Review article

Social spatial cognition

Alex Dorfman, Omri Weiss, Zohar Hagbi, Anat Levi, David Eilam *,1

School of Zoology, George S. Wise Faculty of Life-Sciences, Tel-Aviv University, Ramat-Aviv, 6997801, Israel

ARTICLE INFO

ABSTRACT

Social spatial cognition refers to the interaction between self, place, and partners, with emphasis on the impact of the social environment on spatial behavior and on how individual spatial representations converge to form collective spatial behavior - i.e., common places and routes. Recent studies suggest that in addition to their mental representation (cognitive map) of the physical environment, humans and other animals also have a social cognitive map. We suggest that while social spatial cognition relies on knowledge of both the physical and the social environments, it is the latter hat predominates. This dominance is illustrated here in the modulation of spatial behavior according to dynamic social interactions, ranging from group formation to an attenuation of drug-induced stereotypy through the mere presence of a normal subject. Consequently we suggest that the numerous studies on the biobehavioral controlling mechanisms of spatial behavior (i.e. - the hippocampal formation, animal models for mental disorders) should also consider the social environment rather than solely focusing on the spatial behavior of lone animals.

1. Prolog

Finding places and orienting in the environment constitute basic behavioral performances in humans and other animals. Various biobehavioral mechanisms have been identified in the process of exploring places, 'homing', or concatenating short navigational segments into long routes. These mechanisms, which were first identified in animals, have since become the foundation for understanding human spatial performance. Perhaps the first significant milestone in the study of spatial behavior was introduced by Edward C. Tolman (1886–1959), an American experimental psychologist, who suggested that rats find their way in a labyrinth by means of an internal representation of the environment, which he termed a 'cognitive map'. Moreover, he suggested, by analogy, that the performance of rats in mazes be viewed in relation to the '*God-given maze which is our human world*' (Tolman, 1948). Ever since Tolman, the notion of a 'map in the head' (Kuipers, 1982) has intrigued a large number of scholars from a wide spectrum of research domains and disciplines: neurobiology, psychology, ethology, architecture, geography, urban planning, computer sciences, and others (Portugali, 2005). A few decades after Tolman's seminal studies, it was suggested that, during exploration, spatial information is encoded in a specific brain region - the hippocampus: *"hippocampal locale system is assumed to form the substrate for maps of environments an animal has experienced; these maps are established in the hippocampus during exploration"* (O'Keefe and Nadel, 1978; p. 242). The study of spatial behavior has subsequently flourished, revealing place cells (O'Keefe and Dostrovsky, 1971), head-direction cells (Taube et al., 1990b), grid cells (Hafting et al., 2005), border cells (Lever et al., 2009), and speed cells (Kropff et al., 2015) as the building blocks of spatial representation. However, the above studies on spatial behavior all focused on lone subjects, overlooking the changes that could occur in the presence of others. Here we focus on how spatial behavior is affected by the presence of others, by what others do (e.g. - behave normally or abnormally), by the number of "others" present, and by how the environment is spatially shared. Indeed, social animals should necessarily coordinate their behavior with conspecifics, whereas solitary animals should avoid their conspecifics (Fig. 1). **Social spatial cognition** thus relies on knowledge of both the physical and the social environments. For example, imagine entering an unfamiliar room where no-one is present - you will probably soon begin to explore the room. Now imagine the same situation, but with your boss in the room – surely you will first pay attention to the boss and only then to the room. Imagine too, entering an unfamiliar room full of both familiar and unfamiliar people – whatever you do in this case will differ from that in the two previous situations. This example attests to the important role played by the social environment in spatial behavior, and suggests the predominance of the social over the
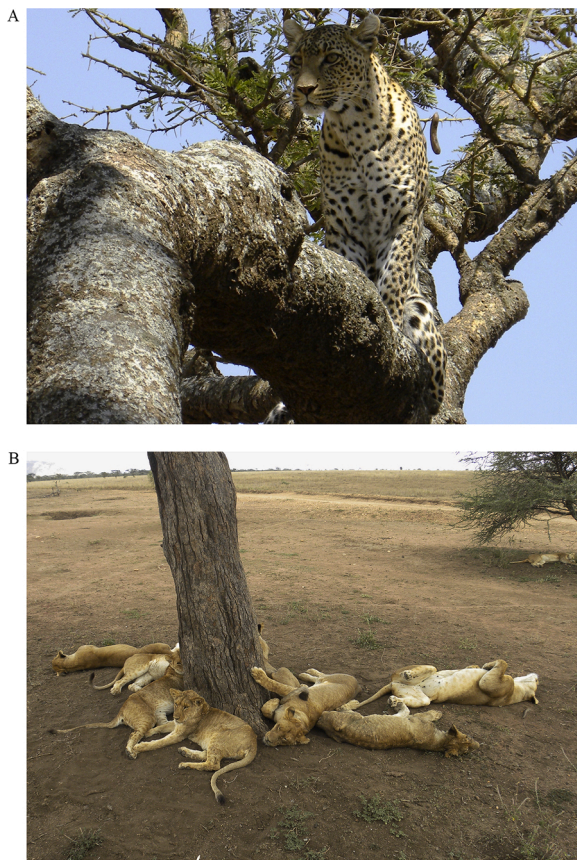
Fig. 1. Solitary and social big cats. A: Leopard (*Panthera paradus*) is a solitary big cat, in which the female and male meet one another only for mating, and separate immediately afterwards. B: Lions (*Panthera leo*) typically spend their lifetime in extended families of several females with their cubs, a dominant male, and a few young males.

