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LOVE: AN EMERGENT PROPERTY OF THE MAMMALIAN AUTONOMIC NERVOUS SYSTEM

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SUMMARY

The evolution of the autonomic nervous system provides an organizing principle to interpret the adaptive significance of mammalian affective processes including courting, sexual arousal, copulation, and the establishment of enduring social bonds. According to the Polyvagal Theory (Porges, 1995, 1996, 1997), the well-documented phylogenetic shift in the neural regulation of the autonomic nervous system passes through three stages, each with an associated behavioral strategy. The first stage is characterized by a primitive unmyelinated visceral vagus that fosters digestion and responds to threat by depressing metabolic activity. Behaviorally, the first stage is associated with immobilization behaviors. The second stage is characterized by the sympathetic nervous system that is capable of increasing metabolic output and inhibiting the visceral vagus to foster mobilization behaviors necessary for 'fight or flight'. The third stage, unique to mammals, is characterized by a myelinated vagus that can rapidly regulate cardiac output to foster engagement and disengagement with the environment. The mammalian vagus is neuroanatomically linked to the cranial nerves that regulate social engagement via facial expression and vocalization. The Polyvagal Theory provides neurobiological explanations for two dimensions of intimacy: courting and the establishment of enduring pair-bonds. Courting is dependent upon the social engagement strategies associated with the mammalian vagus. The establishment of enduring pair-bonds is dependent upon a co-opting of the visceral vagus from an immobilization system associated with fear and avoidance to an immobilization system associated with safety and trust. The theory proposes that the phylogenetic development of the mammalian vagus is paralleled by a specialized communication, via oxytocin and vasopressin, between the hypothalamus and the medullary source nuclei of the visceral vagus, which facilitates sexual arousal, copulation, and the development of enduring pair-bonds. © 1998 Elsevier Science Ltd. All rights reserved.

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INTRODUCTION

There is no fear in love; but perfect love casteth out fear. 1 John 4:18

Love has had a variety of expressions. Foremost in our culture is the love between individuals of different genders. The products of this love are observed in terms of children, of cooperative and shared responsibilities to survive, of the transmitting of culture, and of pleasure and ecstasy. Although we assume that love is a unique human emotion, several neurobiological processes involved in the experience and expression of

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love are shared with other mammals. The phylogenetic origins of these processes reflect their antecedent adaptive function. In mammals, these processes have evolved into an integrated neurobehavioral system, which promotes proximity, reproduction, and physical safety. Central to the neural mediation of these processes is the autonomic nervous system. The focus of this paper is to describe how the autonomic nervous system is involved in the processes associated with feelings of love and behaviors linked to reproduction. The paper proposes a hypothetical model, which speculates that the phylogenetic changes in the autonomic nervous system are related to the emergence of two components of love: an appetitive phase associated with courting and seductive behaviors and a consumatory phase associate with passionate sexual behaviors and the establishment of enduring pair-bonds. According to this model, courting and seduction are dependent on phylogenetically newer structures. For example, the cortex, via corticobulbar pathways, regulates facial expressions and vocalizations to express availability to a prospective mate. In contrast, passionate visceral feelings are dependent upon phylogenetically older structures such as the hypothalamus and medulla, which involve phylogenetically more recent neuropeptides (oxytocin and vasopressin).

Polyvagal Theory: Three Phylogenetic Systems of Affective Regulation

The Polyvagal Theory (Porges, 1995, 1997) proposes that the evolution of the mammalian autonomic nervous system provides the neurophysiological substrates for the emotional experiences and affective processes that are major components of social behavior. In this context, the evolution of the nervous system limits the range of emotional expression, which in turn may determine proximity, social contact, quality of communication, and opportunities to reproduce. The polyvagal construct was introduced (Porges, 1995, 1997) to emphasize and to document the neurophysiological and neuroanatomical distinction between two branches of the tenth cranial nerve (i.e. vagus) and to propose that each vagal branch was associated with a different adaptive behavioral strategy. The current paper expands the Polyvagal Theory to explain affective strategies associated with love. The expanded theory proposes that behaviors and psychological states associated with emotions of love, courting behaviors, and intimacy are derivative of the evolutionary processes that produced changes in the structure and function of the cranial nerves, especially in the regulation of cardiac function and of the striatal muscles of the face, larynx, and pharynx.

Table I. Neural regulation of the heart as a function of vertebrate phylogeny

Phylogenetic Group	**CHM**	**DMX**	**SNS**	**AND**	**NA**
Cyclostome myxinoids	x^+				
lampreys	x^+	x^+			
Elasmobranch	x^+	x^-			
Teleost	x^+	x^-	x^+		
Amphibian	x^+	x^-	x^+		
Reptile	x^+	x^-	x^+	x^+	
Mammal	x^+	x^-	x^+	x^+	x^-

CHM, chromaffin tissue; DMX, vagal pathways originating in the dorsal motor nucleus of the vagus; SNS, spinal sympathetic nervous system; AND, adrenal medulla; NA, vagal pathways originating in the nucleus ambiguus; $^+$ increases cardiac output; $^-$ decreases cardiac output.

Table I illustrates the phylogenetic differences in the structures that regulate the heart in vertebrates (Morris and Nilsson, 1994; Santer, 1994; Taylor, 1992). The heart has been selected because the regulation of the heart determines the proximity between potential mating partners. For example, cardiac output must be regulated to remain calm in safe environments, to mobilize for fight or flight behaviors, or to immobilize for death feigning or avoidance behaviors. To regulate cardiac output several efferent structures have evolved. These structures represent two global and often opposing systems: one, a sympathetic-catecholamine system including chromaffin tissue and spinal sympathetics; and two, a vagal system (a component of the parasympathetic nervous system) with branches originating in medullary source nuclei (i.e. dorsal motor nucleus of the vagus and nucleus ambiguus). In addition, vertebrates have chromaffin tissue containing high concentrations of catecholamines. The chromaffin tissue is defined as having morphological and histochemical properties similar to the adrenal medulla. Classes of vertebrate that do not have an adrenal medulla have relatively more chromaffin tissue, which regulates circulating catecholamines.

In the most primitive fish, the cyclostomes, the neural control of the heart is very primitive. Some cyclostomes such as the myxinoids (hagfish) use circulating catecholamines from chromaffin tissue to provide the sole excitatory influences on the heart. Other cyclostomes such as the lampetroids (lampreys) have a cardiac vagus. However, in contrast to all other vertebrates that have a cardio-inhibitory vagus that acts via muscarinic cholinoceptors, the cyclostome vagal innervation is excitatory and acts via nicotinic cholinoceptors. One striking feature of the cyclostome heart is the location of chromaffin tissue within the heart that stores large quantities of epinephrine and norepinephrine. As in other vertebrates, the circulating catecholamines produced by the chromaffin tissue stimulate β-adrenergic receptors in the heart. Thus, for the cyclostomes there appear to be only excitatory mechanisms to regulate the heart.

The elasmobranchs (i.e. cartilaginous fish) are the first vertebrates to have a cardioinhibitory vagus. The vagus in these fish is inhibitory and the cholinoceptors on the heart are muscarinic as they are in other vertebrates. The cardioinhibitory vagus is functional in the elasmobranchs as a response to hypoxia. In conditions of hypoxia, the metabolic output is adjusted by reducing heart rate. This modification of neural regulation may provide a mechanism to enable the elasmobranchs to increase their territorial range, by providing a neural mechanism that adjusts metabolic output to deal with changes in water temperature and oxygen availability. However, unlike the phylogenetically more recent fish and tetrapods, the elasmobranchs do not have direct sympathetic input to the heart. Instead, cardiac acceleration and increases in contractility are mediated via β-adrenergic receptors stimulated by circulating catecholamines released from chromaffin tissue. Thus, since activation of metabolic output is driven by circulating catecholamines and not by direct neural innervation, once the excitatory system is triggered, the ability to self-sooth or calm is limited.

In general, the teleosts may be considered phylogenetically the first class of vertebrates in which the heart is regulated by both sympathetic and parasympathetic neural pathways. With opposing neural mechanisms from sympathetic and vagal pathways, rapid transitory changes in metabolic output are possible to support immediate changes in behavior from mobilization to immobilization. In teleosts this is observed as 'darting' and 'freezing' behaviors. Amphibia, similar to the teleosts, have dual innervation of the heart via systems with direct neural components from the spinal cord via the sympathetic chain producing increases in heart rate and contractility, and direct neural pathways from the brainstem via the vagus producing cardioinhibitory actions.

