Modulatory Effects of Oxytocin on Learning and Memory: Evidence from Animal and Human Studies

Authors: Zhou Menghan, Zhang Yuan, high mountain, KeithM.Kendrick, Yao Shuxia, Yao Shuxia

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Abstract

As a neuropeptide, oxytocin exerts extensive modulatory effects on individual social behavior and emotional processing, including its influence on learning and memory functions that play a critical role in human work and daily life. Animal and human studies employing various modality techniques have consistently demonstrated that oxytocin plays a significant modulatory role in learning and memory. This effect may be mediated by oxytocin binding to widely distributed oxytocin receptors in key brain networks underlying learning and memory, such as the dopamine reward pathway and limbic system, thereby modulating their functional states. However, the facilitatory or inhibitory effects of oxytocin on learning and memory vary depending on factors such as experimental paradigm, stimulus materials, administration timing, dosage, and location. Future research should integrate the respective advantages of animal and human studies, adopt standardized experimental task designs and administration protocols to overcome current limitations in this field, and actively explore the therapeutic potential of oxytocin in intervening with learning and memory processing deficits in patients with related psychiatric disorders.

Full Text

The Modulatory Effects of Oxytocin on Learning and Memory: Evidence from Animal and Human Studies

ZHOU Menghan, ZHANG Yuan, GAO Shan, Keith M. Kendrick, YAO Shuxia (Key Laboratory of Neuroinformation, Ministry of Education, School of Life Science and Technology, University of Electronic Science and Technology of China)

Abstract: As a neuropeptide, oxytocin plays a crucial modulatory role in social cognition and emotional processing, including its influence on learning and memory activities that are essential in daily life and work. Animal and human studies employing different modalities have consistently demonstrated that exogenous oxytocin exerts important modulatory effects on learning and memory. These effects likely occur through oxytocin's binding to widely distributed oxytocin receptors in key brain networks for learning and memory, such as the dopamine reward pathway and limbic system, thereby modulating their functional states. However, the facilitatory or inhibitory effects of oxytocin on learning and memory vary depending on experimental paradigms, stimulus materials, administration timing, location, and dosage. Future research should leverage the respective advantages of animal and human studies, employ standardized experimental protocols and administration procedures to overcome current limitations, and actively explore oxytocin's therapeutic potential for addressing learning and memory deficits in psychiatric disorders.

Keywords: oxytocin, learning, memory, neural mechanism

Oxytocin is a neuropeptide synthesized in the magnocellular neurons of the hypothalamic paraventricular and supraoptic nuclei (Swaab et al., 1975; Vandesande & Dierickx, 1975). Early research revealed its indispensable role in animal reproduction and its ability to enhance maternal behaviors such as offspring protection and nursing (Pedersen et al., 1979). Subsequent studies have shown that oxytocin plays a significant role in regulating human social behavior and emotional processing (Fehm-Wolfsdorf & Born, 1991; Keverne & Curley, 2004; Meyer-Lindenberg et al., 2011; Striepens et al., 2011), making it a major focus in psychology and neuroscience research over recent decades. Oxytocin's modulatory functions encompass enhancing empathy and social recognition abilities (Domes et al., 2007; Marsh et al., 2010) and alleviating anxiety and stress responses (Heinrichs et al., 2003), including its influence on individual learning and memory processes (Guastella et al., 2008; Hurlemann et al., 2010).

Learning refers to relatively permanent changes in behavior or behavioral potential resulting from experience in a given situation, while memory represents the fundamental psychological processes of encoding, retention, and retrieval or recognition of information (Peng Danling, 2001). These two cognitive activities are closely intertwined yet fundamentally distinct. Learning cannot proceed without memory, which serves as its foundation and guarantee, and learning outcomes are typically evaluated through various forms of memory tests. Both processes are crucial for daily work and study activities and have clinical applications, such as developing therapeutic protocols for post-traumatic stress disorder and drug addiction patients based on manipulating memory reconsolidation (Clark, 2018). Many cognitive studies have examined learning and memory in combination (Cohen et al., 2019; Goode & Maren, 2017), and accumulating neuroimaging evidence indicates they share common cortical and subcortical neural substrates, including the frontal cortex and striatum (Poldrack et al., 2001; Rapp & Wiley, 2019). Consequently, learning and memory are often

discussed together in research on oxytocin's cognitive effects.

