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Opinion

Territorial blueprint in the hippocampal system

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As we skillfully navigate through familiar places, neural computations of distances and coordinates escape our attention. However, we perceive clearly the division of space into socially meaningful territories. 'My space' versus 'your space' is a distinction familiar to all of us. Spatial frontiers are social in nature since they regulate individuals' access to utilities in space depending on hierarchy and affiliation. How does the brain integrate spatial geometry with social territory? We propose that the action of oxytocin (OT) in the entorhinal–hippocampal regions supports this process. Grounded on the functional role of the hypothalamic neuropeptide in the hippocampal system, we show how OT-induced plasticity may bias the geometrical coding of place and grid cells to represent social territories.

Highlights

Space is a primary resource, which has led many species to evolve territorial behavior intertwining the spatial mapping of utilities with their socially regulated access.

In addition to supporting navigation in space, the hippocampal system encodes social stimuli, thereby providing essential elements to represent territorial ownership.

Oxytocin (OT), the prosocial neuropeptide, modulates the processing of social stimuli in ways relevant to territorial behavior.

Central OT long-range projections and receptors present in the hippocampal system provide a direct route for the modulation of hippocampal activity. OT-induced neural plasticity may bias the geometrical coding of place and grid cells to represent social territories.

Territorial behavior, a common thread in evolution, should be investigated using a readout of spatial metrics in terms of utility ownership, social attachment, and hierarchies.

Origins of territoriality in humans: the social contract for land partition

The human diaspora, which began *ca* 70 000 years ago as *Homo sapiens* expanded out of Africa, was probably stimulated by massive local ecological changes [1]. The scarcity of resources such as food and shelter pushed humans to conquer new territories offering better prospects [2]. This adaptation is hypothesized to result from a genetically based proclivity for social group cooperation, coupled with the tendency to exploit dense and predictable nutritional sources [3]. Much later, the emergence of agriculture and animal domestication in Levant Natufian communities about 10 000 years ago was likely to have been fostered by an increasingly sedentary lifestyle [4]. **Philopatry** (see Glossary) was in turn increased by the investments made in territory needed for farming. Humans transitioned from hunter–gatherer habitats to settlements, thereby providing the foundations of today's territorial landscape with villages or towns [5] with massive reorganization in workloads and division of labor. Even more consequential was the subsequent establishment of communal and private property, with increasing territorial control through societal organization, politics, and sometimes war enforcement [4].

It is striking that territorial behavior has not declined over recent human evolution and still strongly shapes individuals' views of space in terms of private, public, and neutral (no-man's land). The scope of the phenomenon extends from the individual to society, with land use regulated between families, groups, cities, and countries, as embodied by legal and political agreements. Humans follow social contracts that govern the territorial use of land and its frontiers depending on hierarchy and kinship [6]. Traditional and modern cultural agreements of land sharing include filiation, marriages, and between-group alliances [7]. Thus, space in the territorial format is essentially social.

We propose that this territoriality is underpinned by adaptive neural substrates linking the memory of resources via orienting and navigation to those controlling group interactions leading to land partition. In support of this idea, we adopt a neuroethological perspective and synthesize findings in several disciplines to explore the relationships between spatial and social cognition as a basis of the expression of territorial behavior (Figure 1). We propose possible brain mechanisms of

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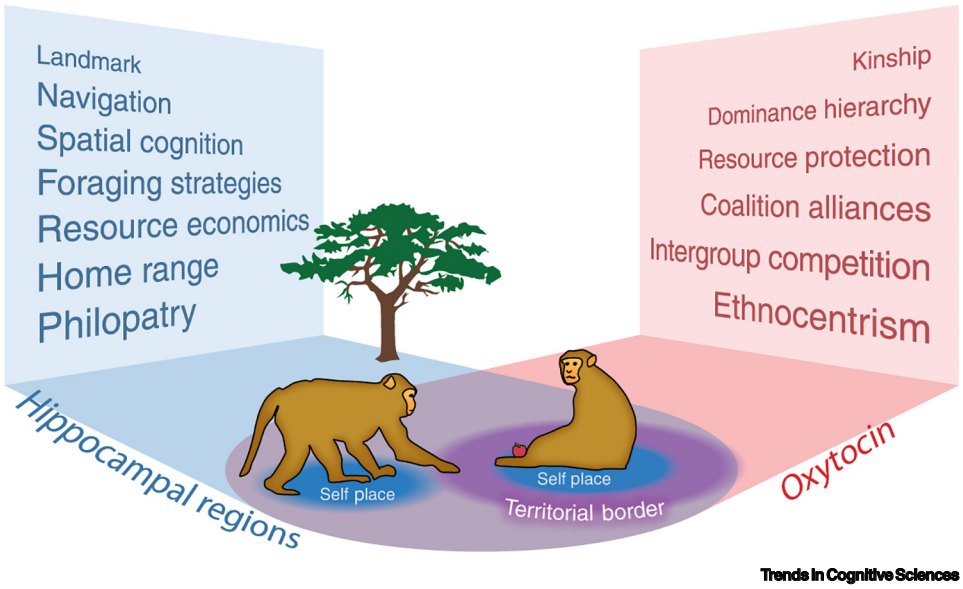

