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Biological Mechanisms for Observational Learning

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Abstract

Observational learning occurs when an animal capitalizes on the experience of another to change its own behavior in a given context. This form of learning is an efficient strategy for adapting to changes in environmental conditions, but little is known about the underlying neural mechanisms. There is an abundance of literature supporting observational learning in humans and other primates, and more recent studies have begun documenting observational learning in other species such as birds and rodents. The neural mechanisms for observational learning depend on the species' brain organization and on the specific behavior being acquired. However, as a general rule, it appears that social information impinges on neural circuits for direct learning, mimicking or enhancing neuronal activity patterns that function during pavlovian, spatial or instrumental learning. Understanding the biological mechanisms for social learning could boost translational studies into behavioral interventions for a wide range of learning disorders.

Introduction

Observational learning is the capacity to acquire or optimize behavior by witnessing a similar or relevant experience in another animal. Observational learning, and the more general concept of social learning, was proposed and demonstrated in humans by Albert Bandura, in an effort to bridge behaviorist and cognitive learning theories [1,2,3]. Bandura's most famous and controversial result is the Bobo doll experiment on the social acquisition of

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aggressive behavior, in which children observed an adult that verbally and physically ‘attacked’ an inflatable Bobo doll. After this episode, children manifested increased aggressive behavior towards the doll, often imitating the manner in which the adult behaved [2,3,4]. Thus Bandura clearly enunciated that learning novel behaviors can rely purely on observation or direct instruction, even in the absence of classical reinforcement [1,2,3,4]. Bandura’s theory was particularly relevant to the acquisition of language, which could not be satisfactorily explained by previous behaviorist or cognitive theories [4,5].

Over the last few decades, there have been an increasing number of studies documenting evidence for observational learning in non-human primates, birds, rodents, fishes and invertebrates [6,7,8,9]. The range of behaviors that can be acquired by observational learning appears to be extensive, from fear associations to vocal learning, tool use and prey catching behavior [9,10,11,12,13]. Observational learning paradigms usually consist of a model (i.e., a demonstrator or actor) that experiences an event or that executes a behavior, and an observer that voluntarily or involuntarily witnesses the behavior of the model or the consequences of the event experienced by the model. During social learning, new behaviors can be acquired by different mechanisms [14]. For certain behaviors, like the social transmission of stress or maternal behavior in rodents, the mere social presence of a conspecific represents a sufficient trigger (Fig. 1a)[15**,16,17]. In other cases, the demonstrator simply draws the attention of the observer to a specific location (local enhancement) or a specific object (object enhancement) that will be relevant for producing the behavior (Fig. 1b) [6,18]. Imitation of actions is another variant of social learning, where the observer copies a movement or a sequence of movements, usually with the purpose of obtaining a reward or of averting punishment. Imitation has been demonstrated in a number of species by the two-action paradigm where the observer reproduces the movement of the demonstrator to obtain a reward that could have been reached by at least one other action (Fig. 1c)[12,19,20,21,22]. Finally, social learning can also refer to emulation, where the observer learns the goal of the behavior from the demonstrator but attains that goal by an action that is different from the one observed [23,24,25].

The different mechanisms of social learning likely rely on different cognitive processes: attention to the model, retention of the observed event or behavior, inferring the goal of the action, reproduction or implementation, motivation to reproduce the observed behavior, anticipation of consequences and response to feedback [2,3,14]. The detailed neural substrates for these complex processes seem to involve brain structures implicated in perception of social stimuli (e.g., sensory and insular cortex), executive control (e.g., the anterior cingulate cortex, ACC), memory formation (e.g., amygdala, hippocampus), and movement control (e.g., mirror neurons in the premotor cortex). Several recent studies suggest that social information might feed into circuits involved in more conventional direct learning or conditioning, and therefore might employ partially overlapping functional connectivity and/or synaptic plasticity mechanisms to adjust behaviors in an effective manner. We will review here some of the evidence supporting this hypothesis.