Numerous studies have demonstrated that oxytocin can influence learning and memory activities in both animals and humans (Benelli et al., 1995; Evans et al., 2010; Kovács et al., 1979; Guastella et al., 2008; Hurlemann et al., 2010; Tomizawa et al., 2003). Molecular biology research reveals that oxytocin receptors are extensively distributed throughout the classic reward pathways in mammalian brains, such as the dopamine reward pathway (Hollerman & Schultz, 1998; Schultz, 2006), including core nodes like the ventral striatum, nucleus accumbens, and ventral tegmental area (Baskerville & Douglas, 2010; Huber et al., 2005; Lee et al., 2009). Additionally, oxytocin receptors have been identified in brain regions closely associated with associative learning, prosocial learning, and memory, including the amygdala, anterior cingulate cortex, and hippocampus (Li et al., 2011; Lin & Hsu, 2018; Lockwood et al., 2016; Boccia et al., 2013). Therefore, oxytocin likely modulates learning and memory processing by binding to receptors within reward and learning circuits, thereby influencing their functional states. Although these studies indicate oxytocin can affect learning and memory, no comprehensive review has yet detailed the specific conditions under which these effects occur or their underlying neural mechanisms. A systematic review of this field would not only expand our understanding of oxytocin's role in modulating social behavior and emotional processing but also deepen our knowledge of its mechanisms of action on learning and memory, providing new directions for future research.

Based on this background, the present review examines the specific modulatory effects of oxytocin on learning and memory in animal and human studies and their potential neural mechanisms. We focus on analyzing how experimental settings, stimulus materials, administration timing, dosage, and location influence oxytocin's modulatory effects on learning and memory processing (see Figure 1 [Figure 1: see original paper]), and conclude by summarizing current limitations and future research directions.

2.1 Modulatory Effects of Oxytocin on Animal Learning

Animal model research serves as a crucial foundation in life sciences, offering unique advantages for revealing specific cognitive processing mechanisms due to its fine-grained methodological approaches and fewer ethical constraints, providing valuable insights and translational potential for human studies. The accumulated body of oxytocin research in animals is substantial, with research focus shifting from early investigations of instinctual social attachment behaviors like maternal and affiliative behaviors (Carter et al., 1992) to more recent examinations of social cognition and behavior, including social recognition (Ferguson et al., 2000) and aggression (Bales & Carter, 2003). As a higher-order cognitive activity and essential basis for organism-environment interactions, learning plays a vital role in animal adaptation and survival, making the investigation of oxytocin's modulatory effects on learning particularly significant.

Early animal studies investigating oxytocin's effects on learning frequently employed passive avoidance learning tasks (see Table 1), which were developed based on rats' preference for darkness over light and their fear memory of aversive stimuli such as foot shocks. In these experiments, rats were placed on a lit platform connected to a dark chamber, with baseline latencies to enter the dark chamber measured during the first two phases. During the third learning phase, foot shocks were delivered upon entry into the dark chamber to induce avoidance behavior (Bohus, Urban, et al., 1978; Kovács et al., 1979). In 1978, Bohus and colleagues administered oxytocin intracerebroventricularly (0.1/1.0 ng) after learning and found that rats showed significantly reduced latencies to enter the dark chamber 24 hours later, indicating impaired avoidance learning. This suggested that oxytocin may have interfered with fear memory consolidation, thereby inhibiting avoidance behavior (Bohus, Urban, et al., 1978), an effect not modulated by the interval between learning and oxytocin administration (0/3/6/23 hours) (Bohus, Kovács, & de Wied, 1978). Peripheral administration of oxytocin showed no significant modulatory effect on avoidance learning (Bohus, Urban, et al., 1978). Using the same paradigm, subsequent research examined direct microinjections into specific brain regions, revealing that oxytocin injection into the dorsal septal nucleus (25 pg) significantly prolonged latencies, indicating facilitated avoidance learning. Conversely, injections into the hippocampal dentate gyrus (25 pg) and dorsal raphe nucleus (50 pg) significantly reduced latencies, demonstrating inhibitory effects on avoidance learning (Kovács et al., 1979). Similar to peripheral administration, injection into the central amygdala (25 pg) produced no significant effect. These findings demonstrate that oxytocin's modulatory effects on avoidance learning are dissociable depending on administration site, possibly due to differential metabolic degradation across brain regions or functional differences between regions (Kovács et al., 1979).