True adrenal glands, in which there is a distinct medulla formed of chromaffin tissue, are only present in birds, reptiles and mammals (Santer, 1994). Neural regulation by the spinal sympathetics of the adrenal medulla provides a neural mechanism for rapid and controlled release of epinephrine and norepinephrine to increase cardiac output to match the metabolic demands of mobilization behaviors. In teleosts, chromaffin tissue is primarily related to parts of the cardiovascular system, but there also is chromaffin tissue associated with the kidney. However, in amphibia chromaffin tissue is primarily associated with the kidney and substantial aggregations of chromaffin cells are located along the sympathetic chain ganglia. Thus, we can observe a phylogenetic shift in the location of chromaffin tissue, and the concurrent evolution of a distinct adrenal medulla near the kidney.

Unlike other vertebrates with cardioinhibitory vagi, the mammalian vagus contains two branches. One branch originates in the dorsal motor nucleus of the vagus and provides the primary neural regulation of subdiaphragmatic organs such as the digestive tract. However, at the level of the heart, the dorsal motor nucleus of the vagus does not play a major role in the normal dynamic regulation of cardiac output. Rather, during embryological development in mammals, cells from the dorsal motor nucleus of vagus migrate ventrally and laterally to the nucleus ambiguus (Schwaber, 1986). There they form the cell bodies for visceromotor myelinated axons that provide potent inhibition of the sinoatrial node, the pacemaker for the heart.

By transitory down-regulation of the cardioinhibitory vagal tone to the heart (i.e. removing the vagal brake), the mammal is capable of rapid increases in cardiac output without activating the sympathetic-adrenal system. By engaging this system, rather than the sympathetic-adrenal system, mammals have the opportunity to rapidly increase metabolic output for immediate mobilization. Under prolonged challenge, the sympathetic system also may be activated. However, by rapidly re-engaging the vagal system, mammals have the capacity to inhibit sympathetic input on the heart (Vanhoutte and Levy, 1979) and rapidly decrease metabolic output to self-soothe and calm.

Three phylogenetic principles can be extracted from Table I. First, there is a phylogenetic shift in the regulation of the heart from endocrine communication, to unmyelinated nerves, and finally to myelinated nerves. Second, there is a development of opposing neural mechanisms of excitation and inhibition to provide rapid regulation of graded metabolic output. Third, with increased cortical development, the cortex exhibits greater control over the brainstem via direct (e.g. corticobulbar) and indirect (e.g. corticoreticular) neural pathways originating in motor cortex and terminating in the source nuclei of the myelinated motor nerves emerging from the brainstem (e.g. specific visceral efferent nerves).

These phylogenetic principles provide a basis for speculations regarding the behavioral repertoire of various classes of vertebrates. The speculations support the premise that the phylogenetic development of the autonomic nervous system provides an organizing principle for affective experiences and determines the range of social and affective behavior. In general, phylogenetic development results in increased neural control of the heart via a mammalian vagal system, which can promote transitory mobilization and the expression of sympathetic tone without requiring sympathetic or adrenal activation. With this new vagal system, transitory incursions into the environment can be initiated without the severe biological cost of either metabolic shut down, via primitive vagal inhibition, or metabolic excitation, via sympathetic-adrenal activation. Paralleling this change in the neural control of the heart is an enhanced neural control of the face, larynx, and pharynx

Table II. Physiological functions of autonomic subsystems

Physiological functions/systems	VVC	SNS	DVC
Heart rate	+/−	+	−
Bronchi	+/−	+	−
Gastrointestinal		−	+
Vasoconstriction		+	
Sweat		+	
Adrenal medulla		+	
Tears	+/−		
Vocalization	+/−		
Facial muscles	+/−		
Eyelids	+/−		
Middle ear muscles	+/−		

VVC, ventral vagal complex; SNS, sympathetic nervous system; DVC, dorsal vagal complex. DVC slows heart rate, constricts bronchi, and stimulates gastrointestinal function. SNS increases heart rate, dilates bronchi, inhibits gastrointestinal function, promotes vasoconstriction, increases sweating, and activates catecholamine release from the adrenal medulla. Depending on degree of neural tone, VVC either slows or speeds heart rate, constricts or dilates bronchi, lowers or raises vocalization pitch, regulates middle ear muscles to foster perception of human voice, and increases or decreases facial expressivity

that enables complex facial gestures and vocalizations. This phylogenetic course results in greater central nervous system regulation of behavior, especially behaviors needed to engage and disengage with environmental challenges including behaviors involved in social interactions.

The mammalian autonomic nervous system retains components of three interactive, but distinct, phylogenetically dependent neural systems associated with: (1) the dorsal vagal complex (DVC); (2) the sympathetic nervous system (SNS); and (3) the ventral vagal complex (VVC). Each of these three neural systems is linked with a specific emotion subsystem observable in humans. Each emotion subsystem carries out specific, but different adaptive functions. The DVC promotes immobilization and the conservation of metabolic resources. (DVC), The SNS promotes mobilization behaviors and is metabolic costly. The VVC provides mechanisms to communicate that require minimal energy expense. The constituent responses associated with each subsystem are listed in Table II. Changes in affect regulation can be seen as an emergent property of this evolutionary trend.

With the increased neural complexity paralleling phylogenetic development, the organism's behavioral and affective repertoire is enriched. The DVC represents the phylogenetically oldest stage. The DVC is characterized by a primitive unmyelinated vegetative vagal system that fosters digestion and responds to novelty or threat by reducing cardiac output to protect metabolic resources. Behaviorally, the DVC is associated with the use of immobilization behaviors as an avoidance strategy. The SNS, the second stage, evolved as a neural regulator of metabolic output. The SNS can rapidly increase metabolic output and inhibit the primitive vagal system's influence on the gut to foster mobilization behaviors necessary for fight or flight. The VVC represents the phylogenetically most recent stage and is unique to mammals. The VVC is characterized by a myelinated vagal system that can rapidly regulate cardiac output to foster engagement and disengagement with the environment. The VVC consists of the myelinated vagus and portions of other cranial nerves (i.e. V, VII, IX, XI) that regulate structures derived from the embryonic branchial arches (i.e. ancient gill arches). Collectively, these neural pathways regulate the

branchiomeric muscles and have been categorized as special visceral efferent fibers. In mammals the branchiomeric muscles control facial expression, sucking, swallowing, breathing, listening and vocalization.

Ventral Vagal Complex (VVC). The VVC is unique to mammals and represents the most recent phylogenetic stage. According to the Polyvagal Theory this mammalian vagal system (including the special visceral efferent fibers associated with other cranial nerves) fosters the development of complex social behaviors. In addition, the mammalian vagal system has an inhibitory effect on sympathetic pathways to the heart, and thus, promotes calm and prosocial behaviors.

The VVC, by providing a voluntary system for communication and limited mobilization, serves as the neurophysiological basis for the courting behaviors associated with seduction. For example, structures related to the VVC signal availability and promote proximity. The VVC includes motor pathways that originate in the nucleus ambiguus (i.e. source nucleus for the glossopharyngeal (IX), the myelinated portion of the vagus (X), and the accessory (XI) cranial nerves) and the sensory and motor pathways of the closely related trigeminal (V) and facial (VII) nerves. The cortical control of the VVC is mediated by corticobulbar pathways that originate in motor areas of the frontal cortex and terminate in the nucleus ambiguus and in the source nuclei of trigeminal and facial motor pathways (Kuypers, 1958). Because the system involves and mediates voluntary actions (e.g. facial expressions, vocalizations), it has been labeled the smart vagus, in contrast to the vegetative vagus that is associated with visceral homeostasis (e.g. digestion) mediated by unmyelinated vagal fibers originating in the dorsal motor nucleus of the vagus (Porges, 1995).

Somatomotor fibers originating in the VVC control the branchiomeric muscles including those of the face, mouth, neck, larynx, pharynx, esophagus, and middle ear. Visceromotor efferent fibers originating in the VVC control salivary and lacrimal glands, and the heart and bronchi. The primary inputs to the VVC come from facial and oral afferents traveling through the sensory components of the facial and trigeminal nerves and from the visceral afferents terminating in the nucleus of the solitary tract. The VVC is involved in the control and coordination of sucking, swallowing, and vocalizing with breathing. By controlling facial expression, vocalization, and head tilt, the VVC is intimately involved in the communication of affect.