Imitation and emulation in humans and other primates

The highly evolved capacity for social learning in people is thought to contribute to the development of traditions and culture, and is at the core of several educational theories and successful pedagogical approaches [27,28]. In particular one form of observational learning, emulation, is highly developed and sophisticated in the human population. This is likely facilitated by the use of spoken and written language, a fast mean to communicate instructions [26]. However, even pre-lingual infants can acquire behaviors by emulation and by imitation [29]. The drive for this is possibly the evolutionarily selected advantage of bonding with the adult that can provide protection [30]. Adult humans and non-human primates can also form social attachments by non-verbal imitation [31,32], and this appears to be part of self-sustained behavioral loop: social interactions are generally rewarding for primates (as well as other mammals), and could play the role of a positive reinforcer in learning to imitate [31,32,33]; imitation then boost the rewarding nature of the specific interaction. Generally, in primates and other mammals, social information appears to modulate neuronal activity in structures of the classical reward pathway (ventral tegmental dopamine neurons, ventral striatum, medial prefrontal cortex), a major circuit for direct learning [34,35,36,37]. Social information is also encoded in the amygdala, a structure known to play an important role in aversion [38]. This evidence points to the neural mechanisms by which social information could substitute for reward and punishment during observational learning.

Many species of non-human primates use tools to obtain food in the wild. For example, chimpanzees manufacture appropriate sticks and use them to fish termites out of their mounds. This involves a complex sequence of actions that would be difficult to achieve by an individual through trial and error. It is more likely that chimpanzees and other primates acquire the knowledge of tool use as juveniles, by observing their parents or other adults perform the task, and then imitating the behavior [39]. This hypothesis has been tested by two-actions tasks designed for laboratory or field conditions. A common approach is using an ‘artificial fruit’, a device that has a reward at the center and one or several ‘protective’ layers that need to be removed by the animal. These layers can be removed by at least two different actions, only one of which is witnessed by the observing animal. Consistently, following observation, the method of opening the artificial fruit is the same as the one used by the demonstrator conspecific [12,19,40]. Some primates can acquire such imitative behavior from a human actor, showing that information can be transmitted not only within species but also across species [40].

An important step towards understanding the physiological substrate for action imitation was the discovery of mirror neurons in the premotor area, inferior frontal gyrus and inferior parietal lobule of macaque monkeys by Giacomo Rizzolatti and colleagues [41]. These neurons fired robustly when the monkey made a certain hand movement and also when it observed the human researcher produce the same hand movement. Similar neurons were later found to mirror mouth and facial movements [42]. It appears that mirror neurons integrate sensory and motor information, therefore it is believed that they could play an important role in understanding the action of another animal, and perhaps in the implicit learning of an action in order to reproduce it later [43]. Both of these roles would be

important steps in imitative learning, however there is no clear evidence to date that mirror neurons might be implicated in observational learning or in direct motor learning [30].

Since this discovery, the existence of mirror-like neurons has been reported in birds and humans [44]. In humans, functional imaging studies described a mirror system, localized in similar brain areas as originally described in the macaque [45]. The existence of mirror systems for facial gestures in particular, generated much speculation on their possible role in the social transmission of emotional states. Humans and other primates that are capable of complex facial expressions are also experts in quickly detecting and recognizing the emotional state of another individual [9]. Often, this results in emotional contagion, where the observer assimilates the emotion perceived in another [9,16]. The neural substrate seems to involve the amygdala, a structure that is important for processing certain emotions such as fear or avoidance [9,46]. For example, if humans either observe another person experiencing negative consequences or are simply told about negative consequences, similar levels of amygdala activation occur as would be expected from directly experiencing the negative outcomes themselves [9]. If mirror neurons were important for emotional recognition and contagion, they would be expected to be functionally connected to the amygdalar complex or to subcortical structures including brainstem nuclei, the hypothalamus and the dopaminergic ventral tegmental area, important in encoding punishments or rewards. There is much to be learned about the development and plasticity of mirror neuron circuitry, an endeavor that could be helped in the future by new developments in using optogenetic and transgenic approaches in primates that show robust imitative behaviors, such as marmosets [47], or by identification of clear behavioral analogs in rodent models.

Social transmission of song production and tool use in birds

In birds, vocal imitation is the best documented form of social learning [48,49]. Juvenile songbirds such as zebra finches sequentially acquire their father's song by listening and then reproducing it, progressing from an unstructured vocal output to a precisely structured mature song. Songbirds seem to have an internal drive for copying the song of their father (or another tutor), and they can do this when the song is played back in isolation or produced by a robot [50**].