Oxytocin's modulatory effects on animal learning also vary across different learning types. In contrast to the inhibitory effects of intracerebroventricular oxytocin on passive avoidance learning (Bohus, Urban, et al., 1978), intracerebroventricular administration (2 ng) significantly enhanced long-term spatial learning in nulliparous female mice in a maze task (Tomizawa et al., 2003), consistent with findings that female mice exhibit enhanced spatial learning and memory during estrus when endogenous oxytocin levels are elevated (Dawood et al., 1979; Kinsley et al., 1999; Kumaresan et al., 1979). Furthermore, administration of oxytocin antagonists to maternal rats that had already demonstrated good spatial learning during pregnancy (day 14 to experiment end) effectively inhibited their spatial learning and memory performance, further confirming oxytocin's critical role in modulating spatial learning (Tomizawa et al., 2003).

Given the close relationship between the nucleus basalis of Meynert and spatial learning in animals (González et al., 2004), Wu and Yu (2004) systematically investigated the effects of different oxytocin doses (0.2/2/10 nmol) injected into this region on spatial learning in rats. Results showed that rats in the 2 nmol and 10 nmol conditions took significantly longer to complete the maze task com-

pared to the 0.2 nmol and control (2 l saline) groups. Pre-treatment with an equivalent dose of oxytocin antagonist before 2 nmol oxytocin administration counteracted the inhibitory effect on spatial learning (Wu & Yu, 2004), demonstrating that oxytocin's inhibitory effect on nucleus basalis-mediated spatial learning is essential. Although the study did not examine whether antagonist pre-treatment would similarly counteract the inhibitory effect at the 10 nmol dose, the differential effects observed between 0.2 nmol and 2/10 nmol conditions suggest that oxytocin's modulatory effects may require sufficient dosage to manifest.

These studies reveal dual modulatory effects of oxytocin on animal learning: inhibitory effects observed following intracerebroventricular (0.1/1.0 ng), hippocampal dentate gyrus (25 pg), and dorsal raphe nucleus (50 pg) injections on passive avoidance learning, and nucleus basalis injections (2/10 nmol) on spatial learning; and facilitatory effects demonstrated by dorsal septal nucleus injections (25 pg) on passive avoidance learning and intracerebroventricular injections (2 ng) on spatial learning. Notably, the same administration route (e.g., intracerebroventricular) produced opposite effects on different learning types (passive avoidance vs. spatial learning), while the same learning type (e.g., passive avoidance) showed different effects depending on administration route (peripheral vs. intracerebroventricular), location, and dose. Despite this complexity, these studies consistently demonstrate the essential role of oxytocin in modulating learning, providing valuable insights for future animal research and offering translational implications for human studies.

2.2 Modulatory Effects of Oxytocin on Human Learning

Research on human learning in psychology and cognitive neuroscience has primarily focused on associative learning, with behaviorist stimulus-response theories serving as the main theoretical foundation. This framework posits that learning involves establishing connections between environmental stimuli and behavioral responses, with reinforcement being one of the primary mechanisms. Building upon numerous findings from animal models, human studies on oxytocin's modulatory effects on learning have made substantial progress. Given that oxytocin's effects on human behavior are highly context-dependent (Bartz et al., 2011; Kendrick et al., 2017), we will examine oxytocin's influence on human learning according to different learning types and discuss potential underlying mechanisms (see Table 2).