Figure 1. Conceptual framework of territorial coding interfacing spatial and social domains. Oxytocin inputs (red) on brain areas dedicated to spatial processing (blue) yield a territorial representation where space is mapped in the social domain. This process merges: (i) the ability to know a terrain such as a home range through its resources and borders; and (ii) the ability to identify others allowed in that terrain (self, mate, kin, affiliated) and those excluded (any other conspecific, any non-kin). Thereby, territoriality results from the controlled access to spatial resources by social determinants between and within groups.

territorial implementation driven by **OT** input into the hippocampal–entorhinal complex. We suggest that space as a territory is a novel domain in cognitive neuroscience that should be further investigated using a readout of spatial metrics in terms of ownership, utilities, attachment, and social hierarchies.

Territorial behavior is at the crossroads between spatial and social representations

Territorial behavior is not unique to humans. Limited resources such as food, shelter, and mates have led many species, including birds, carnivorans, rodents, and primates, to exclude conspecifics from regions of space, granting them continuous access to resources [8]. Thus, a portion of space becomes a territory when an animal maintains a presence in a fixed limited area (philopatry) and defends it against intruders. This operational definition puts the concept of territory at the interface between the physical attributes of space and the social interactions relating to the acceptance or rejection of conspecifics in that space (Figure 1). That a territory possesses stable contours makes its definition parallel with that of '**home range**', which for many species comprises recurrent visits to specific feeding, caching, or sleeping sites [9,10]. **Spatial cognition** is therefore a common capacity that enables the exploitation of home-range resources in species subject to a wide variety of evolutionary pressures[11,12] and can be adapted to manage the economics of important resources in a social competitive context. For example, in the monogamous territorial prairie vole, the expression of territorial behavior can be directly linked to spatial cognition: animals submitted to high sexual competition, which increases territorial behavior, display better performance in laboratory spatial memory tests [13,14].

Space becomes a territory only when ownership is claimed by an individual or group and is challenged by others [15]. In gregarious species, the capacity of the home range to fulfill the increased nutritional needs of a thriving group often results in territorial defensiveness and conflict with other

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conspecific groups [15]. Male chimpanzees (*Pan troglodytes*) patrol and actively defend their borders through the formation of coalitions during intergroup aggression [16]. This aggressive strategy results in territorial home-range expansion for the victorious chimpanzees following a lethal conflict [17], improving the feeding success of individuals in their own community [18]. Male bonding plays an important role when raids involve coalitions [19], a pattern that parallels human behavior in belligerent contexts [20]. Even in macaque species not known to exhibit strong territorial defense, such agonistic behavior between groups can emerge when animals are confronted with a lower food supply and higher population density [21]. Within the group, to reconcile possessive behaviors with the need to thrive, many mammalian species, including humans, compromise on the use of territory according to social status and group affiliation [6]. The presence of marked levels of hierarchies and systems of dominance inherited through affiliation and kinship [22] strongly influences access to food and mates [23] and individual position within the group [24]. The overall intricacy of spatial distribution as a function of social determinants led us to hypothesize that a common neural substrate is responsible for territorial behavior.

From spatial cognition to space ownership

To navigate between locations in space, humans and other animals rely on a range of spatial information. Knowledge about self-position, heading direction, and distance with respect to geographical landmarks or goals greatly enhances the exploitation of a home range. The past four decades of neuroscience research have confirmed that many of the building blocks essential to support an internal cognitive map of space [25] are present in the hippocampal formation (broadly defined as the hippocampus, the subiculum, and the entorhinal cortex). The cognitive spatial map is now believed to be embodied by neurons with unique functional properties, such as place cells and grid cells (Figure 2A,B) in the hippocampus and the entorhinal cortex [25]. Such cells, first demonstrated in rodents, display selective neuronal activity for a place that depends on the animal occupying that place. Other notable functional cell types identified in species evolving under various ecological settings (rats, bats, and macaques) include cells encoding a particular direction in space with respect to an object, a goal, or a reward [26–29] (Figure 2C) and cells that are active when animals roam along the physical limits of a place [27] (Figure 2D). Thus, the hippocampal formation harbors the essential building blocks to encode the physical attributes and resources available in a territory.

An important issue is how territorial behavior relates to the mechanisms underlying a sense of ownership associated with one's own territory. While other animals may not have the same concept of ownership as humans do, it is plausible that territorial defense may be a form of rudimentary ownership expression. A prerequisite for territorial behavior is that a partition of land is recognized as one's own. Such sense of ownership might arise from: (i) long-term familiarity, which may help in recognizing what is one's own; and (ii) a bias to return to rewarding places. These processes may be mediated by the hippocampal formation's ability to learn about rewards in a home range and to bias future exploitation of rewards in a known place [30,31]. In this respect, the hippocampus might contribute to territorial cognition before that territory is shared with or protected from others.

