interactions are buttressed by research illustrating increases in functional connectivity when watching a demonstrator's painful reactions, for example between the PAG and superior temporal sulcus (STS) [10], between the amygdala, STS, and temporoparietal

junction (TPJ), as well as between the AI and TPJ [31[•]]. The STS and TPJ are key regions in social cognitive processes that integrate perceptual and abstract social information [39] and the attribution of beliefs to others, respectively [40]. Recent studies in humans reveal that an area in the gyrus of the ACC (gACC) allocentrically represents information about the consequences of another's actions—in contrast to egocentric representations about the outcomes of one's own actions [41]. The mapping of direct anatomical connections between the gACC and the BLA in primates [42] lends support to the speculation that projections from the ACC to the BLA are critical for learning through observing consequences to others, similar to what has been shown in mice [17^{••}].

As reviewed so far, vicarious learning is realized through the interactions between basic survival circuits and higher social cognitive brain networks. Recent research also reveals that the brain regions common to Pavlovian and vicarious learning might process the information differently (see Figure 2). For example, a recent study using dynamic causal modelling of cross-regional connectivity between the amygdala, ACC and AI revealed that the flow of information between regions in a network common to direct and vicarious learning differed between the two learning types. In particular, information about the US (self and other experienced shock) was most likely to enter the network through the amygdala during direct conditioning and through the AI during observational learning [31[•]]. This functional role of the AI resonates well with other research showing that AI is a key region

Figure 2



Schematic illustration of a basic learning circuit that interacts with regions processing social information during vicarious and direct (Pavlovian) threat learning in humans (described in Ref. [31]). Bold arrows to the right indicate likely inputs of vicarious and direct information, respectively. Circular bold arrows refer to connectivity between three core regions during both direct and vicarious threat learning, and dashed lines indicate connectivity during threat learning. ACC: anterior cingulate cortex; AI: anterior insula; PAG: periaqueductal gray; STS: superior temporal sulcus; TPJ: temporoparietal junction.

for empathic processes [43–45] and is further supported by the finding that, together with activity in the AI [36], empathic appraisals [46] predict the expression of observational threat learning.

Evidence that the AI relays information to the ACC and the amygdala dovetails with the aforementioned research in rodents [17] which describes the critical role cortical regions play in communicating with the amygdala when learning from others. This relay of information from cortical to subcortical regions central for basic learning suggests that vicarious learning relies on a hierarchical organization from higher to lower level processing. It should be noted, however, that the amygdala swiftly responds (approx. 70 ms) to social information, such as facial expression of fear [47], before these stimuli are even processed in visual cortical areas. Hence, it is likely that bidirectional information transfer between basic learning networks and more executive cortical regions are at play during vicarious learning.

Research that indicates integration of social information into basic Pavlovian mechanisms does not only include learning about threats, but recent studies have further revealed associative learning mechanisms when learning safety from others. In particular, observation of others' safety experiences when being exposed to a CS extinguishes conditioned responses [48], which is paralleled by

decreased responses in the amygdala towards CS (as compared to control stimuli). Furthermore, pre-exposure to CS through an identical vicarious safety procedure reduces the subsequent acquisition of vicarious learning, an effect that might indicate latent inhibition of vicarious learning [7].

Recent studies have further outlined the integration of social information through modulation of social factors specific to both the demonstrator, the observer, and their relationship during social threat learning. For example, as with other animals, demonstrator-observer similarity enhances observational learning of threat (as well as safety [49,50]); however, the neural circuitry involved in the regulation of these social factors during threat and reward learning has yet to be investigated.

Similar to enhanced social learning seen in inbred gregarious mice strains [51], humans scoring higher in trait empathy, show greater learning rates in a vicarious learning task [52], which can lead to higher rates of altruistic behavior [53]. Moreover, analogous to the role of dominance in non-human primates in learning [2], ascribed demonstrator dominance [54] and skill [55] facilitates human threat learning and avoidance, respectively. For example, attributed dominance can be learned by observing the outcomes of confrontations between dyads, and such attribution is modulated by the amygdala [54], supporting the idea that social information is integrated in basic learning circuits that mediate learned defensive responses. The integration of social information with basic aversive learning extends to how individuals learn about social rewards. For example, individuals who take the advice of others, or make bets about monetary rewards based on those with expertise, exhibit engagement of the mPFC, striatum, and TPJ [56,57,58].

Learning about another's social value

To survive and adaptively engage with others in the community, individuals must also learn who they should trust, rely on, and cooperate with. This requires constant learning—and updating when prediction errors ensue—about the social value of others: Should I avoid this aggressive looking individual? (Figure 1C). Should I trust the advice of this stranger? (Figure 1D). A growing body of research suggests that just as objects and experiences can acquire value through several avenues, so too can individuals use various routes to learn about the social value of others.