2.2.1 Social Learning Oxytocin is widely recognized for its prosocial effects in human research (Striepens et al., 2011), and it demonstrates positive modulatory effects on social learning. Hurlemann et al. (2010) employed a between-subjects, randomized, double-blind, placebo-controlled design using a number classification task to investigate oxytocin's modulation of social associative learning. Participants classified number strings through binary choices and optimized subsequent behavioral selections based on feedback. Results showed

that intranasal oxytocin selectively enhanced performance under social feedback conditions without significantly affecting performance under nonsocial geometric feedback, providing the first evidence for oxytocin-enhanced human learning. A subsequent study using the same paradigm combined with functional magnetic resonance imaging (fMRI) further examined the neural mechanisms of this effect. Behavioral findings replicated Hurlemann et al.'s results, with oxytocin selectively improving learning performance under social feedback conditions compared to placebo. At the neural level, fMRI revealed that oxytocin enhanced activation in learning and emotion-processing regions including the amygdala, hippocampus, and thalamus, and increased functional connectivity between the right amygdala and left insula as well as left caudate nucleus (Hu et al., 2015). Since these regions, particularly the amygdala, contain abundant oxytocin receptors (Boccia et al., 2013; Gimpl & Fahrenholz, 2001), oxytocin likely modulates learning by acting on receptors within brain regions involved in emotion regulation, reward, and stimulus salience (Hu et al., 2015). Hurlemann et al. further demonstrated that patients with bilateral amygdala damage showed impaired learning under social feedback but normal performance under nonsocial feedback, confirming the amygdala's essential role in oxytocin's mechanism of action on socially reinforced learning. Oxytocin enhances the encoding of social feedback information in the amygdala and increases its functional connectivity with the insula and caudate nucleus to heighten the salience of social feedback, enabling synergistic integration of social information processing and reinforcement learning, ultimately facilitating social learning. This aligns with the social salience hypothesis of oxytocin (Shamay-Tsoory & Abu-Akel, 2016).

A recent event-related potential study using a more complex probabilistic learning task investigated whether oxytocin differentially modulates learning under positive (happy faces) versus negative (angry faces) social feedback. Results demonstrated that oxytocin facilitated learning under both positive and negative feedback conditions, an effect accompanied by reduced feedback-related negativity (FRN) at the neural level, suggesting that oxytocin makes evaluations of positive and negative feedback more similar to promote learning. During a test phase without feedback, oxytocin's facilitatory effects persisted behaviorally, as evidenced by increased accuracy for stimuli associated with positive feedback. Neurally, oxytocin decreased error-related negativity (ERN) while enhancing late positive error (Pe) amplitude, indicating that although oxytocin reduced early conflict detection between actual errors and expected correct responses, it promoted later error awareness and correction motivation. These findings suggest that oxytocin facilitates probabilistic associative learning under complex conditions primarily by enhancing processing of positive feedback to make it more similar to negative feedback, reducing conflict detection and enhancing error awareness to ultimately promote learning (Zhuang et al., 2020).

Clinical research examining oxytocin's modulation of social learning remains limited. One study using a probabilistic reinforcement learning task investigated oxytocin's effects on classification learning in high-functioning autism patients. Results showed that oxytocin effectively improved learning performance under

both social target-nonsocial feedback and nonsocial target-social feedback conditions, indicating that oxytocin's effects depend on social information involvement. This behavioral effect was accompanied by enhanced fMRI activation in the nucleus accumbens, a region involved in reward prediction error processing, suggesting that oxytocin can promote social learning in autism by modulating reward-related brain regions, offering promising clinical implications (Kruppa et al., 2018).