Mapping social information in the hippocampal regions

Recent evidence indicates that the hippocampus displays complexity along social dimensions comparable with that described above for spatial dimensions. In humans, macaque monkeys, and rodents, hippocampal neurons carry information related to other individuals' identity [32–34], a requirement for territorial representation. Notably, in humans these neurons respond selectively to a specific person's visual image or spoken name or when the person's identity is recalled from memory [35]. In rodents, several findings support the involvement of all regions of the

Glossary

Ethnocentrism: the tendency of humans to favor their own ethnicity in their judgment and, by extension, display kin or own-group preference.
Hippocampal CA2: a small region comprising large pyramidal cells between the CA3 and CA1 subfields, specifically important for the processing of social stimuli. Lesioning of CA2 or blocking neurotransmission in CA2 disrupts social memory.
Hippocampal CA3 recurrent collaterals: in hippocampal CA3, the axons of pyramidal cells ramify to reach other pyramidal cells throughout all of the hippocampus, enabling each neuron in CA3 to make contact with many other cells in the hippocampus. The recurrent collateral autoassociative network, present in rodents and primates, provides a scaffolding to link memories about places with memories about social stimuli.
Home range: the living area of an animal containing primary resources such as shelter, mates, and food. Its maintenance and exploitation benefits from spatial cognition mapping the location of utilities in space.
Oxytocin (OT): neuropeptide secreted by the paraventricular and supraoptic nuclei of the hypothalamus. In addition to its peripheral actions linked to sexual reproduction and labor, the central action of OT is to modulate attachment and prosocial behavior. The hormone also plays a role in anxiety management. The central actions of OT result from diffusion of OT in the brain or local release through the activation of long-range oxytocinergic axons. OT action results from its effects on OTRs.
Philopatry: originally used to refer to the tendency of animals to return to their birthplace to breed. By expansion, this term refers to a manifest attachment to a land in animals or humans.
Social memory: defines the ability to discriminate between a previously known individual (familiar) and a new one. Such memory is measured in rodents via the animals' natural tendency to explore a new conspecific more than a familiar one, which demonstrates that rats can recognize others. Such individual recognition is essential to many social interactions guided by kinship and dominance hierarchies supported by the history of interaction with individuals.

hippocampus in the encoding and maintenance of **social memory**, the ability of an animal to remember a conspecific. Recent attention has been drawn specifically to **hippocampal CA2**, the region interposed between CA3, the input region, and CA1, one of the output regions of the hippocampus. Silencing of neuronal activity in CA2 [36] and its projection to CA1 impacts the encoding, consolidation, and recall of social memory [37] and induces specific changes in CA1 neural dynamics [38]. Conversely, optogenetic activation of CA2 enhances social memory if applied during encoding [39]. Beyond CA2, direct optogenetic manipulation of ventral hippocampal CA1 neurons in mice shows that this output region possibly stores social memory [37,40,41]. Specific alterations of the input region of the hippocampus, in ventral CA3, via blockage of glutamate (NMDA) receptor plasticity also produces deficits in social memory [42].

Recent neurophysiological findings reveal the convergence of social and spatial signals in the hippocampus. Specifically, rodent pyramidal cells in CA2 [37,43] and CA1 [34] exhibit spatial firing rates that change or remap' depending on the presence of conspecifics. Further, **social place cells** found in CA1 in rats and bats (Figure 2E,F) encode the observed position of conspecifics in turn-taking tasks in which the other's position in place was monitored [44,45]. These cells fire distinctively (in different locations) or jointly (in same locations) for self or observed others' position in space and can even acquire spatial selectivity through observation prior to actual self-exploration [46]. Recent intracranial recordings in human patients during ambulation show that hippocampal oscillatory activity is modified by the presence of another individual, indicating a boundary anchoring effect [47]. Thus, the hippocampus possesses the functional cell types that may support the computation of self and others' place most suitable to define self and others' territory. Finally, functional neuroimaging studies in humans show that hippocampal activity

Social place cells: in rats and bats, social place cells in the hippocampus exhibit spatially selective activity during their own movement in an environment and also while observing another conspecific moving in that environment. Thus, the cells enable the representation of others' presence in a place.
Spatial cognition: refers to the cognitive abilities enabling learning of the layout of elements in a place and navigation between them in a goal-directed and flexible manner. Spatial cognition depends mainly on the integrity of the hippocampal formation.
Territoriality: defines the defensiveness expressed by an individual to exclude others from its home range. In humans, territoriality refers to the social contract regulating land ownership and access.