physical environment. The following survey describes how the presence of social partners alters exploration of an unfamiliar environment in humans and other animals (especially rats). Such understanding is a prerequisite in the search for the biobehavioral controlling mechanisms of social spatial cognition, a field of neurosciences that is currently gaining ground.

2. "The Hippocampus as a Cognitive Map … of Social Space" (Eichenbaum, 2015)

The above provocative title featured in an editorial on a pioneering study (Eichenbaum, 2015) revealing that the encoding of spatial representation in the hippocampal formation (mainly in CA1 ventral neurons) extends to the social space by mapping social relations, resulting in a map of social navigation in the human brain (Tavares et al., 2015). Similarly, hippocampal neurons in mice were found to modulate and store social memories, which are manifested as recognizing familiar conspecifics (Okuyama et al., 2016). Furthermore, following recording of the activity of hippocampal place cells in rats that traveled in a T-maze in which one rat was required to observe another rat's trajectory in order to successfully retrieve a reward, four types of social spatial representations in the hippocampus were suggested: (i) own place fields; (ii) joint place fields; (iii) other's place fields; and, (iv) common place fields (Danjo et al., 2018). While that study demonstrated that hippocampal spatial representations include dimensions for both self and non-self, the question remained open as to how these types of representations are manifested in the way that animals share the land. This is discussed later on in the present article.

Another seminal study on social place cells in bats (Omer et al., 2018a) revealed several types of hippocampal social spatial representations. Specifically, in observer bat there were neurons that represented the position of another, demonstrator bat, in allocentric coordinates. About half of these neurons also represented the position of the observer bat when it subsequently took the same flight path of the demonstrator, and therefore functioned like "spatial mirror cells". This was also supported in the finding that these neurons also represented the positions of inanimate moving objects. Notably, about half of the social place cells became silent during the observer bat's flight (Omer et al., 2018a). Further studies reported a large hippocampal firing rate in the presence of conspecifics, varying with sex and identity of the conspecific (Rao et al., 2019); and that oxytocin receptors in the hippocampus of mice are necessary for discrimination of social stimuli but not of non-social stimuli (Raam et al., 2017). Social spatial information is indeed an integral part of spatial representation and, when traveling, one may follow, avoid, or move independently of others. The question thus arises as to how two or more individuals explore and share the environment compared with lone explorers.

In biology, studies on groups of two or more individuals have focused on collective behavior, on the adaptive benefits of being in a group, and on the particular form of social action (Nagy et al., 2020), while hardly referring to the dynamics of group formation. In social psychology, models for group formation were developed by focusing on social interactions and/or reflecting the dynamics of group formation as assessed via group functioning towards achieving a goal or accomplishing a task (Chidambaram and Bostrom, 1997). Unlike the above approaches, it is suggested here that proximity (social distance) among individuals is an objective and measurable proxy for socialization and for becoming socially organized or coordinated in time and space. Below we show that measuring this parameter may serve to unveil the controlling biobehavioral mechanisms of social spatial behavior.