2.2.2 Monetary Reward Learning The extensive distribution of oxytocin receptors in human dopamine reward circuits (Schorscher-Petcu et al., 2009; Skuse & Gallagher, 2009) provides a basis for oxytocin to modulate reward-related learning. In one monetary reward associative learning task, two facial expression images from the same individual were paired with high- and low-probability monetary rewards. Participants learned these associations to maximize rewards. Reinforcement learning model analyses revealed no modulatory effect of oxytocin on learning efficiency under positive or negative facial expression conditions. However, when angry faces served as high-probability reward stimuli, the oxytocin group showed greater preference for angry faces, suggesting that oxytocin may reduce aversion to angry expressions (Evans et al., 2010). A follow-up study added neutral faces and punishment conditions (monetary loss), requiring participants to choose between two identical emotional expressions from different individuals. Results showed that oxytocin significantly impaired reward learning under happy face conditions without affecting negative face or punishment learning (Clark-Elford et al., 2014). Oxytocin may have enhanced the interfering effect of emotional faces on the learning task, thereby impairing efficiency under happy face conditions, consistent with its role in promoting happy face recognition and approach behavior toward positive social stimuli (Schulze et al., 2011; Yao et al., 2018). While both studies combined monetary reward with emotional faces, their different experimental designs yielded divergent results. Neither study found a general facilitatory effect of oxytocin on reward learning, possibly because oxytocin does not modulate pure monetary reward processing, or because the confounding effect of emotional face processing—which oxytocin does modulate (Clark-Elford et al., 2015; Domes et al., 2010)—obscured interpretation of its effects on monetary reward learning.

Oxytocin modulates reward circuit function in psychiatric patients. Nawijn et al. (2016) used a monetary incentive delay task to investigate oxytocin's effects on reward learning in PTSD patients. fMRI results showed that oxytocin enhanced activation in reward- and uncertainty-related regions including the putamen, insula, and anterior cingulate cortex, revealing for the first time oxytocin's modulatory effects on brain regions involved in monetary reward processing. Another study in autism patients added a social condition using emotional faces as feedback stimuli to the classic monetary incentive delay task. fMRI results showed that oxytocin selectively enhanced activation in the mesolimbic system involved in reward processing under nonsocial (monetary) reward conditions without significant effects under social feedback conditions (Greene

et al., 2018). Despite the physiological overlap between oxytocin receptor distribution and reward circuits (Skuse & Gallagher, 2009) and clinical evidence for oxytocin's modulation of reward-related circuit activation in psychiatric patients, neither study found behavioral facilitation of monetary reward learning. This dissociation between neural activity and behavior raises questions about whether oxytocin truly lacks modulatory effects on monetary reward learning or whether cognitive deficits in psychiatric patients (potentially causing floor effects) masked behavioral effects, warranting further investigation.

2.2.3 Fear Conditioning and Extinction Learning Both humans and other species exhibit fear and anxiety responses when facing danger, which are crucial for survival and environmental adaptation. Animal studies have shown that oxytocin effectively modulates fear and anxiety responses (McCarthy et al., 1996), and human research indicates that oxytocin reduces excessive fear responses in individuals including generalized anxiety patients by modulating amygdala activation (Kanat et al., 2015; Kirsch et al., 2005). Neuroimaging research demonstrates that fear extinction is primarily regulated by interactions between the medial prefrontal cortex and amygdala (Milad & Quirk, 2012; Vouimba & Maroun, 2011), regions that contain abundant oxytocin receptors (Boccia et al., 2013). These findings provide a strong rationale for investigating oxytocin's modulation of fear conditioning and extinction learning.

Eckstein et al. (2016) pioneered research on oxytocin's modulation of fear conditioning using a classic fear conditioning paradigm. Participants received intranasal oxytocin or placebo 30 minutes before undergoing fear conditioning with social (neutral faces) or nonsocial (houses) stimuli. The oxytocin group showed significantly faster responses to conditioned stimuli (CS+) than to CS- stimuli, and higher skin conductance responses to CS+ than CS- during late conditioning, effects absent in the placebo group. fMRI results revealed that oxytocin significantly enhanced activation in the anterior cingulate cortex—a region critical for fear representation and learning—in response to CS+ stimuli. These convergent behavioral, electrophysiological, and neural findings demonstrate oxytocin's facilitatory effect on fear conditioning, independent of stimulus sociality. Rapid threat detection is an evolutionarily conserved core function essential for survival, and these findings suggest the oxytocinergic system may play an important role in this process.