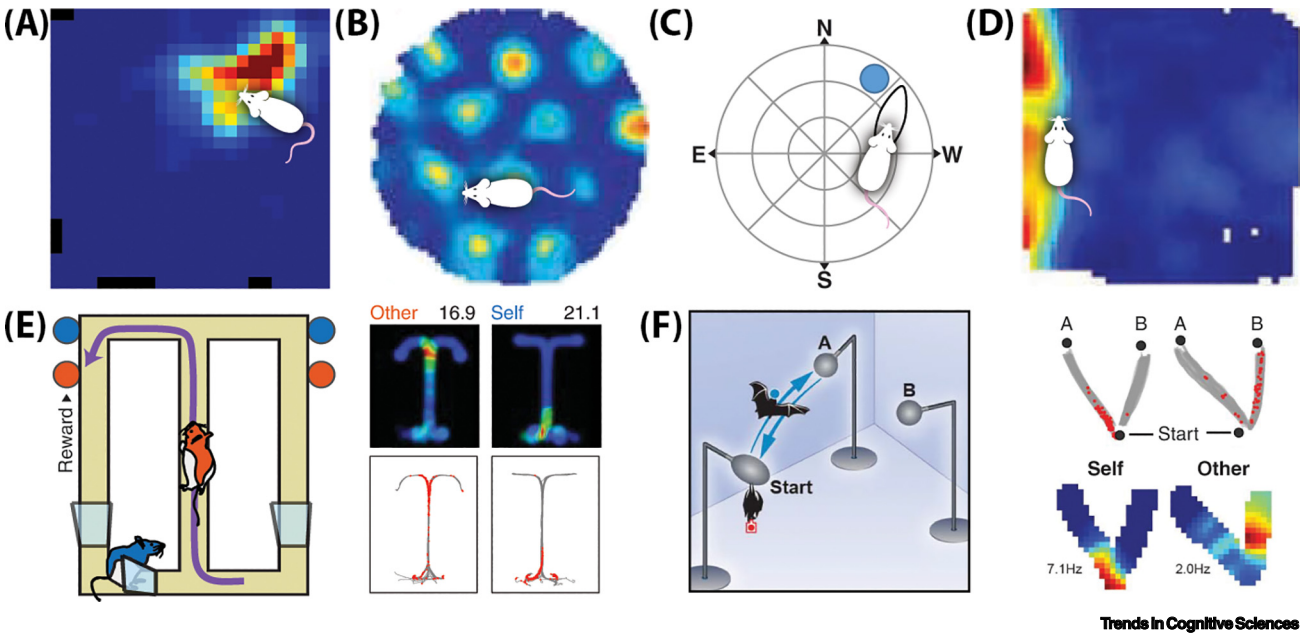

Figure 2. Spatial and social codes in the hippocampus and entorhinal cortex of rodents and bats. (A) Place cells in rodent CA1. Adapted from [119]. (B) Grid cells in rodent medial entorhinal cortex (MEC). Adapted from [120]. (C) Object vector cells in rodent MEC. Adapted from [108]. (D) Border cells in rodent MEC. Adapted from [27]. (E) A social place cell in the rodent hippocampus. Adapted from [45]. Left panel: Turn-taking task in which the correct reward location for one rat depended on the observed trajectory of the other rat. Right panel: Example cell's activity (bottom) and firing rate map (top) for self and other's trajectories. (F) Social place cell in the hippocampus of the bat. Adapted from [44]. Left panel: A bat (with a red mark) observes a demonstrator during successive flights between two goal positions, A and B. Right panel: Neural activity (top) and firing rate map (bottom) for self and other's trajectories.

encodes social distances along axes representing dominance and affiliation [48] and tracks dynamic social behavior, such as hierarchical status [49]. The social factors in these studies are relevant to territorial compromises with others in one's group or with out-groups. Hence, the hippocampus could provide an important contribution to territorial representation. Next, we explore how this role may be linked to OT actions.

Although the role of canonical neurotransmitters, such as glutamate, glycine, and GABA, in the hippocampal formation has been studied for decades, the impact of non-conventional neurotransmitters, such as neuropeptides, remains poorly explored. OT and arginine vasopressin, both synthesized in the hypothalamic paraventricular and supraoptic nuclei of mammals, are of interest in territoriality because they are both released in the hippocampus [50]. However, direct OT-ergic projections to the hippocampal regions are the best documented [50–52]. Therefore, basing this opinion on evidence from the literature and our own results, we focus on OT and propose that, by virtue of its role in the processing of social information, this neuropeptide influences territorial representation via the hippocampal–entorhinal circuit.