When learning about the value of others, there is evidence that basic learning mechanisms provide an efficient and fruitful way of representing social and moral value. The emotional value acquired through pairings of stimuli (e.g. an individual paired with a negative social experience) can come to flexibly shape how we learn about another's moral value, independent of any instrumental

influence [59]. One early study found that pre-exposure effects, in this case providing subjects with information that a potential social partner is either morally good or bad, is enough to override any additional—and directly experienced—information that the partner is in fact morally upright or morally debased [60]. These initial and lasting moral impressions formed through pre-exposure effects were found to be encoded by the striatum, a neural learning hub observed in both rodents and humans that encodes instrumental value.

Other work following in the tradition of associative learning finds that, just as in the non-social domain, Pavlovian mechanisms govern how we learn the social value associated with other people. One phenomenon of associative learning is ‘blocking’, which describes how learning about the value of one stimulus becomes blocked if another stimulus, already known to predict certain outcomes, is presented in compound with it. In general, this phenomenon illustrates how previously learned information about one stimulus can effectively ‘block’ learning about a concurrent stimulus [61,62] a process that involves the mPFC and its ability to integrate information [63,64]. Two recent studies extended this effect to learning about social information [61,62]. For example, one study found that, in accordance with Pavlovian learning theory, pre-existing social value (e.g. generosity) associated with people you know prevents you from learning about other individuals who act in the same way and are present at the time of learning [13]. Similar to what is observed during basic instrumental learning mechanisms that rely on the mPFC to update behaviors through positive or negative reinforcement, these highly complex social behaviors have also been shown to be mediated by the mPFC [63].

More recent work has made inroads in precisely characterizing the role of the mPFC as a hub for integrating and orchestrating social value information to guide adaptive choice. Specifically, the mPFC appears to support how humans perceive and judge others, through both direct and indirect learning mechanisms. One study revealed that the mPFC modulates the perception of faces during learning [65], while another study illustrated that this region also integrates the information directly gleaned from faces with higher-order conceptual knowledge to bias these visual perceptions [66]. Even without any direct experience, however, the mPFC can govern social Pavlovian learning processes through an efficient learning process known as stimulus generalization (where an animal learns about one stimulus and applies that knowledge to other similar stimuli [67]). For example, encountering a stranger who resembles an individual known to be untrustworthy results in the stranger being trusted less—a putatively adaptive choice subserved by the mPFC and amygdala selectively encoding the transfer of moral value [11••].

Another avenue by which humans acquire social value is through instrumental associations, where a valenced outcome becomes yoked to a discrete choice. Decades of work in economics and psychology reveal that such instrumental associations—which often take the form of direct and repeated exchanges—can imbue an individual with either positive or negative moral value. Research has shown that social outcomes, such as emotional expression, can serve as reinforcers similar to non-social rewards and punishments [68,69]. Moreover, information, that a person is kind or cruel, is then used to guide adaptive decision-making. For example, learning about a person’s trustworthiness [70] or cooperative tendencies [71] unfolds quickly and only takes a few exchanges, a seemingly domain-general process that is governed by prediction errors generated by the striatum and VTA [72–74]. Interestingly, moral information that a person generally behaves in certain prosocial or antisocial ways is so useful for subsequent adaptive choices, that it can supersede purely rewarding actions [75].

Conclusions and future directions

Research across species and research traditions has begun to describe the ways social situations regulate the actions of a range of survival functions, such as defensive responses that are linked to Pavlovian and instrumental learning processes. We suggest that a basic domain-general learning circuit mediates Pavlovian and instrumental learning processes by integrating direct experiences, as well as social information from or about others. Such a framework can aid our mechanistic understanding of many social phenomena, from simple social aversions to moral judgments. These basic learning phenomena, including extinction, generalization, and latent inhibition, are useful for explaining how more complex social behaviors are learned.

Recent research reveals, however, that while there are shared core computational and neural processes for personal and social experiences, there are also divergences, as social learning is uniquely dependent on social cognitive functions and the specific interaction between associated brain regions. Important future research questions will be to examine the precise computational and neural mechanisms governing the interaction between basic learning and social cognition, and to determine to what extent social learning can be explained by referencing non-social processes. Another challenge for future research of social regulation of survival circuits will be to improve the integration of knowledge about *function* and *mechanism* of social learning. This will require the joint forces of both ethologists studying functional learning strategies across species [76], and social and affective neuroscientists studying the neural mechanisms of these strategies [11••,77].

Conflict of interest statement

Nothing declared.

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