Petrovic et al. (2008) also employed a fear conditioning paradigm, administering intranasal oxytocin or placebo (32 IU) after fear conditioning completion, with extinction beginning 45 minutes later. Participants rated face stimuli for likability before conditioning, after conditioning (pre-drug), before extinction testing (post-drug), and after extinction testing. Results showed that oxytocin eliminated differences in likability ratings between CS+ and CS- faces during extinction by increasing CS+ ratings, effectively reducing negative emotional responses to conditioned stimuli. Consistently, oxytocin abolished reaction time differences between CS+ and CS- during extinction and suppressed amygdala

and anterior cingulate responses to CS+ faces in fMRI. A follow-up study using a similar paradigm with added nonsocial stimuli (houses) found that oxytocin significantly reduced skin conductance responses to both social and nonsocial CS+ during late extinction and suppressed amygdala activation during both early and late extinction (Eckstein et al., 2015). While the former study focused on emotional responses to conditioned fear stimuli and the latter examined sociality effects, both consistently revealed that oxytocin inhibits activation in the fear processing network, particularly its core node the amygdala, during encoding of fear-conditioned stimuli. The latter study further elucidated dynamic changes throughout extinction by dividing the phase into early and late periods.

Acheson et al. (2013) incorporated fear-potentiated startle measurement into a fear extinction paradigm and added an extinction recall test 24 hours after conditioning to investigate oxytocin's effects on extinction memory consolidation. Consistent with previous studies, intranasal oxytocin or placebo was administered after fear conditioning, with extinction beginning 45 minutes later. During extinction, oxytocin showed no significant modulatory effects on anxiety ratings or startle amplitude. However, during the 24-hour extinction recall test, oxytocin significantly reduced electromyographic responses to CS+, indicating enhanced consolidation of extinction learning memory. Although direct comparison with previous studies is limited by differences in paradigms and data modalities, this study importantly extends previous findings by demonstrating oxytocin's facilitatory effect on extinction recall, advancing our understanding of oxytocin's mechanisms in fear processing intervention.

Abnormal fear conditioning and extinction in response to threatening stimuli are implicated in anxiety disorders, depression, and PTSD, with impaired extinction following fear acquisition being a key mechanism underlying excessive and persistent fear responses (Grisanzio et al., 2018; Marin et al., 2017). Current interventions for fear-related psychiatric disorders, such as cognitive behavioral therapy and pharmacological treatments, often show limited efficacy or substantial side effects (Bradley et al., 2005; Carpenter et al., 2018; Wang et al., 2017), making the search for effective extinction-enhancing agents clinically important. These three studies provide convergent evidence from different perspectives for oxytocin's facilitatory effects on fear extinction learning and memory consolidation, offering valuable preclinical proof-of-concept support for future therapeutic applications in fear-related psychiatric disorders.

These studies investigated oxytocin's modulatory effects on human learning from behavioral, electrophysiological, EEG, and fMRI perspectives. Similar to animal models, oxytocin's effects on human learning are complex, showing facilitatory effects on social learning, fear conditioning, and extinction learning, but no significant effects on monetary reward learning. Moreover, even within similar learning types, oxytocin's effects are influenced by stimulus sociality (social vs. nonsocial) and valence (positive vs. negative vs. neutral), consistent with findings that oxytocin's modulation of other social behaviors is modulated by task context and individual differences (Bartz et al., 2011; Kendrick et al.,

2017). Overall, oxytocin demonstrates effective modulation of human learning with preliminary but promising evidence in clinical populations, though future clinical applications must carefully consider these moderating factors.

3.1 Modulatory Effects of Oxytocin on Animal Memory

Animal research on oxytocin's memory-modulating effects has primarily focused on social recognition (see Table 3). Social recognition refers to the process whereby an animal initially requires substantial time to familiarize itself with a novel conspecific, with recognition time decreasing across repeated exposures (Love, 2014). This process requires short-term and working memory, making it a common paradigm for studying memory. In social recognition tasks, a rat is placed in a cage and exposed to a juvenile rat for an initial interaction. Oxytocin is administered intracerebroventricularly after this interaction, and after a delay, the juvenile is reintroduced. Social recognition is indicated when the adult rat displays focused behaviors such as sniffing and following, with the time required defined as social recognition time. Oxytocin's facilitatory or inhibitory effects are determined by the interval between exposures: failure to recognize at a 30-minute interval indicates inhibition, while successful recognition after 120 minutes indicates facilitation. When the interval was 30 minutes, oxytocin-treated rats (6 g/kg) showed no difference in recognition time between first and second exposures compared to saline controls, indicating an inhibitory effect on social recognition memory consolidation (Dantzer et al., 1987).