In mammals, the myelinated efferent pathways from the VVC to the heart function as a vagal brake. The intrinsic rate of the heart in the healthy human, even without sympathetic excitation, is faster than resting heart rate. Thus, under most conditions the vagus, primarily via myelinated pathways that originate in the nucleus ambiguus, actively inhibits heart rate. However, when there is a need to engage actively with select elements in the environment, cortical neurons inhibit homeostatic needs, and cardiac output is rapidly increased to match metabolic demands. Under these situations there is a transitory withdrawal of the vagal tone to the heart to increase heart rate, which defines the removal of the vagal brake (Porges et al., 1996). When environmental demands require a calm behavioral state and prosocial behavior, the re-engagement of the vagal brake produces a reduction in heart rate and an increase in self-soothing behaviors. In fact, the mammalian or smart vagus actively inhibits sympathetic excitation of the cardiac pacemaker (Vanhoutte and Levy, 1979). Thus, the VVC may be recruited in two behavioral dimensions of seduction and courting: (1) a signal system of gestures and vocalizations denoting reproductive availability; and (2) a tightly regulated mobilization system to foster proximity with a prospective mate.

Based on the Polyvagal Theory, the function of the corticobulbar pathways in regulating brainstem structures is dependent upon the perception of whether the environment is safe or dangerous. Cortical control of the brainstem is state dependent with increased cortical control being expressed during states of cortical activation associated with alertness (Parmeggiani, 1985). According to the Polyvagal Theory, cortical regulation of the VVC is maximized during periods of cortical activation when the individual is alert and perceives the environment as safe (Porges et al., 1998). During a perceived threat, the VVC is depressed (i.e. withdrawal of the vagal brake) to facilitate the expression of the SNS to promote mobilization for fight or flight behaviors. Thus, access to the flexible communication and visceral regulatory processes of the VVC, which is required for courting and the signaling of social availability, occurs only in environments perceived as safe, which have low demands for aggressive and defensive behaviors.

The Sympathetic Nervous System (SNS). The second emotion subsystem is dependent on the SNS. The SNS is a mobilization system, which promotes fight or flight behaviors. The SNS responds to threat and metabolic challenge. The SNS prepares the body for emergency by increasing cardiac output, stimulating sweat glands to protect and lubricate the skin, and by inhibiting the metabolically costly gastrointestinal tract. The evolution of the SNS follows the segmentation of the spinal cord, with cell bodies of the preganglionic sympathetic motor neurons located in the lateral horn of the spinal cord. The SNS provides a mechanism for mobilization and has long been associated with intense emotion. The SNS, not only contributes to the fight and flight behaviors associated with protection of self and significant others, but also promotes the general physiological activation associated with sexual arousal. During the initial phases of sexual arousal when signaling via facial expressions and vocalizations is important to communicate reproductive availability, there may be co-activation of the SNS and the VVC.

Dorsal Vagal Complex (DVC). The third and phylogenetically oldest emotion subsystem is dependent on the DVC. The DVC is a neural component of a vestigial immobilization system. The DVC contributes to an active defense response system for reptiles by allowing them to inhibit cardiopulmonary function, while freezing or submerging. The DVC is primarily associated with digestive, gustatory, and hypoxic responses in mammals. The DVC includes the dorsal motor nucleus of the vagus, the nucleus of the solitary tract, area postrema and the interneuronal communication among these structures. The efferents for the DVC originate in the dorsal motor nucleus of the vagus and the primary vagal afferents terminate in the nucleus of the solitary tract and area postrema. The DVC provides the primary neural control of subdiaphragmatic visceral organs. In mammals, as an evolutionary vestige from the reptilian vagal control of the heart and lungs, the DVC provides low tonic influences to the heart and bronchi.

In contrast to reptiles, mammals have a great demand for oxygen and are vulnerable to depletions in oxygen. The metabolic demand for mammals is $\approx 5\times$ greater than for reptiles of equivalent body weight (Else and Hulbert, 1981). Thus, reptilian dependence on the DVC as an avoidance system provides a shutdown of metabolic activity to conserve resources during diving or death feigning. The DVC provides inhibitory input to the sinoatrial node of the heart via unmyelinated fibers and thus, is less efficiently controlled than the myelinated fibers from the VVC. Hypoxia or perceived losses of oxygen resources are the main stimuli that trigger the DVC. Once triggered, severe bradycardia and apnea are observed, often in the presence of defecation. A similar response strategy is observed

in the hypoxic human fetus, who responds with bradycardia and defication (i.e. meconium). In children and adults, a perceived loss of oxygen might elicit panic symptoms, which initially are associated with sympathetic excitation (e.g. tachycardia, profuse sweating) and may be followed by syncope, mediated via the DVC. Although adaptive for reptiles, the hypoxic triggering of the DVC may stop or profoundly slow the beating of the heart and, thus, could be lethal for mammals.

The DVC has beneficial functions in humans. Under most normal conditions, the DVC maintains neural tone to the gut and promotes digestive processes. However, if up-regulated, the DVC contributes to pathophysiological conditions including colitis and the formation of ulcers via excess gastric secretion. Although recent research confirms that the unmyelinated vagal fibers originating in the DVC contribute to bradycardia in mammals, it is debated whether the unmyelinated vagal fibers, independent of the myelinated vagal fibers from the VVC, are capable of the massive bradycardia observed in mammals (Daly, 1991; Jones et al., 1995). Alternately, one might hypothesize that the massive bradycardia would require the recruitment of myelinated vagal pathways by the DVC following withdrawal of neural tone by the VVC. Thus, during periods when the VCC tone is depressed, the myelinaed vagal pathways originating in the nucleus ambiguus might come under control of the dorsal motor nucleus of the vagus.

Mammals may employ the DVC in response to a severe threat. Especially in an unavoidable situation, the DVC may promote behavioral strategies of sudden prolonged immobility or feigned death (Hofer, 1970), which may result in fear induced death (Richter 1957). In humans, a similar neurophysiological reaction may explain syncope. The triggering of this system is powerful and costly, since the vagal surge may result in life threatening bradycardia and apnea causing the disruption of normal brain regulation. The reported physiological and psychological responses to rape or other severe trauma may provide examples of the potent effect of this system.

Evolution and Dissolution: A Hierarchical Response Strategy During Mate Selection

The evolution of the autonomic nervous system provides substrates for the emergence of the three emotion subsystems described above. Although reminiscent of the triune brain proposed by MacLean (1990), the Polyvagal Theory emphasizes that even the phylogenetically more primitive structures have changed in structure and function. This phylogenetic adjustment of the autonomic nervous system represents an exaptation (i.e. a shift in the function) of structures to express emotions. The ancient gill arches that characterize primitive vertebrates evolved into structures that convey emotional state via facial expressions, gestures and vocal communication.

The Polyvagal Theory proposes a hierarchical response strategy to environmental challenges, with the most recent modifications employed first and the most primitive last. However, the response strategy is not all-or-none and may include transitional blends between the boundaries of the three emotion subsystems. These transitional blends may be determined by both visceral feedback and higher brain structures (including vasopressinergic and oxytocinergic pathways that communicate between the hypothalamus and the DVC). Thus, the neurophysiological substrate of specific states and behaviors may incorporate activation of more than one emotion subsystem. For example, sexual arousal, with features of facial and vocal expressiveness in concert with facial flush, sweating and tachycardia, may reflect a blend defined by the activation of the VVC and the SNS.

The proposed hierarchical response strategy provides a model for the exploration of human social behavior. This phylogenetic strategy can be observed in human mating strategies. Our mating behavior is usually initiated by communication via facial expressions and vocalizations, a strategy with low metabolic cost. If appropriately used, communication will determine availability, induce proximity and promote reproductive behavior. Or, the strategy will determine unavailability, induce social distance, and promote a search for another prospective mate. An important feature of this mate selection strategy is that it limits vulnerability and risk by allowing participants to rapidly switch between engagement and disengagement behaviors (i.e. speaking then switching to listening; moving toward then rapidly retreating).