Linking OT to territorial behavior

OT is released into the bloodstream as a hormone controlling various physiological processes such as parturition, lactation, energetic metabolism, and cardiovascular functions [53]. In conjunction, OT acts centrally in the brain as a noncanonical neurotransmitter or neuromodulator, regulating a number of behaviors ranging from pain to social behaviors [50,54]. Many actions of OT are key to territorial behavior because they influence emotions and reactions to others, such as attachment and affiliation or distancing and aggression [53,55,56]. For example, a key difference between the monogamous territorial prairie vole and the polygamous non-territorial montane vole lies in the way that the OT system controls their behavior, which stems from distinct patterns of OT receptor (OTR) expression [57–59]. Direct OT infusion into the cerebral ventricles of the monogamous prairie vole's brain alters not only pair bonding but also tolerance towards competitors [60], a behavior that subserves territoriality in this monogamous species [58]. Specifically, in monogamous males, OTR expression was greater in individuals that exhibited high reproductive success and expressed high territoriality [58]. By contrast, in polygamous mammalian species, OT increases social affiliation and contact [61], which may enhance tolerance to others and contribute to the regulation of the peri-personal space defining the territory of self. In line with this possibility, firing of OT neurons in the paraventricular nucleus increases gradually when female rats approach each other [62]. Thus, OT may regulate territoriality in rodents by acting on variables controlling social tolerance and affiliation by species, sex, and reproductive strategies.

In both human and nonhuman primates, intranasally administered OT, which crosses the blood–brain barrier [63–65], globally increases attention to the eye region [66,67] and gaze following in monkeys [68,69] and facilitates the reading of emotions in humans [70]. Within a group of macaques, OT reduces the normally hierarchized gazing behavior between dominant and subordinate monkeys [71,72], suggesting that OT increases tolerance across levels of the hierarchy within a group. Similarly, in chimpanzees, plasma OT levels assessed from urine are correlated with the strength of social bonding among individuals in a group [73]. In humans, intranasal OT administration increases trust in other individuals [74,75] and alters social distance in personal space [76]. Overall, these results suggest that OT increases the saliency of social elements [77], which, in a context of spatial competition, could reinforce individual and collective territoriality. OT promotes in-group favoritism by increasing biases in a test of stereotypes [78] and increases in-group cooperation when attacking out-group competitors [79]. This fits with results supporting OT involvement in chimpanzee intergroup conflict [80]. Together, these findings

support a role of the neuropeptide in **ethnocentrism**, important for the expression of territorial behavior when confronted with a resource limitation of space. This is not direct evidence for the involvement of OT in territorial behavior, but it indicates that OT acts on the social variables that modulate tolerance to other individuals and group cohesion, which in turn influence territorial defense.

The central action of OT in the hippocampal formation

Although it circulates peripherally, OT does not cross the blood–brain barrier in behaviorally relevant amounts [81,82], and local concentrations of the hypothalamic neuropeptide in the brain are surprisingly much higher than in the blood [83]. Beyond its classic peripheral targets (e.g., the uterus, mammary glands) [84], the central action of OT supports a wide range of physiological and behavioral effects mediated by its actions on OTRs, which are distributed in many regions such as the basal forebrain and the amygdala (for reviews see [52,54]). Here we focus on OT signaling in the hippocampal–entorhinal regions specifically relevant to the processing of spatial and social information linked to territoriality (Figure 3). In rodents, OTRs have been found in all fields of the hippocampus (but most abundantly in CA2 and CA3) and entorhinal cortex [53,85,86] despite the fact that mice, rats, and voles have their own peculiarities in OTR distribution patterns in other brain regions. Interestingly, in prairie voles, the pattern of hippocampal OTR expression predicted the animals' territorial profile (i.e., maintaining and defending a portion of space) in the context of sexual competition [58].

Evidence for hippocampal OTR expression has also been reported in primates. More specifically, OTR binding was found in the entorhinal cortex of the rhesus macaque [87] and in whole hippocampal regions in the titi monkey [87,88]. In the latter species, OTR hippocampal binding was increased depending on parental experience, suggesting a direct role for the OTR in affiliative behavior [88]. Using a highly sensitive RNA-seq technique, OTR gene expression has been found in the human hippocampus [89]. However, this latter finding awaits confirmation for functional OTRs by advanced techniques with cellular and molecular resolution, such as precise *in situ* hybridization (RNAscope) and region-specific real-time PCR. Nevertheless, intranasal administration of OT in humans modulates fMRI signals in the hippocampus when subjects