Dosage also influences oxytocin's modulatory effects on social recognition. Compared to controls, low-dose intracerebroventricular oxytocin (0.09 $ng \cdot kg^{-1}$ to 6 $ng \cdot kg^{-1}$) facilitated social recognition in adult rats, whereas higher doses (24 $ng \cdot kg^{-1}$) impaired social recognition behavior (Popik & Vetulani, 1991; Popik et al., 1992). Expanding the dosage range (1 fg to 10 ng), Benelli et al. (1995) confirmed that low-dose oxytocin facilitated social recognition, with the most significant effects at 10 fg and 1 ng. Pre-treatment with an equivalent dose of oxytocin antagonist 5 minutes before low-dose oxytocin (1 ng) administration eliminated the facilitatory effect. Adding a novel juvenile during the recognition phase revealed that oxytocin-treated rats (0.1 ng/kg) spent significantly more time investigating the novel versus familiar juvenile, further confirming low-dose oxytocin's facilitatory effect (Gard et al., 2012). Beyond intracerebroventricular injection, Ferguson et al. (2000) used gene knockout technology to demonstrate oxytocin's essential role in social recognition: oxytocin knockout mice ($Oxt^{-}/^{-}$) showed impaired social recognition compared to wild-type mice ($Oxt^{+}/^{+}$) during maternal interactions, with intracerebroventricular oxytocin injection (1 ng) rescuing this deficit in knockout mice and antagonist administration impairing recognition in wild-type mice. These results establish the indispensability of oxytocin in social recognition memory from a genetic perspective.

In summary, although direct studies of oxytocin's memory-modulating effects in animal models are fewer than learning studies, this field has revealed oxytocin's crucial role in animal memory through intracerebroventricular injection,

antagonist administration, and gene knockout approaches. Notably, oxytocin's memory-modulating effects are primarily dose-dependent, with low doses generally facilitating and high doses inhibiting memory. Future animal research should investigate the precise mechanisms underlying oxytocin's memory effects at more refined scales.

3.2 Modulatory Effects of Oxytocin on Human Memory

Similar to animal research revealing diverse modulatory effects, oxytocin's effects on human memory vary across experimental tasks and memory materials (see Table 4). Bruins et al. (1992) first investigated oxytocin's effects on memory using verbally presented abstract words and visually presented face images (positive/negative). Participants received intranasal oxytocin or placebo after learning, with memory testing conducted one week later. Oxytocin impaired memory for verbal abstract words but did not affect visual face memory. Using a similar post-learning administration design, Savaskan et al. (2008) presented male happy, angry, or neutral faces during encoding and tested neutral face identity recognition 30 minutes and 24 hours after drug administration. Oxytocin effectively enhanced identity recognition for neutral and angry faces at both short and long intervals, regardless of participant gender, but showed no effect on happy face recognition.

Pre-learning administration primarily affects memory encoding rather than consolidation and has been more extensively studied, predominantly using face memory paradigms. Heinrichs et al. (2004) administered intranasal oxytocin or placebo 50 minutes before encoding and examined its effects on explicit and implicit memory for reproduction-related versus neutral words. Oxytocin significantly reduced explicit recognition scores for both word types but impaired implicit memory only for reproduction-related words. Subsequent research has focused primarily on face memory. Guastella et al. (2008) used face images as stimuli and required participants to make "remember," "know," or "new" judgments during testing. Compared to angry and neutral faces, oxytocin-treated participants made more "remember" or "know" judgments for previously presented happy faces, indicating selective enhancement of happy face memory. Rimmele et al. (2009) extended this work by adding nonsocial stimuli (houses, landscapes) to examine whether oxytocin's memory effects were specific to social stimuli. Oxytocin selectively increased familiarity ratings for social face stimuli, with consistent effects for both positive and negative faces, but showed no significant modulation of nonsocial stimuli. Herzmann et al. (2013) further investigated how oxytocin modulates memory for same- versus other-race faces (happy/neutral). Oxytocin enhanced familiarity ratings for face stimuli, particularly happy faces, in both male and female participants, regardless of face race. Oxytocin increased amplitudes of memory-related ERP components (FN400 and parietal old/new effect) without affecting early perceptual processing components, indicating direct modulation of memory-related neural encoding rather than perceptual processing. Interestingly, oxytocin impaired recognition mem-