This phylogenetically based hierarchical response strategy is consistent with the concept of dissolution proposed by John Hughlings Jackson (1958) to explain diseases of the nervous system. Jackson proposed that "the higher nervous arrangements inhibit (or control) the lower, and thus, when the higher are suddenly rendered functionless, the lower rise in activity". The Polyvagal Theory (Porges, 1997) proposed dissolution, not in response to disease or brain trauma, but as a response strategy to differential challenges. The VVC with its mechanisms for signaling and communication provides the initial response to the environment. The VVC inhibits, at the level of the heart, the strong mobilization responses of the SNS. Withdrawal of the VVC, consistent with Jacksonian principles, results in a disinhibition of the sympathetic control of the heart. Similarly, withdrawal of sympathetic tone results in a disinhibition of the DVC control of the gastrointestinal tract and a vulnerability of the bronchi and heart. There are several clinical consequences to unopposed DVC control including defecation, due to a relaxation of the sphincter muscles and increased motility of the digestive tract; apnea, due to constriction of the bronchi; and bradycardia, due to stimulation of the sinoatrial node. Thus, when all else fails, the nervous system elects a metabolically conservative course that is adaptive for primitive vertebrates, but may be lethal for mammals. Consistent with the Jacksonian principle of dissolution, specific psychopathologies defined by affective dysfunction may be associated with autonomic correlates consistent with the three phylogenetic levels of autonomic regulation.

The Social Engagement System: An Emergent Property of the Ventral Vagal Complex

Phylogenetically, the VVC is the most recent neurophysiological affect system. The VVC is composed of a somatomotor component consisting of the special visceral efferents and a visceromotor component consisting of the myelinated vagal pathways from the nucleus ambiguus to the sinoatrial node of the heart and the bronchi. As illustrated in Fig. 1, the special visceral efferents and the vagal brake collectively constitute an emergent social engagement system. The somatomotor components of the VVC contribute to the regulation of behaviors involved in exploration of the social environment (e.g. looking, listening, ingesting) and behaviors involved in acknowledging social contact (e.g. facial and head gestures, vocalizing). More specifically, the somatomotor components of the VVC are involved in head turning (via cranial nerve XI), vocalizations (IX, X), facial expression (VII, V), the filtering of low frequency sounds via the middle ear muscles to extract human voice from backgrounds sounds (VII) and mastication (V). The visceromotor components of the VVC contribute to the rapid modulation of vagal (X) control of the heart and the bronchi (X), which provides metabolic resources to engage and disengage in a social setting.

Three important features define the social engagement system. First, the efferent pathways that regulate the social engagement system originate in medullary structures (i.e. nucleus of cranial nerve V, nucleus of cranial nerve VII, nucleus ambiguus). Second, corticobulbar pathways, which originate in frontal cortex (i.e. upper motor neurons), enable the possibility of efficient cortical regulation of these medullary source nuclei (i.e. lower motor neurons). Third, on the medullary level, the structures that regulate the efferent regulation of social-communication behaviors neuroanatomically communicate with structures that regulate ingestion (e.g. sucking, swallowing, salivation) and cardiac output. Thus, modulation of the vagal brake may either promote calming and self-soothing states (i.e. attenuate the influence of the sympathetic nervous system on the heart) or support mobilization (i.e. potentiate the influence of the sympathetic nervous system on the heart).

Mammals have a unique vagal system that includes myelinated fibers that regulate heart rate. The mammalian vagus functions as an active vagal brake (Porges et al., 1996) in which rapid inhibition and disinhibition of the vagal tone to the heart can change cardiac output to promote immediate engagement and disengagement with objects and individuals. Thus, the autonomic components, coincident with social interactions, may be mediated by changes in vagal tone to the heart, rather than the assumed changes in sympathetic arousal. Consistent with the Polyvagal Theory, difficulties in regulating the vagal brake may result in the phylogenetically older systems (i.e. neural regulation of the adrenal and the sympathetic nervous system) being recruited to regulate metabolic output to deal with environmental challenges. Consistent with the Polyvagal Theory, during states of mobilization, characterized by classic 'fight–flight' behaviors and sympathetic excitation, both the vagal brake and the behavioral components of the social engagement system are not easily accessible.

The functional impact of the mammalian vagus on the heart produces a heart rate pattern known as respiratory sinus arrhythmia (RSA). RSA is the rhythmic increase and

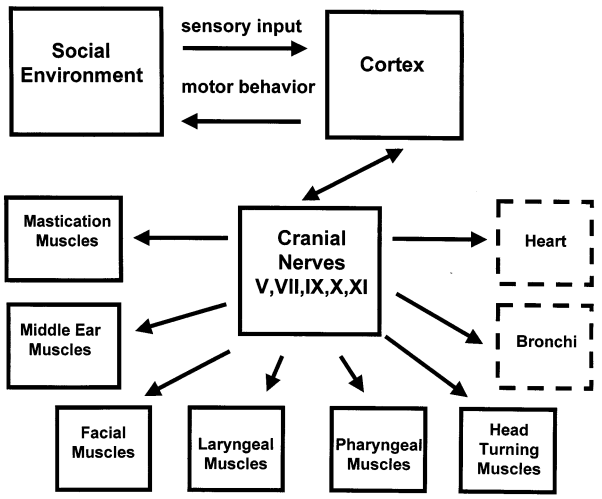

Fig. 1. The social engagement system: social communication is determined by the cortical regulation of medullary nuclei via corticobulbar pathways. The social engagement system consists of a somatomotor component (special visceral efferent pathways that regulate the muscles of head) and a visceromotor component (the vagal brake that regulates the heart and bronchi).

decrease in heart rate observed at the frequency of spontaneous breathing. Because the brainstem nuclei that regulate the mammalian vagus are neuroanatomically and neurophysiologically linked to the brainstem source nuclei of the special visceral efferents that regulate facial expression, monitoring dynamic changes in RSA and heart rate (i.e. the vagal brake) provides an efficient and noninvasive method of assessing the status of the social engagement system.

Courting and Seduction: Specialized Functions of the Social Engagement System

Seduction and courting behaviors convey an invitation to reduce physical and psychological distance. Primates express this invitation via cortical regulation of the brainstem source nuclei of the VVC that control facial expressions, head movements, and vocalizations. Mammalian social behaviors appear to be an emergent property of the cortical regulation of the VVC and the peripheral structures identified in Fig. 1. Courting and other behaviors of social engagement require direct cortical modulation of the medullary source nuclei of the VVC. This cortical regulation of brainstem inhibits protective and defensive response strategies that are dependent upon subcortical structures (e.g. amygdala, hypothalamus). However, courting and other expressions of social behavior are not independent of neurophysiological state. When the brainstem is under subcortical control, such as in states associated with fight–flight behaviors, cardiac output is increased by activation of the sympathetic nervous system to support the mobilization behaviors necessary to avoid or to respond to potential conflict. During these states, cortical modulation of the visceromotor control of the heart (i.e. the vagal brake) would substantially reduce cardiac output and compromise the effectiveness of the adaptive fight–flight behaviors. Thus, cortical regulation of the VVC requires the setting to be perceived as safe. The perception of safety, or at least the lack of fight–flight responses, would provide a neurophysiological state in which cortical regulation of medullary nuclei could promote proximity and increase the probability of reproductive behaviors.

Love and the Polyvagal Theory

Based upon the Polyvagal Theory, one would expect a neurobehavioral model of love to contain three phases, one representing each of the three emotion subsystems described above. The first two phases are easily identified. The first phase would be associated with the social engagement system, which would systematically signal and engage a prospective mate, and the regulation of vagal brake, which would modulate the metabolic resources necessary to carry out the behaviors. The first system would function only during periods of perceived safety. The second phase would be associated with mobilization and would provide the energy, via sympathetic excitation, to defend and to facilitate proximity for reproductive behaviors when separated. However, a third phase associated with immobilization is more difficult to conceptualize within the Polyvagal Theory. Although sexual behaviors often incorporate a state of immobilization, immobilization during coitus is not consistent with the state of fear predicted by the Polyvagal Theory. In addition, the initial description of the Polyvagal Theory made no statement regarding experiences of pleasure and ecstasy associated with sexual behavior. Therefore, to provide a neurophysiological explanation of love, the configuration of the Polyvagal Theory requires modification.