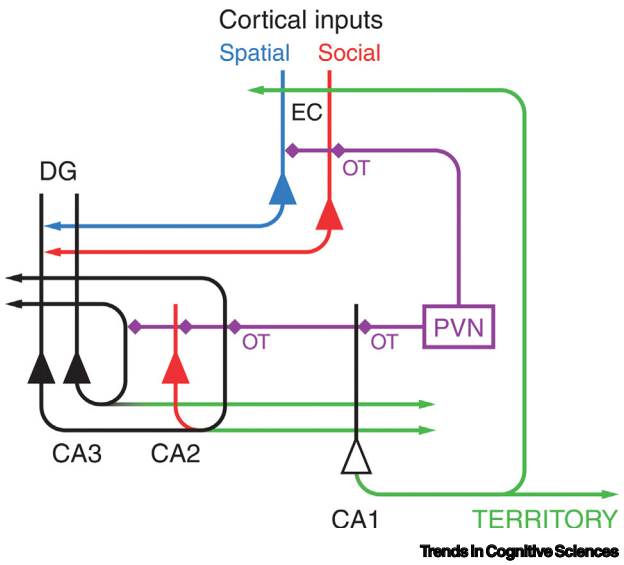

Figure 3. Oxytocin (OT) action in the hippocampal system. Schematic representation of the sites of OT action in the hippocampal system in the CA regions. OT-induced plasticity may promote the combination of spatial and social inputs in the hippocampal circuit via CA3 recurrent collaterals or by its action in the entorhinal cortex. The outputs of this circuit convey territorial information to the cortex, the amygdala, and septal regions. Abbreviations: EC, entorhinal cortex; PVN, paraventricular nucleus of hypothalamus.

perceive faces having a social value [90]. Further, central OT infusion into the lateral ventricle of rhesus macaques affects hippocampal binding of serotonin, a neurotransmitter known to regulate emotional responses and approach–avoidance behaviors [91].

How does OT reach its target in the hippocampal formation? Although longstanding theory proposes passive diffusion of the neuropeptide from the dendrites of hypothalamic neurons (in the paraventricular and supraoptic nuclei) through the entire brain [92], such passive diffusion would have a limited ability to elicit temporally locked and brain-region-specific behaviors. An alternative concept, supported by numerous circuit-intervention manipulations [51,93–96] argues for the precise release of OT from axon terminals of OT neuronal projections terminating in distant brain regions. Although both mechanisms of OT transmission can be considered, it is crucial for our hypothesis that long-range oxytocinergic axonal projections have been found in all fields of the hippocampus and in subdivisions of the entorhinal cortex of rats [51,52,97–99].

There is ample evidence for the functional significance of evoked endogenous release of OT in the hippocampal–entorhinal system in rodents [97]. Direct activation or inactivation of OTRs via optogenetic, chemogenetic, or pharmacological approaches reveals three important cellular effects of OT signaling. First, their activation increases bursting firing in CA2 pyramidal cells as well as in fast-spiking CA2 interneurons [100,101], thereby enhancing spike transmission and the tuning of CA1 neuron output. Second, it promotes long-term potentiation of synaptic activity in CA1 pyramidal neurons [102] and depression in the dentate gyrus [103]. Third, their inactivation reduces synaptic transmission from pyramidal CA2 neurons to CA1 [98] or to the entorhinal cortex [104].

At the behavioral level, chemical or genetic silencing of OTR in CA2/CA3 and/or the dentate gyrus reveals that they are essential for social memory [98,104]. Further, during the processing of a social stimulus, the activation of OTRs in CA2/CA3 neurons results in the recruitment of population-based coding mechanisms through ensembles of neurons [98]. The connectivity of this CA2/CA3 population may be maintained by OT because the deletion of OTR reduces the complexity of the basal dendritic arbors of CA2 pyramidal neurons [98,104]. This suggests that OT controls the neural signal strength of social stimuli in the hippocampus. These effects set the stage for a specific role of OT signaling by means of information selection and plasticity in the hippocampus prior to the output to other regions. We suggest that, in addition to social memory, OT might enable the definition of own and others' space, depending on the ecological context.

A neural implementation of territorial behavior: a role for OT inputs in the hippocampal networks

How might OT inputs affect territorial representations? An elementary implementation of a territory can be based on the hallmark of hippocampal function: its multimodal associative ability supported by extensive **hippocampal CA3 recurrent collateral** connections [105,106] (Figure 3). Given input from the entorhinal cortex and dentate gyrus through the trisynaptic circuit, neurons in any part of CA3 can form connections with neurons in CA3, CA2, and CA1 and can, by associative learning, create cell assemblies linking neurons with different representations [107] (Figures 3 and 4). A parsimonious expression of territory might be encoded by links (in green on Figure 4) between spatial representations (carried by CA3 or CA1 place cells) and social representations (carried by social cells and identity cells in CA2 and CA1) and further embodied by neurons coding the learned association between a set of locations and an individual. As they are formed only in a competitive context, we term any such neurons territory' cells. These cells could encode locations within a territorial boundary in a position-invariant manner (in green in Figure 4) reduced to personal or other property dimensions and support the memory of territorial interactions similar to place cells representing familiar locations. Given this associative