Much has been discovered about the neural and synaptic mechanisms for vocal learning in zebra finch. The HVC forebrain nucleus is important for song imitation, and acts as an interface between the sensory information received from higher order auditory areas and the motor commands generated internally [50**]. A recent study by Vallentin et al. showed that inhibitory synaptic inputs to HVC projection neurons are involved in vocal imitation [50**]. Intracellular recordings in awake birds showed that auditory cues from the tutor song evoked robust and temporally precise firing in about half of the HVC projection neurons in juvenile but not adult birds (Fig. 2a). Vallentin et al. used two-photon guided in vivo voltage-clamp recordings to reveal sensory-evoked excitatory events in projection neurons and then show that in adult birds, the played-back song recruits robust local inhibition in HVC that suppresses spiking of motor neurons. Played-back tutor song drives inhibitory cells spiking in both adult and juvenile birds, as revealed by directly recording interneuron activity (Fig. 2b). This produced temporally-precise inhibitory currents in HVC projection neurons for the

parts of the song that had already been learned but not for the rest of the song that had yet to be correctly imitated (Fig. 2c). Thus, activity of inhibitory neurons was driven by social auditory cues to induce structured firing of HVC projection neurons, and appeared to orchestrate the development of social learning for song production.

Birds can also learn other behaviors by observation. Chicks, for example, can learn the association between an object and an aversive taste after witnessing a single event in which a demonstrator bird pecks a bead covered in an aversive substance [51]. Budgerigars and other birds can learn to use tools in order to acquire food by observing other birds and even humans using that tool [23,52,53]. Zebra finches can acquire nest building behavior by watching streamlined videos of conspecifics building their nest [54]. The neural mechanisms for these other forms of observational learning are less well understood.

Social transmission of threat avoidance in rodents

In laboratory rodents, the best documented form of observational learning is the ability to associate a context or a stimulus with fear, after being exposed to a conspecific that experiences classical fear conditioning [9,55,56**]. To learn this behavior, the animals have to recognize fear responses in conspecifics. In mice and rats, this recognition is probably done via multiple modalities: visual (the freezing or escaping behavior of the demonstrator), auditory (distress calls produced in response to pain), and/or olfactory (pheromones that can be discharged during painful and dangerous conditions) [15**,57*]. Sterley et al. found that a mouse experiencing foot shocks secretes an anogenital pheromone that can be investigated by conspecifics [15**]. Exposure to this pheromone is sufficient to induce in the receiver mouse increased levels of circulating cortisol, and metaplasticity of excitatory synapses on corticotropin-releasing hormone neurons in the hypothalamus. Similarly, monogamous prairie voles can detect the emotional state of the partner after the later experienced fear conditioning to a tone [58**]. When the stressed vole freezes in response to the conditioned stimulus, its partner also freezes and experiences a surge in cortisol levels. In rats, the ultrasonic distress calls (in the 22 kHz band) seem to be capable of transmitting information about the emotional state of a conspecific that received foot shocks [57*]. It is therefore likely that witnessing the stress of a conspecific represents an aversive stimulus in rodents, similar to the unconditioned stimulus during classical fear learning. The speed with which the observer rodent acquires the novel fear association depends on how much access it has to these fear-related behavioral outcomes, and in some cases on the relationship with the demonstrator [55*,58**].

The multiple processes implicated in observational learning require complex interactions between key brain structures. In particular, in the case of observational fear learning in rodents, interactions between limbic structures seem to play an important role [55,56,58]. In the observer mouse, ACC activity is necessary for expressing freezing behavior after witnessing a conspecific that undergoes contextual or cued fear learning, and for retaining the memory of the aversive stimulus 24 hours later [55*,56**]. Immediate/early gene expression, a marker for neuronal activity, was also demonstrated in the ACC in voles during exposure to a stressed partner [58**]. This indicates that the ACC might be an important brain structure responsible for processing social stimuli. Information from ACC appears to

be transmitted to the basolateral amygdala (BLA), a brain structure known to encode fear learning during classical conditioning [46]. During observational learning, the activity in ACC and BLA is synchronized in the theta range [55*]. Significantly, ACC neurons fire in response to both the cue and the shock delivered to the demonstrator mouse [56**]. Following conditioning by proxy, BLA neurons also start responding to the paired cue (Fig. 3a). This BLA plasticity during observational learning depends on direct projections received from ACC. During observational learning, BLA- projecting ACC neurons have increased firing compared to non-BLA projecting neurons, and their suppression decreases cue-evoked responses in the BLA during observational learning. When ACC to BLA projection neurons are silenced, observational learning is impaired (Fig. 3b). However, if the behavior has already been acquired by observation, inhibiting the cingulate neurons projecting to the amygdala does not impair the production of learned behavior. These experiments indicate an important role for functional connectivity between the cingulate cortex and the amygdala during observational learning of threat avoidance in rodents. It remains to be determined if ACC plays an important role in other forms of socially transmitted behavior in rodents.