Love Without Fear: Hypothalamic Regulation of the Dorsal Vagal Complex. The third emotional subsystem of the Polyvagal Theory assumes that immobilization is adaptive

only in response to danger. A state of fear would be inconsistent with the acknowledged behavioral states associated with seduction and passion. However, for many mammals behavioral immobilization of the female is required for intromission. This active inhibition of motor activity optimally occurs in humans, not in a state of terror or fear, but in a state defined by safety and trust of the mate. If trust and safety do not characterize the period of copulation, intercourse may be painful and produce tissue damage. Alternatively, if a faulty sense of safety is perceived, both male and female may be vulnerable to predation.

How do mammals immobilize without fear? And, what are the physiological mechanisms underlying the mating rituals that allow behavioral immobilization without the physiological consequences of fear-induced shutdown responses?

Although the Polyvagal Theory has emphasized the potentially lethal shutdown behaviors associated with massive surges from the dorsal motor nucleus of the vagus, the DVC is involved in other functions. The DVC, with motor fibers originating in the dorsal motor nucleus of the vagus and afferent fibers terminating in the nucleus of the solitary tract and area postrema, has been assumed to be involved primarily in homeostatic functions (Leslie, 1985). The DVC promotes anabolic activities related to the restoration and conservation of bodily energy and the resting of vital organs. The DVC regulates digestion by modulating digestive polypeptides and gastric motility (Rogers and Hermann, 1992). In addition, Uvnas-Moberg (1989, 1994) has proposed a parallel between DVC regulation of gastrointestinal hormones and the regulation of visceral states including stress, hunger, and satiety. Without external challenges, the DVC optimizes the function of the internal viscera. In contrast, by increasing metabolic output to deal directly with external challenges, the SNS attempts to optimize the organism's relationship with the environment. Thus, increases in ambient temperature, noise, pain, and pyrogenic agents produce not only increased sympathetic activity, but an active inhibition of DVC actions on the gut (Uvnas-Moberg, 1987).

Paraventricular Nucleus and the Dorsal Vagal Complex. The paraventricular nucleus of the hypothalamus is an important regulator of the DVC. Neural communication between the paraventricular nucleus and the DVC is involved in responses that are not only homeostatic but protective and defensive (e.g. nausea and vomiting, conditioned taste aversion, behavioral defense) (Lawes, 1990). Communication between the paraventricular nucleus and the DVC changes with experience and thus, may exhibit a type of learning or memory. Associations may be established rapidly between environmental features or experiences and visceromotor responses. Perhaps, as in conditioned taste aversion, this memory is expressed as a learned association between a specific environmental feature and nausea. Once the association is made, subsequent exposure to the environmental feature may result in immediate nausea and defensive avoidance behaviors. These speculations regarding the changing communication between the paraventricular nucleus and the DVC with experience are consistent with general theories of aversion learning (Garcia et al., 1985).

The paraventricular nucleus regulation of the DVC evolved in phylogenetically older vertebrates in which escape and avoidance behaviors contributed to the maintenance of visceral homeostasis (Lawes, 1990). Because the early vertebrates lacked an elaborate nervous system to control their viscera, behavior was a primary mechanism for the maintenance of homeostasis (e.g. moving to regulate thermoregulatory and oxygen requirements). As the nervous system evolved, an autonomic nervous system and neuroendocrine mechanisms emerged and displaced the need to use behavior to regulate internal

state. The neural and neuroendocrine regulation of internal state allowed behavioral processes to be directed toward environmental challenges. However, the brain structures, specifically the paraventricular nucleus, that governed the homeostatically driven behaviors in the phylogenetically older species, evolved into the structures responsible for regulating internal homeostatic functions in the phylogenetically newer species (Leslie et al., 1992).

The role of the paraventricular nucleus in the regulation of the DVC in modern vertebrates retains phylogenetically older functions and continues to respond to threatening situations by contributing to visceral and endocrine responses. However, this phylogenetic organization results in vulnerabilities, because perceived challenges to survival, whether or not truly life threatening, may elicit visceral and endocrine reactions that compromise normal physiological function.

The phylogenetic emphasis of the Polyvagal Theory emphasizes that defense and avoidance behaviors have a vagal component manifested through the DVC. For example, a physiological shutdown mediated by the DVC would support avoidance behaviors such as death feigning or freezing. However, the evolution of hypothalamic regulation of the DVC provides response alternatives. Specifically, in mammals, the paraventricular nucleus produces two neuropeptides, oxytocin and vasopressin, that differentially communicate with the sensory and motor portions of the DVC. Using the push-pull perfusion technique, Landgraf et al. (1990) demonstrated that both oxytocin and vasopressin are released in the DVC. Binding sites for vasopressin are prevalent in the sensory component, but are not represented in the motor component (Fuxe, et al., 1994). In contrast, oxytocin appears to provide a primary pathway from the paraventricular nucleus to the dorsal motor nucleus of the vagus with oxytocin injections into the DVC mimicking the vagal responses normally observed immediately following feeding (Rogers and Hermann, 1992). Direct pathways from the nucleus of the solitary tract to the paraventricular nucleus provide a potential source of feedback for hypothalamic influences on visceromotor functions (Sawchenko and Swanson, 1982). The communication between the DVC and the paraventricular nucleus appears to modulate specific visceromotor reflexes involving cardiovascular (Nissen et al., 1993) and gastrointestinal systems (Bray, 1985).

Oxytocin and Vasopressin. Oxytocin and vasopressin are synthesized primarily in the paraventricular and supraoptic nuclei of the hypothalamus and released centrally via parvocellular neurons and systemically via magnocellular neurons (Swanson and Sawchenko, 1977). The central and systemic effects of these neuropeptides are different. Central release of oxytocin regulates the output of the dorsal motor nucleus of the vagus, usually maintaining output within levels optimal to support homeostasis. Peripheral release of oxytocin is related to milk ejection, uterine contractions, and ejaculation (Arletti et al., 1992; Wakerley et al., 1994). Central release of vasopressin appears to modulate afferent feedback from the viscera and to shift set points, independent of sensitivity, for vagal reflexes such as the baroreceptor reflex (Michelini, 1994). The raising of the baroreceptor set point would, by increasing cardiac output, potentiate fight–flight behaviors and allow sympathetic excitation of the heart to be unopposed by homeostatic vagal reflexes. Thus, central levels of oxytocin have been assumed to be associated with vagal processes and central levels of vasopressin have been assumed to be associated with sympathetic processes (Uvnas-Moberg, 1997).

Because the peripheral influences of oxytocin and vasopressin function through feedback, primarily via the sensory component of the DVC, the effects are less clear and may

be level dependent. For example, it is possible that peripheral vasopressin may, by stimulating vagal afferents, trigger massive vagal responses via the dorsal motor nucleus of the vagus. In support of this speculation, it is known that in humans, peripheral vasopressin, and not oxytocin, is related to the nausea experienced during motion sickness (Koch et al., 1990). In addition, systemic vasopressin may induce a baroreceptor-mediated withdrawal of sympathetic tone, which is observed in increases in baroreceptor-elicited bradycardia and a fall in plasma concentration of norepinephrine (Buwalda et al., 1992; Michelini, 1994).

Under certain conditions, such as during periods of perceived safety, small increases in peripheral vasopressin might trigger parvocellular release of both oxytocin and vasopressin. Potentially, this could occur via stimulation of either peripheral vagal afferents or vasopressinergic receptors in the area postrema. This stimulation would initiate communication between the paraventricular nucleus and both the sensory and motor nuclei of the DVC. The simultaneous central release of oxytocin and vasopressin would activate both vagal and sympathetic activity. This unique physiological state might characterize sexual arousal and would support intimate behaviors. Since vestibular stimulation elicits systemic vasopressin release (Koch et al., 1990), the perception of motion or environments that move might elicit visceral states vulnerable for intimacy. This could explain the selection of porch swings, trains, boats, planes, water beds, or even roller-coasters as preferred arenas for eliciting and experiencing passionate love.