3. Home in lone contexts compared with home in social ones

The spatial behavior of rodents in an unfamiliar environment is conceived of as a set of roundtrips of exploration (or excursions) that start and end at a specific location, termed 'home-base' (Eilam and Golani, 1989). This location is characterized by a behavior that is seldom performed in other locations. Indeed, home is first and foremost a behavior (Blumenfeld-Lieberthal and Eilam, 2016). Excursions from and to the home-base have a typical structure: they usually comprise an upper boundary of 8–10 stops at other locations; their outbound segment is slow and interrupted by stops, and the inbound segment is fast and includes fewer, if any, stops (Golani et al., 1993). The neural control of home-base behavior and excursions of exploration was extensively studied (see Thompson et al., 2018) for a comprehensive review). In short, lesions to the fimbria-fornix or hippocampus produce specific impairments in the homeward-bound segment of exploratory excursions (Wallace and Whishaw, 2003; Wallace et al., 2002a, b; Winter et al., 2013). Unlike control rats, the ability to dash to the home base was impaired in hippocampal-lesioned rats tested in a dark open field (Wallace and Whishaw, 2003). In the same vein, stopping behavior (Golani et al., 1993) is involved in the onset of place-cell activity at the various stopping locations (Monaco et al., 2014). Notably, allowing rats to first explore an arena and then introducing their home cage into the arena did not result in explicit home-cage representation, and both head-direction cells and grid cells remained globally stable (Sanguinetti-Scheck and Brecht, 2020). This lack of remapping of head-direction and grid cells indicates that orientation and navigation are mainly governed by the more stable distal landmarks and less by local ones (Zadicario et al., 2007).

Rats establish their home-base in a shelter; or, in the lack of shelter, near a salient landmark; and, in the lack of landmarks, at the point of entering the open field (Clark et al., 2006; Nemati and Whishaw, 2007; Yaski and Eilam, 2008). Interestingly, head-direction cells are then
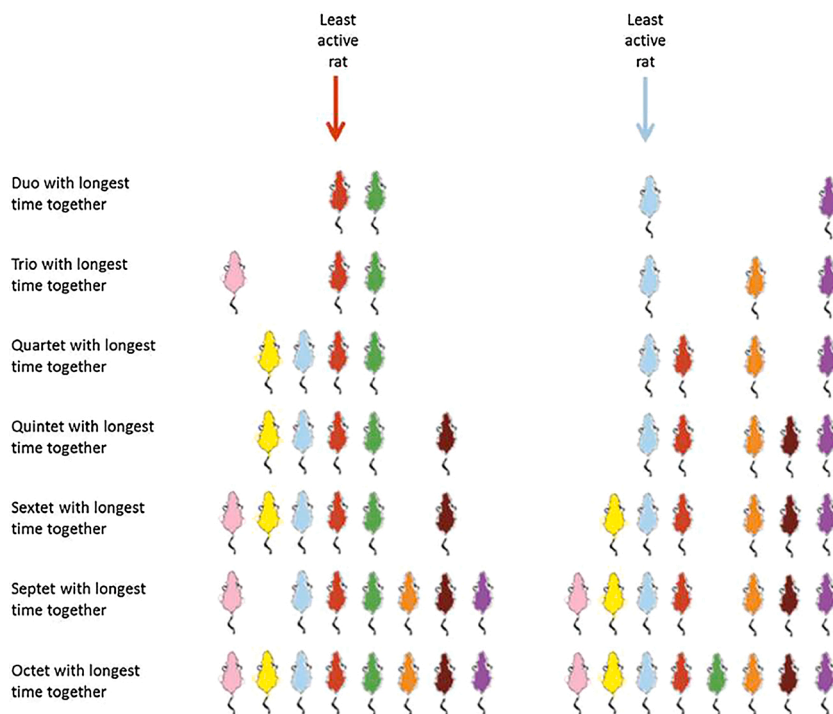
Fig. 2. The formation of a group around the least mobile rat (marked with ↓) is illustrated in two groups of eight unfamiliar rats. Each column (color) represents one rat, and each row represents the combination of rats that spent the greatest length of time together compared with other possible combinations of rats for this group size. As shown, in both groups the marked rat participated in all group sizes (i.e., duo, trio, quartet, etc.), spending the longest total time, as if the group had been formed around it. Further analyses revealed that, indeed, the least active rat demonstrated the greatest social connectivity (see Weiss et al., 2018, from which this figure was taken).