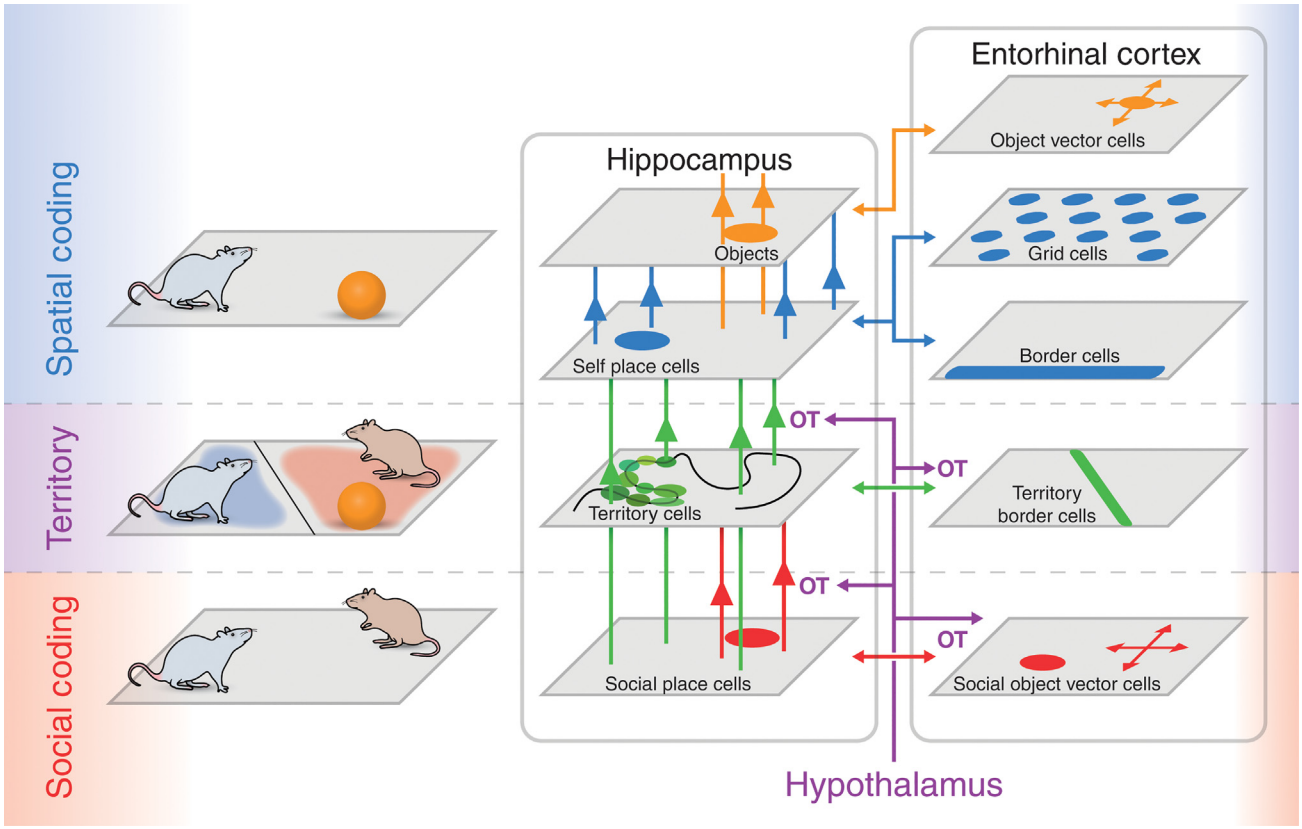

Figure 4. Theoretical territorial neural representation implementing putative oxytocin (OT) action sites to modulate diverse cell types in the hippocampus and entorhinal cortex of rodents. In the hippocampus, promoted by OT action on synaptic plasticity, a territory might be encoded by synaptic links (green cells) between cells representing space (in blue) and social stimuli (in red). These converging inputs might lead to the appearance of 'territory cells' displaying large place fields encompassing all positions in a territory. In the entorhinal cortex, cells might encode the social border between self and others' territory (green territory border cells) or one's bearing with respect to others in space (social object vector cell in red). OT may modulate the activity of social place cells and territory cells in the hippocampus and entorhinal cortex via its axonal projections originating from the paraventricular nucleus of the hypothalamus (in purple) (Figure 3). The cells encoding territory may coexist with other cells encoding physical attributes of the environment (in blue) or social stimuli (in red).

scheme, and in a manner consistent with the cellular and behavioral effects of OT in the hippocampus described above, OT may directly modulate synaptic weights to facilitate learning between spatial and social representations. In addition, OT might influence territorial representation by its inputs to layers II and III of the entorhinal cortex. In this region, signals carried by grid cells and border cells could provide socially biased input to the hippocampal CA1 via the trisynaptic pathways depending on OT release in the entorhinal cortex during a social encounter (Figure 3). We speculate that entorhinal object vector cells [108] could anchor on social stimuli instead of physical objects. In this framework, as shown in Figure 4, a representation of the geometric space may coexist in conjunction with a representation of the same space in a territorial format when social context is gated by entorhinal input. Switching between these representations could depend on the presence or absence of other individuals and be facilitated by the increase in the signal-to-noise ratio provided by OT actions in the hippocampus [97,104]. In addition to the well-documented trisynaptic pathway, the entorhinal cortex also provides a more sparse monosynaptic input to CA1 [109] whose role is less understood but is hypothesized to relate to novelty detection. By modulating entorhinal cortex neurons via this dual input, OT actions can occur during territorial initiation, recall, and updating of the existing territorial map.