Social-guided spatial navigation in rodents

Spatial navigation and spatial learning use place cells in the hippocampal CA1 region, and grid cells in the entorhinal cortex in rodents and in humans [59,60]. Place cells develop in response to allocentric and vestibular cues, and fire to indicate where the animal is located in space. During many types of observational learning, it is essential that the observer correctly locates the position of the demonstrator in space. How is this achieved? Two recent papers identified social place cells in rats and bats, in the same part of the hippocampus where the classical place cells are located [61*,62*]. These cells fired to indicate the spatial position of a demonstrator conspecific. Remarkably, up to 13–15% of all place cells were also social place cells; conversely, about half of all social place cells could also be characterized as classical place cells. These findings indicate that there is partial overlap in neural circuitry encoding the position of self and the position of a behaviorally relevant other. Future studies should investigate if grid cells and other neurons important for spatial navigation are also capable of encoding trajectories of others, in both rodent models and humans.

Conclusions

The ability to learn from the experience of a conspecific likely provides selective advantage during evolution, and therefore should be present in many species. Indeed, in addition to the mammalian examples discussed here, there is evidence for social learning in invertebrates, whether these are highly social (eusocial insects like bees and ants) or minimally social (asocial octopuses) [63,64].

In most species studied, the neural substrate for social learning seems to at least partially overlap with neural circuits for learning from direct experience. Social information could feed into these circuits at several different ‘entry points’. For example, during fear learning, social information appears to be processed in the cortex, particularly the ACC and the insula, and from there transmitted to the amygdala where it substitutes for the representation of the

unconditioned stimulus or of a secondary reinforcer. In the case of action learning such as vocal and tool use learning, social information seems to control the activity of motor neurons or of action-planning neurons. In the case of spatial navigation, social inputs can modulate the activity of place cells in the hippocampus. Future studies are required to determine how much neural circuit mechanisms for direct and observational learning resemble each other and how much they differ, and to what extent the overlap might explain efficacy of observational learning. Finally, understanding the mechanisms for observational learning could eventually refine social behavioral interventions that are currently used only minimally and empirically.

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prevented, both partners exhibit high stress levels, indicating that the emotional state was socially transmitted. The behavioral response to the stress of the partner is mediated by oxytocin receptor neurons in ACC.

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Highlights

- Many animal species can learn by observing the behavior of a conspecific
- Recent studies are investigating the neural circuits for observational learning
- Observational learning uses similar circuits as for other forms of learning
- Social information can substitute for reward, punishment, or motor plan
- Plasticity of excitatory and inhibitory synapses is likely involved

(a) Emotional Contagion

(b) Local/Object Enhancement

(c) Imitation in a two-action task

Figure 1:
Mechanisms of social learning

- (a) Emotional contagion in rodents. The observer animal displays distress in response to a stimulus after detecting fear conditioning to that stimulus in another animal.
- (b) Local enhancement in fish. One fish can direct the trajectory of others that observe its location during foraging.

(c) Two-action device for testing imitation in primates. The device has 2 or more ways of allowing access to reward. The observer picks the option successfully used by a demonstrator animal.

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Figure 2:

Vocal learning in song birds

(a) Juvenile birds have an underdeveloped song and tutor song-evoked spiking responses in HVC projection neurons. Adult birds have a mature song and HVC projection neurons are silent during played back song.

(b) Inhibitory interneurons in HVC have song-evoked spiking activity.

(c) Inhibitory currents in HVC projection neurons are temporally precise for the parts of the song that have been learned.

Figure 3:

Social transmission of stress in rodents

(a) ACC activity induces plasticity in BLA neurons

(b) Activity of ACC→BLA projection neurons is necessary for observational learning of fear responses.