re-oriented to the direction of the home base (Valerio and Taube, 2012), and this could be the key to understanding the above-noted home-base behaviors. For many animals, 'home' in nature is usually regarded simply as a den, nest, burrow, or other type of sheltered location. The role of home as a hub for spatial behavior and as an 'organizer' of spatial behavior has also been noted in humans, and human mobility is characterized by deep-rooted regularities (Song et al., 2010), with over 50 % of daily trips being home-generated (Golledge, 1999; p.26). These and other perspectives of home in humans and other animals have been discussed elsewhere (Blumenfeld-Lieberthal and Eilam, 2016). The term 'home-base' refers to a behavioral template in which a vantage point is used as an anchor for roundtrips to the surrounding environment. Social animals tend to establish their home-base with or near their social partners. For laboratory rat pups that were placed as a huddle in a circular open-field, the location of the huddle became a 'social home-base' for roundtrips in the arena, regardless of the location of the huddle, which continuously drifted from one place to another as littermates attempted to crawl under other pups, thereby pushing and changing the location of the huddle (Loewen et al., 2005). In other words, it was the huddle of littermates and not its location that served as a home-base. Another example is that of chimpanzee infants, which like other primates, ride on their mother's back while exploring the environment and then take roundtrips from her into the environment. Since the mother could be moving when the infant is away from her back, the infant has to keep track of both its own location in the environment and the changing location of its mother, who constitutes a sort of 'mobile' home-base (Menzel, 1973). This example illustrates the greater complexity imposed on social compared with lone spatial behavior (Dorfman et al., 2016). When tested together with conspecifics, laboratory rats, which are descendants of social animals (Barnett, 1963), tend to share their home-base location with their mates when in a duo, trio, quartet, and octet (Weiss et al., 2017a, 2018; Weiss et al., 2015, 2017b). When eight unfamiliar rats were placed in a large complex apparatus in which each of them could have selected a separate corner as a "private" home-base, they nonetheless soon converged together to share the same place as their home base (Weiss et al., 2018). This process is illustrated in Fig. 2, where the least active rat, which became stationary, was gradually joined by the other rats in an order corresponding to their descending

level of activity, until they all huddled together in the same location. In other words, the least active individual was joined by another rat, and together they constituted the least active dyad (duo) of all the other dyads that were fission-fused by the six other rats. The least active dyad was then joined by a third rat, to form a least active triad (trio), and so on until all eight rats were crouching together in the same location. A similar propensity was described in garter snakes (*Thamnophis sirtailis*), which prefer to remain in larger aggregates and to enter shelters that are already occupied by conspecifics, rather than enter empty shelters (Skinner and Miller, 2020). Moreover, both snakes and rats displayed a similar social trend in which the shyer snakes and the least active rats were more social and had a higher weighted degree in the social network (snakes: Skinner and Miller, 2020; rats: Weiss et al., 2018). Similarly, ducks established their nest site according to the local density of conspecifics and not according to the previous year's nest location (Ringelman et al., 2017), indicating that the social environment was more influential than the physical one. This similarity among remote vertebrate species indicates a propensity that could suggest a general pattern in social animals.

In contrast to the tendency of social animals to settle together, solitary animals tend to settle away from conspecifics. This is illustrated in Figs. 3 and 4, depicting the behavior of social and non-social rodents with no access to a shelter that were exposed to an owl perceived as attacking them via a wire mesh barrier. The six individuals of the social species (voles; *Microtus güntheri*) huddled together, whereas the six individuals of the non-social species (common spiny mice; *Acomys dimidiatus*) scattered away from each other. This pattern was general, as shown in the frequency distribution of distance between each two individuals in 10 groups (n = 6) of each of these two species (Fig. 3c), as well as in additional social and non-social species (Rabi et al., 2017). Home-base behavior thus presents a spatio-temporal behavioral template in which animals anchor their traveling in a specific location. While in the case of a lone animal this location is established in reference to the physical structure of the environment (typically a shelter or near a salient landmark), in the social environment it is established according to the location of conspecifics. Since the hippocampal formation is deeply involved in both home-base behavior and exploratory excursions of lone animals (Thompson et al., 2018), and since animals in groups of

a. Gunther's vole (*Microtus guntheri*)
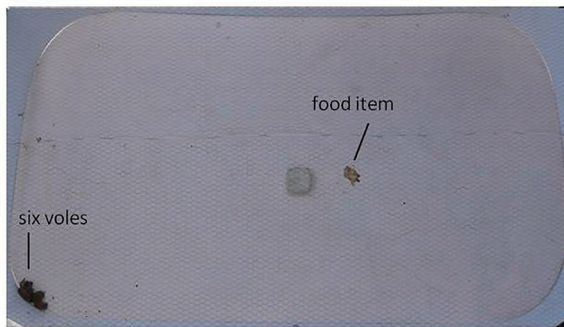
b. Common spiny mouse (*Acomy dimidiatus*)