Oxytocin may be part of a complex response profile related to the perception of the environment as safe. Consistent with this view, Uvnas-Moberg (1997) and Carter and Altemus (1997) propose that oxytocin promotes states resistant to stress (i.e. anti-stress), In contrast, vasopressin may be part of a complex response profile related to the perception that the environment is challenging or dangerous. In fact, central vasopressin could potentiate mobilization responses via sympathetic excitation, while high levels of systemic vasopressin may potentiate a physiological shutdown associated with fear (e.g. bradycardia) via feedback to the dorsal motor nucleus and inhibition of sympathetic outflow (Ferguson and Lowes, 1994). In addition, lesions of vagal afferents, which functionally block the visceral input to the sensory component of the DVC (areas sensitive to vasopressin), attenuate or abolish specific conditioned taste aversions (Andrews and Lawes, 1992).

Based on the Polyvagal Theory, the mammalian or smart vagus, with myelinated motor fibers originating in the nucleus ambiguus, provides a system for voluntary engagement with the environment with special features associated with the prosocial behaviors of communication. Paralleling this evolutionary shift in the vagus, is a mammalian modification of the hypothalamic regulation of the DVC via both oxytocin and vasopressin. The advent of specific receptors for oxytocin and vasopressin increases the range of adaptive functions involving the DVC. In mammals, the dorsal motor nucleus of the vagus, the motor component of the DVC, is sensitive to oxytocin, and insensitive to vasopressin. In contrast, the sensory components of the DVC, the nucleus of the solitary tract and area postrema, are most sensitive to vasopressin. Although the nucleus of the solitary tract has receptors for oxytocin (Landgraf et al. 1990), area postrema may not be directly influenced by oxytocin (Carpenter, 1990). The differential sensitivity of specific components of the DVC to these two neuropeptides (the differential effects of central and systemic release on visceral function and a potential level dependency) results in a wider range of response options and the co-opting of the primitive vagal system to support avoidance (death feigning, vomiting), engagement (e.g. nursing, feeding) and copulation.

Conditioned Love: Physiological Mechanisms Involved in the Learning and Memory of Intimacy. Classical conditioning provides a potential neurophysiological process to associate gastrointestinal responses with specific sensory events. Classical conditioning may incorporate oxytocinergic and vasopressinergic pathways connecting the paraventricular nucleus with the dorsal motor vagal complex. Garcia et al. (1985), in presenting a general theory of aversion learning, speculated that two specialized coping systems evolved in mammals. The first coping system includes behaviors to protect oneself from predatory attack. This system employs instrumental mobilization behaviors including active approach and avoidance behaviors. The second coping system deals with protecting the gut from toxic foods and includes the hedonic appraisal of visceral stimulation during eating and copulation. The second system produces rapidly conditioned and difficult to extinguish gustatory–visceral associations. Garcia et al. speculated that to approach a receptive mate is a product of the first system and to find a sexually satisfying mate more desirable is a product of the second system. This distinction between approach behaviors and conditioned visceral feelings is convergent with the proposed neurobiological theory of love, which distinguishes between seduction and conditioned or passionate love.

Consistent with the hypothesis that a conditioned association between positive visceral feelings and the mate are a product of copulation, Carter et al. (1995, 1997) have shown that sexual interactions, probably mediated through oxytocin and/or vasopressin, can faciliate pair-bonding. Oxytocin has been associated with positive states such as physical proximity, touching, prosocial behavior, and the ingestion of food (Carter et al., 1997; Uvnas-Moberg, 1997). Oxytocin also has been implicated in the cephalic phase of digestion. The cephalic phase, the initial digestive phase, is stimulated by psychological factors such as sight, smell, taste, or associations with food before food enters the stomach. The cephalic phase is characterized by increased gastric secretion and reduced gastric motility, providing a receptive environment for the passage of food and allowing the gastric secretions to more efficiently aid in digestion of food in the stomach (Rogers and Hermann, 1992).

Oxytocin and vasopressin are related to other learned responses. For example, intracerebroventricular injection of oxytocin attenuates passive avoidance (Kovacs and Telegdy, 1982), whereas vasopressin enhances passive avoidance (De Wied, 1971). Although these findings may be paradigm dependent, there is consistent evidence that central levels of both neuropeptides are involved in learning social cues and in the development of partner preferences (Carter, 1998; Engelmann et al., 1996). In addition, it is well known that the oxytocin release during milk ejection can be conditioned (Wakerley et al., 1994). Likewise, it is plausible that the oxytocin released during coitus could be conditioned and associated with specific social cues. Thus, engagements between the pair-bonded mates would trigger a release of oxytocin, which might decrease the latency for subsequent sexual encounters.

Communication Between the Paraventricular Nucleus and the Dorsal Vagal Complex: A Mammalian System for Love and Fear. The neural and neuropeptide communication between the paraventricular nucleus and the DVC, with its involvement in both emotional and learned associations, may provide the physiological mechanism that enables mammals to respond reliably to both fear-related and safety-related environmental cues. Thus, this communication, through the partitioned roles of two related peptides, vasopressin and oxytocin, may promote several classes of behavior. First, the oxytocinergic pathways from the paraventricular nucleus to the dorsal motor nucleus of the vagus appear to co-opt the ancient immobilization fear system that characterizes reptiles. By blunting the shutdown

fear response mediated by the dorsal motor nucleus of the vagus, oxytocin modulates vagal function to promote homeostasis and shifts the function of the visceral organs to support progenitive behavior and experiences of passion. Second, in the absence of central oxytocin communication with the dorsal motor nucleus of the vagus, increases in systemic vasopressin would facilitate a fear-induced avoidance, consistent with phylogenetic origins, as a shutdown response system. Third, central vasopressin would facilitate mobilization via sympathetic excitation. Fourth, small increases in systemic vasopressin may trigger a co-excitation of central oxytocin and vasopressin coincident with the peripheral co-excitation of vagal and sympathetic activity characteristic of sexual arousal.

Consistent with the literature on visceral (i.e. vagal) conditioning and pair-bonding (Carter et al., 1997), the oxytocinergic communication between the paraventricular nucleus and the dorsal motor nucleus of the vagus, may provide a neurophysiological mechanism to explain how specific progenitive behaviors including proximity with a mate would be linked with positive visceral feelings. The conditioning process would be facilitated by systemic vasopressin, that could trigger sexual arousal (e.g. sexual arousal) and central oxytocin, which could modulate vagal responses. The conditioning process may provide a plausible mechanism to explain other classes of behavior including parent–child bonding, friendships, and the visceral reactions to the loss of a loved one either through death or violation of vows of love. For example, grief and unrequited love, often characterized by potent unpleasant visceral responses, may be mediated by increases in systemic vasopressin, which can trigger vagal responses (e.g. nausea and syncope), which are no longer protected or modulated within the homeostatic range by oxytocin. Vasopressin and oxytocin may work in concert in other behavioral states. For example, during sexual or nursing behaviors peripheral oxytocin release may enable the visceral organs to be responsive and pliable, while central oxytocin and/or vasopressin release may result in a modulation or an attenuation of painful tactile stimulation, such as that reported following electrical stimulation of the solitary tract (Ren et al., 1990; Uvnas-Moberg, in press).

Additional neuroanatomical structures may be involved in the establishment of intimacy. The amygdala appears to play a major role in the retention of fear-related or aversive associations (Davis, 1992; LaBar and LeDoux, 1996; LeDoux et al., 1988). For example, lesions of the central nucleus of the amygdala attenuate the conditioned bradycardia, independent of the conditioned corneoretinal potential (Gentile et al., 1986) or the magnitude of the heart rate orienting response (Kapp et al., 1979). This research demonstrates a role for the amygdala in the retention of negative affective states. However, the role of the amygdala in the retention of positive affective states with prosocial consequences, such as a hypothesized conditioned love, has not been investigated.

Immobilization Without Fear: The Importance of Perceived Safety. By incorporating the influence of the neuropeptides, oxytocin and vasopressin, on the DVC, the Polyvagal Theory can be used to explain two classes of immobilization behaviors; one associated with fear and the other with passion. Mammals require a perception of safety to digest food efficiently, to sleep, and to reproduce. During perceived threat or fear these processes are inhibited. The paraventricular regulation of the DVC provides a plausible mechanism for a central switching circuit that determines whether specific DVC processes are fostered or inhibited. Thus, the neuropeptide modulation of the DVC may contribute to two important processes: first, the determination of whether immobilization is due to fear or

security; and second, a specific conditioned association with each behavioral state. Similar to other conditioned vagal responses (e.g. taste aversion), the learned associations with either fear or security may be easily established and very difficult to extinguish.