ory in male participants. Using a within-subjects design with only neutral faces, oxytocin impaired recognition of both neutral faces and nonsocial stimuli in male participants, suggesting that oxytocin's memory effects may be influenced by stimulus emotional valence and experimental design (Herzmann et al., 2012).

Collectively, these studies demonstrate significant modulatory effects of oxytocin on human memory, particularly for social stimuli such as emotional faces. However, oxytocin's effects vary depending on administration timing, memory test interval, test format (recognition vs. familiarity), stimulus valence (positive vs. negative vs. neutral), and stimulus type (faces vs. words). Additionally, few human memory studies have employed neuroimaging techniques, representing an important direction for future research.

4 Summary and Outlook

In summary, oxytocin exerts important modulatory effects on learning and memory processing in animals and humans. Exogenous oxytocin (injection or intranasal) may modulate learning and memory by binding to extensively distributed oxytocin receptors in brain networks involved in these processes, particularly the dopamine reward pathway and limbic system (especially the amygdala and hippocampus), thereby adjusting their functional states. Whether oxytocin's effects are facilitatory or inhibitory depends on multiple factors including task design, administration timing, and stimulus characteristics. While existing research using diverse modalities has substantially advanced our understanding of oxytocin's mechanisms, several limitations and avenues for future research remain:

(1) The complexity of oxytocin's modulatory effects on learning and memory is evident in animal studies showing different effects depending on administration route, dosage, and location. Future animal research should leverage methodological advantages using fine-scale techniques such as optogenetics and single-cell recordings to systematically investigate specific mechanisms rather than merely documenting modulatory effects. In human studies, inconsistent findings often stem from variations in task design, dosage, timing, and stimuli. Future research should first employ standardized tasks and administration protocols to systematically examine oxytocin's effects on specific learning and memory types, enabling cross-study comparisons and clarifying whether oxytocin facilitates or inhibits particular processes and their neural mechanisms. Second, future studies should enhance translational validity between animal and human models. Animal research, less constrained by ethics, offers richer techniques and finer-scale neural mechanism characterization, providing valuable insights for human studies. Conversely, human research with higher cognitive functioning enables more complex experimental designs and reveals more advanced learning and memory patterns, which can inform animal research.

(2) Although a few studies have confirmed oxytocin's modulatory effects on behavioral performance and neural responses during social and monetary reward learning in autism and PTSD patients, most human research has focused on healthy populations, leaving a substantial gap before clinical translation. Nevertheless, oxytocin shows considerable potential for intervening in learning and memory deficits in psychiatric disorders, particularly social information-based learning in autism and fear extinction in fear-related disorders. Future research should evaluate oxytocin's therapeutic potential in clinical populations based on findings from healthy individuals and high-trait groups, while exploring how administration methods, dosages, and frequency optimize effects to promote clinical translation.

(3) Existing human studies have predominantly used intranasal administration and relatively simple paradigms. While research has established relationships between endogenous oxytocin levels (blood/salivary concentrations) and human behavior/emotion (Chen et al., 2020; Engel et al., 2019; Han et al., 2020), no studies have examined relationships between endogenous oxytocin and learning/memory. In terms of paradigms, learning research has primarily used reinforcement learning tasks and memory research has focused on recognition, with relatively few studies investigating learning and memory in complex dynamic contexts. In real-world situations, stimulus-outcome associations are not static and may change with conditions, requiring individuals to adjust decisions based on outcome feedback. Oxytocin's modulatory effects under such dynamic conditions remain unexplored.

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Note: Figure translations are in progress. See original paper for figures.