These hypotheses could be directly tested by measuring the effects of the activation or suppression of OTR actions (via chemo- or optogenetic tools) in the hippocampus while animals navigate in or out of a social territory (Figure 4). The effects of the direct stimulation of OT neurons innervating the entorhinal cortex should also be tested on behavior and on hippocampal neural activity. For example, behavioral measures (exploration, avoidance) and neural activity (via spatial selectivity measures) should be compared before and after an animal's territory has been restricted by partition of the environment creating a neighboring territory. Territory and border cells could be identified while animals access each other's territory or observe another conspecific in their own territory. We predict that silencing or increasing OT action would modulate the signal carried in the hippocampal regions and the expression of territorial behavior.

Territorial behavior is likely to involve other brain regions in conjunction with the hippocampal system to guide behaviors such as acceptance or rejection of intruders within a territory depending on their subordinate or dominance status or affiliation. The two key regions, which are strongly connected with the hippocampus and control behavior relevant to territoriality such as defensive fight–flight responses, are the amygdala [110,111] and the medial septum [112]. Depending on the nature of the social encounter, modulation of the behavior can occur through output projections from the hippocampus to the amygdala [113] or to the septal regions [114]. Thus, based on the memory of previous interactions formed by the hippocampus, these circuits are likely to be important players in guiding specific behavior (submission, approach, attack, and defense) depending on the presence or absence of a threat in a territorial space.

Concluding remarks

Territoriality, often associated more generally with property (i.e., owned objects and land), is an evolutionarily rooted behavior that has a pervasive influence on human individuals and societies. We propose a model based on two evolutionarily conserved systems, the hippocampal formation and the OT neuropeptide, fitting the enduring adaptive relevance of territorial behavior. Although the role of the hippocampus in spatial cognition and more recently in social cognition [49,115], is widely corroborated, it is never formulated in terms of territoriality. Our model proposes a new view of space in which spatial metrics integrate social demands to generate territorial behavior, either as territorial aggression or as a compromise on spatial resources. Exactly how territorial behavior stems from OT action needs to be unraveled and many other questions should be prospectively addressed (see Outstanding questions). In particular, the well-known interaction between OT and its sister peptide arginine vasopressin, both originating from hypothalamic nuclei, may reveal networks with functions complementary to those discussed here [116]. OT, released massively during dramatic behavioral and homeostatic challenges, can bind to arginine vasopressin receptors [116,117]. This is particularly relevant to arginine vasopressin signaling in aggression and individual territory defense [118]. An exploration of the neural mechanisms of territorial behavior is likely to be of significant utility in understanding modern human society, in which territorial boundaries, whether private or national, are the origin of most conflicts and wars. Therefore, advances in the neural underpinning of territoriality could support prospects for translational applications.

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Outstanding questions

How does the activation of OT neurons, triggered by socially relevant signals (vocalization, face–body, touch, or olfactory), result in local OT release in the hippocampal formation? Is there a specialized subpopulation of hypothalamic OT neurons selectively connecting with hippocampal circuits?

What are the temporal dynamics of OT release and the subsequent changes in activity in the hippocampal (CA1, CA2, CA3) and entorhinal circuits? How do they control behavior?

What types of hippocampal cells respond to OT and are they activated directly (i.e., via direct OT action) or indirectly (i.e., via non-OTR-expressing neurons connected with OTR-expressing neurons)?

If OT primarily impacts the activity of social place cells and putative territory cells in either the hippocampus or the entorhinal cortex, the anatomical and functional output of these cells has to be studied. In this respect, does the output affect socially relevant brain regions promoting affiliation or social avoidance, such as the prefrontal cortex, amygdala nuclei, and septum? Do these regions also express OTRs, uniting OT action at several places, including hippocampal formation?

How do other neurotransmission networks (serotonin, dopamine) orchestrate with OT in the emergence of territorial perception in the hippocampus complex in light of the increasing evidence that OT also participates in anxiety and stress regulation?

Are there important interspecies differences in OT signaling in the hippocampus? The precise analysis of OT signaling in the primate brain needs to be compared with the results obtained in rodents at anatomical, electrophysiological, imaging, and behavioral levels. These comparisons should take into account the fact that some social signals/channels in rodents and primates are the same (e.g., somatosensory/tactile stimulation) and some are strictly different (olfaction prevails in rodents, while visual signals are dominant in primates including humans).

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Author contributions

S. Wirth, V.G., and A. Sirigu proposed the original concept framework. All authors contributed to the elaboration of the proposed model. S. Wirth wrote a first draft and A. Sirigu and V.G. provided ongoing review. All authors contributed to and approved the final version of the document.

Declaration of interests

The authors have no interests to declare.

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