The oxytocinergic pathways from the paraventricular nucleus to the dorsal motor nucleus of the vagus modulate the neural stimulation of organs of fear, digestion, and elimination to foster reproduction, feelings of safety, visceral sensations of pleasure and ecstasy and the conditioning of visceral associations with the mate. In contrast, the vasopressinergic pathways from the paraventricular nucleus to the nucleus of the solitary tract and area postrema may inhibit processes associated with digestion, elimination, and reproduction, thereby facilitating fight–flight (mobilization) behaviors. Other neural pathways from the hypothalamus to the DVC may promote either primitive avoidance behaviors such as freezing and death feigning or the more phylogenetically advanced flight–fight behaviors associated with the SNS. In addition, pathways from the amygdala may modulate the communication between the hypothalamus and the DVC (Lawes, 1990) and contribute to specific fear-associated behaviors (LeDoux et al., 1988; Rosen et al., 1996).

Mammalian neuropeptides modulate autonomic functions during love-related behaviors. The Polyvagal Theory emphasizes the phylogenetically more recent vagal pathways that originate in the nucleus ambiguus. The nucleus ambiguus vagal pathways are involved in the voluntary behaviors required for social engagement, including the general category of seduction. However, the visceral experience of ecstasy, diffuse visceral pleasure, and analgesia are related to the phylogenetically older DVC. The DVC, according to the Polyvagal Theory is associated with an immobilization fear system. However, the mammalian neuropeptide, oxytocin, which is released from the paraventricular nucleus of the hypothalamus, provides a neurophysiological mechanism to co-opt the function of the DVC. Oxytocin may modify the function of the DVC from an immobilization fear system to an immobilization passion or love system. Oxytocin, although stimulating vagal activity (e.g. DVC), appears to limit vagal activity to a functional range that protects the organism from experiencing massive vagal surges that would shut down physiological homeostasis.

Seduction or Rape?. The autonomic nervous system is involved in several aspects of human mating behavior. First, as discussed above, the autonomic nervous system can support seduction (behaviors of engagement). The mammalian or smart vagus with its somatomotor regulation of facial expressions and vocalizations provides the neural regulatory structures for this phase of social engagement. Second, by an inhibition of the vagal system and an excitation of the SNS, cardiac output can be increased to support behavioral mobilization including active withdrawal from unwelcomed engagements, fighting behavior to protect the mate, and approach behaviors to reduce distance from the mate. Third, the phylogenetically older DVC (visceral or vegetative vagus) contributes to behavioral immobilization by initiating a primitive shutdown of physiological systems. This form of immobilization is usually in response to fear when there is no option to mobilize. Fourth, by co-opting the DVC, the neuropeptides from paraventricular nucleus can promote sexual arousal, immobilization without fear, copulatory behavior, positive visceral experiences and conditioned associations with the mating partner.

A physiological shutdown response profile may characterize the female during rape, an unwelcomed and physiologically dangerous event. This physiological shutdown, due to a massive surge from the dorsal motor nucleus of the vagus, may be associated with or conditioned to specific events or individuals. This classically conditioned response may

require only a single trial to be learned and may exhibit great resistance to extinction. For example, following the rape, sexual encounters, even with a desired partner, may elicit a vagal syncope. Or, the raped woman may become anxious about sexual encounters and physiologically mobilized via sympathetic excitation to escape. An important aspect of the immobilization phase is that it may follow the well-documented laws of conditioning visceral responses mediated by the DVC (e.g. nausea and vomiting) used to explain conditioned taste aversion (Garcia et al., 1985). A similar response profile may characterize individuals who fear death and believe that they are unable to escape, such as the description of hopelessness (Richter, 1957) and perhaps, clinical disorders such as post-traumatic stress disorder.

Seduction provides a prosocial vehicle for mate selection. Appropriate mate selection, in turn, changes the visceral and psychological experiences associated with female immobilization, which is required for intromission, from fear to passion. Seduction allows intimacy to occur without trauma. When the female perceives the male as providing security, an immobilization love system is initiated. This immobilized love system is physiologically and psychologically incompatible with the immobilized fear system. Although both immobilization response patterns share common physiological substrates, the response profiles are different. The immobilized fear system results in a physiological shutdown and a functional inhibition of social behavior and sexual receptivity and responsivity of the genitalia. The immobilization fear system, when initiated, attempts to turn off behavior and consciousness by lowering heart rate and blood pressure, which may produce syncope. In contrast, the immobilization love system heightens sexual arousal in response to genital stimulation, lubricates genital tissue, maintains blood pressure, and raises pain thresholds. The immobilization love system co-opts the paraventricular communication with the DVC and modifies immobilization from a fear-related psychologically dissociative and physiologically compromised state to a love-related psychologically ecstatic and reproductively available state.

By co-opting the communication between the paraventricular nucleus and the DVC, an immobilized love circuit fosters reproductive behaviors. Reproductive behaviors occurring during states of immobilized love promote enduring associations between the mate and the ecstatic experiences. The development of these associations appears to follow the laws of visceral conditioning, since they are easy to establish and result in relatively permanent bonds (Carter et al., 1997). Love may be a classically conditioned response with enduring resistance to extinction. Perhaps, species differences in monogamy (Carter et al., 1995; Dewsbury, 1987) might be related to differences in the capacity to recruit the paraventricular control over the DVC in prosocial associative learning paradigms. If this is true, the selective nature of the seduction phase and the fight–flight behaviors of the mobilization phase may become a functional barrier to this associative vulnerability. Thus, when we are careful about whom we allow ourselves and our children to be physically close to and to have sexual activities with, we are respecting our vulnerability to the conditioning that characterizes passionate love.

How does our nervous system organize these unique and important behaviors? As illustrated in Fig. 1, the social engagement system and the vagal brake provide neurobiologically-based constructs to describe mechanisms of seduction. Modulation of the social engagement system enables symbolic approach behaviors (e.g. facial expressions, head tilt, and vocalizations) and modulation of the vagal brake provides metabolic support for the behavioral mobilization necessary to engage a prospective mate physically. However, if there is a mismatch between the expectations of the prospective mating partners, mobiliza-

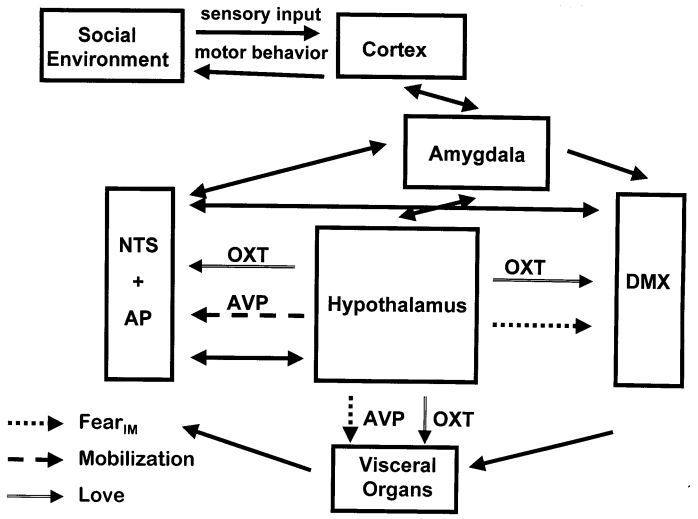

Fig. 2. Neural and neuropeptide regulation of the dorsal motor nucleus of the vagus: fear or love? Higher brain structures including the amygdala and cortex influence hypothalamic–dorsal vagal complex (DVC) communication. The DVC includes sensory nuclei in the nucleus of the solitary tract (NTS) and area postrema (AP) and motor nuclei in the dorsal motor nucleus of the vagus (DMX). During perceived danger, when mobilization is adaptive, central vasopressinergic pathways (AVP) communicate between the hypothalamus and both NTS and AP to change the set-point of vagal reflexes to facilitate sympathetic excitation. Immobilized fear occurs when fight–flight behaviors are not an option. Immobilized fear is fostered by vagal surges from DMX to visceral organs, which are potentiated by systemic AVP. Systemic AVP triggers increased DMX output by stimulating visceral afferents via NTS and AP. During perceived safety, oxytocin (OXT) is released centrally and systemically to foster an immobilized love response pattern. Central OXT limits DMX output to a functional range protecting homeostasis and systemic OXT stimulates visceral organs. Small increases in systemic AVP might, either via vagal afferents or direct stimulation of vasopressinergic receptors in AP, trigger central AVP and OXT and promote sexual arousal.

tion may occur to insure an increase in physical distance. This mobilization response requires sympathetic excitation and a withdrawal of the vagal brake (the smart vagus). If physical escape is not available, the vegetative vagus (DVC) may become activated to provide a primitive avoidance strategy characterized by a physiological shutdown and a possible loss of consciousness due to compromised homeostatic regulation (e.g. decreased blood pressure).

Successful mating and bonding are the product of a different sequence. In this sequence, seduction is successful and proximity between the prospective mating partners is reduced. Mobilization is restricted to the physical activities associated with the preparation to copulate and copulation. Finally, to ease intromission for the female and the post-coitus recovery for the male, an immobilization system is stimulated. This immobilization system is confined to situations of perceived security. Because states of immobilization for mammals are periods of vulnerability, this type of immobilization occurs only in a safe environment with mutual trust as a defining feature. Thus, an important feature of the love experience is not mediated by physical attractiveness, but is driven by trust and security.

As illustrated in Fig. 2, hypothalamic–DVC regulation is flexible. Higher brain structures determine whether the hypothalamic–DVC communication results in an immobilized

fear response or an immobilized love response. The amygdala may play a major role in determining which hypothalamic–DVC circuit is recruited. If Pavlovian conditioning provides a plausible metaphor for the enduring nature of a conditioned love (Garcia et al., 1985), then the amygdala may be involved in maintaining these learned associations.

The proposed model attempts to integrate the role of neuropeptides (i.e. oxytocin and vasopressin) with the autonomic nervous system. As illustrated in Fig. 2, the perceptual mechanisms of higher brain structures determine if a situation is dangerous or safe. During perceived fear, there are two options. The organism may mobilize and express fight–flight behaviors. Or, if the first option is not available, the organism may immobilize. Immobilization results in a behavioral shutdown, death feigning, and a loss of consciousness. The effect of vasopressin released centrally via the parvocellular neurons, communicating between the hypothalamus and the sensory portion of the DVC (nucleus of solitary tract and area postrema), inhibits feedback from the viscera and promotes sympathetic activation and increased mobilization. However, vasopressin released systemically via the magnocellular neurons originating in the hypothalamus stimulates visceral afferents and promotes feedback to the DVC, which may result in the massive vagal surge associated with physiological shutdown.

In contrast, perceived security changes the immobilization system, which originally evolved to cope with fear, to a system that promotes reproduction and provides heightened sensory experiences that are psychologically reinforcing. Perceived security enables the hypothalamic release of oxytocin centrally to modulate the vagal discharge that can stimulate the viscera and systemically to foster reproduction and heightened sensory feedback. Enhanced sensory feedback provides a positive visceral state that acts as a reinforcer to enhance the conditioned association between the mate and reproductive availability. In addition, sensory feedback acts as a modulator of pain (Komisaruk and Whipple, 1995), which allows areas of the body to experience sensations that would have been perceived as painful in other situations. The positive visceral feelings lead to experiences of pleasure, ecstasy, and the less well defined emotional states that we associate with love. Thus, via the influence of oxytocin on the autonomic nervous system, organs of fear and vigilance become organs of pleasure, nurturance and reproduction. Oxytocin, a hormone unique to mammals, co-opts ancient structures changing a fear-induced shutdown system in to a receptive and ecstatic reproductive system. In addition, as stated above there is the possibility that low levels of peripheral vasopressin, perhaps elicited by gentle vestibular stimulation in an environment perceived as safe (e.g. the porch swing or a sail boat) triggers central release of oxytocin.

Of course, the violation of trust changes the context and a mate that once conveyed a sense of safety, would now convey cues of danger. Thus, violation of trust might result in mobilized fight–flight behaviors, or the shutdown behavior associated with immobilized fear. In addition, unrequited love or the loss of a loved one, might result in syncope or visceral feelings associated with nausea, characteristic of vagal activation due to systemic vasopressin release, without the protective or modulated influence of oxytocin.

The Monogamy Switch and the Biological Prenuptial. Love, as an emotional and motivational process, may have evolved to maximize the adaptive benefits associated with reproduction and safety. However, to achieve these benefits, individuals need to negotiate the relative costs of coping with two potent risks: (1) the vulnerability to predation; and (2) the vulnerability of the nervous system to develop enduring social bonds following the mating sequence. The first risk is obvious. The environment is competitive and often

hostile. To survive, coalitions must be developed. Prominent among these coalitions is the social bond between mating partners. The second risk acknowledges that our nervous system may be stimulated to form enduring social bonds with an inappropriate mate. The articulation of the second risk is new to science. Rather, the second risk has been the focus of gender specific myths and cultural expectations regarding chastity, promiscuity, and marriage. In contemporary culture, monogamy is the focal point around which seduction and sexual encounters are expected to revolve. However, not all sexual and love experiences lead to monogamous relationships. Although the partitioning of the love experience into two sequential components (seduction and a conditioned or enduring passionate love) assumes a monogamous end point, many individuals may focus on seduction and opt for relationships that are not monogamous.

Conditioned love with its enduring social bond might require a prerequisite neurophysiological state that might be conceptualized as a monogamy switch. Once a decision is made to become monogamous with a selected mate, the individual may immobilize without fear and the nervous system becomes vulnerable to conditioned love. Alternatively, to protect oneself from monogamy, the monogamy switch may be disabled by mobilization strategies, even during sexual encounters. Mobilization strategies engage SNS mechanisms, which are inhibitory of the conditioning processes associated with DVC mechanisms. For example, promiscuous sexual activity need not lead to enduring bonds, if the sexual activity were physically active and both sexual partners limited periods of immobilization. This strategy would limit oxytocin release, while experiencing the activation of sexual arousal. Illicit affairs fit this model, especially if the sexual activity is brief, intense, and under the threat of discovery.

The risks or vulnerabilities to states of conditioned love have been described in gender specific myths, which promote female chastity and female vulnerability to first love in contrast to male promiscuity. Underlying these myths may be an implicit understanding of the monogamy switch, a neurophysiological mechanism that promotes pair-bonding or conditioned love. For example, female immobilization without fear might heighten a vulnerability to a conditioned or learned love. Thus, the male, who conquers the female's fears and gives her a sense of safety and security, not only is allowed to copulate with her, but she in return may be permanently bonded to him. Possibly, this gender bias might have evolved because copulatory behavior in mammals requires only the female to immobilize, but to immobilize outside the realm of fear. In contrast, the male tends to be more mobilized in the sexual act and only following ejaculation does the male become immobilized and at physical risk from the environment. It is this mobilization that may protect the male from a conditioned love. Perhaps, if the male, following copulation, remained immobilized or slept in the presence of the female, he would be as vulnerable as the female to conditioned love. Cultural and self-imposed prohibitions of spending the night together, even following sex, might reflect an implicit biological awareness of this phenomenon.

The potential gender differences in conditioned love vulnerability may result in an unstated, but assumed biological prenuptial. The biological prenuptial reflects the interactive negotiations between prospective mating partners in which the male requests exclusive copulatory rights of the female's reproductive organs and the female requests that the male insure her security and safety needs before activating the monogamy switch. Violation of the biological prenuptial occurs when the male physically abuses the female or when the female copulates with another male. The valence of these two violations appears to be gender specific. In support of this hypothesis, Buss et al. (1992) reported that men are

more distressed by their mate's sexual infidelity, while women are more distressed by their mate's emotional infidelity. Violations of the biological prenuptial are destructive to the love bond and result in a lack of trust and security for both genders. This gender biased prenuptial is so rooted in our history that it finds its way into our marriage vows and religious tenants, which have been used to support monogamy.

CONCLUSION

The evolution of the neural and hormonal regulation of the autonomic nervous system provides a framework to interpret mammalian love as an adaptive process that facilitates reproduction in a rapidly changing and challenging environment. The development of love and intimacy consists of several sequential processes with adaptive functions that promote safety and progenitive behavior. Love, as a neurophysiological construct, not only promotes reproduction, but it also provides a pair-bond to promote safety in the challenging environment. Within this adaptive context, love may have evolved functionally as a temporal shortcut to bypass the slow, often tedious, and potentially unsuccessful processes of communication and social engagement to foster physical proximity and to promote intimacy and reproductive behaviors.

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