c. Frequency distribution of inter-distances
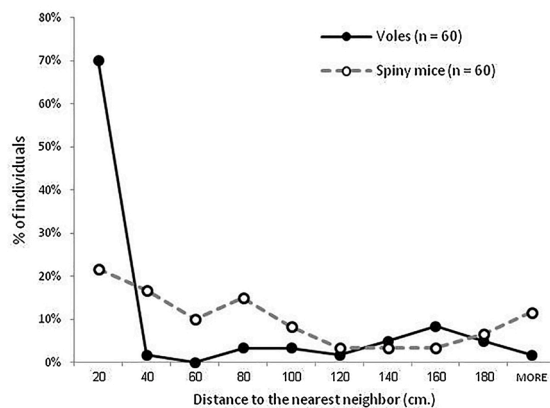
Fig. 3. A snapshot of the response of the voles (a) and common spiny mice (b) following exposure to a barn owl (rodents were protected below a wire-mesh while the owl swooped down on a food item placed on the wire-mesh). As shown, the voles huddled together, whereas the common spiny mice scattered equally along the arena wall. In (c), frequency distribution of the distance between adjacent individuals in bins of 20 cm, as measured for 60 voles and 60 common spiny mice. For each species, 10 snapshots were taken (one frame for each of the ten groups in each species), and the distance between each animal to its nearest neighbor was measured. Data are given as percentage of the total number of distances measured in all 10 groups. As shown, more than 70 % of the voles were at a distance of 20 cm or less from one another, and only a few were at greater distances. In contrast, the common spiny mice were scattered among all distances. (Figure taken from Rabi et al., 2017).

two or more integrate their spatial behavior with their partners, an impact of the social environment on hippocampal formation is expected, and there is indeed currently growing evidence for this (Ahuja et al., 2020; Danjo et al., 2018; Eichenbaum, 2015; Omer et al., 2018b; Tavares et al., 2015).

4. How to share the land when away from home?

4.1. Staying together in various places

Wild rats (*Rattus norvegicus*) live in large colonies made up of subgroups of pairs, harems, unisexual groups, and single males and females. In these groups, mothers have strong bonds with their infants until these are around two months old (Schweinfurth, 2020). A similar social structure was also observed in the black rat (*Rattus rattus*; Ewer, 1971). In laboratory studies, it was shown that rats display social affiliation, being attracted to the spatial locations of their conspecifics (Nagy et al., 2020; see Brown, 2011 for review). This affiliation is manifested in the cumulative time that the partners spend in various locations. Specifically, the most obvious feature of home-base in rats and other rodents is that the time spent there is significantly longer than in any other place (Eilam, 2014; Eilam and Golani, 1989). It was found that during exploration the time spent in different stopping locations follows a power law distribution, resembling other systems that exhibit self-organization (Yadav et al., 2010). Accordingly, the cumulative time spent in a stopping location is considered as a proxy for its importance in the context of spatial behavior: the greater the time spent there, the more important the location. In several rodent species it was found that dyads introduced into a 2 × 2 m open-field displayed a strong correlation between the amount of time that each dyad-partner allocated to similar stopping locations (Fig. 5; Hagbi, 2018). In other words, both partners revealed (together or alone) equal periods of the time spent in the same locations. This strong correlation between dyad partners implies a matching importance of the various stopping locations. Notably, many grazers and browsers do not have a home-base, but a home-range, in which they spend most of the time. In this case, a shared area within home-ranges reflects the affiliation among individuals. For example, reticulated giraffe individuals that were frequently observed together had an overlapping home-range and associated paths (VanderWaal et al., 2014). The above coupling of behavior of social partners in the various locations, as manifested in the time spent and visits paid to these locations, should also be manifested in a matching potentiation of place-cell activity at these locations (Monaco et al., 2014) over repeated visits by the partners.

In order to uncover how dyad partners share a 2 × 2 m open-field area, it was divided into 25 locations, that were classified as follows: **Joint locations**, where the two rodents tended to stop together at the same time; **Common locations**, where both rodents stopped alone at separate times; **Personal locations 1**, where only one partner stopped; and, **Personal locations 2**, where only the other partner stopped (Hagbi, 2018). These types of locations are depicted in Fig. 6 for dyads of six rodent species. As shown, many of the 25 pre-defined locations were joint, and there were only a few personal locations. Note, however, that the low number of personal location could be a product of the relatively limited arena size and the species that were relatively social or of individuals that were raised with conspecifics, a constraint that was imposed in order to avoid aggressive interactions. Comparing this division of locations, which was revealed in spatial behavior, and the various types of social place fields that were revealed by recording from the hippocampus (Danjo et al., 2018; Omer et al., 2018a), results in an intriguing hypothetical similarity, as outlined in Table 1. Altogether, the above parallel between place cell activity and social spatial behavior reflects the impact of the social environment on hippocampal activity during the establishment of mental spatial representation.

4.2. Consistency in the amount of socializing

A data comparison of 154 individual laboratory rats tested in four separate tests as dyads, triads, tetrads, or octads (Weiss et al., 2017a, 2018; Weiss et al., 2015) revealed an interesting consistency. On average, each rat spent about 65 % of the time in the proximity of conspecifics, regardless of the duration of testing and the number of
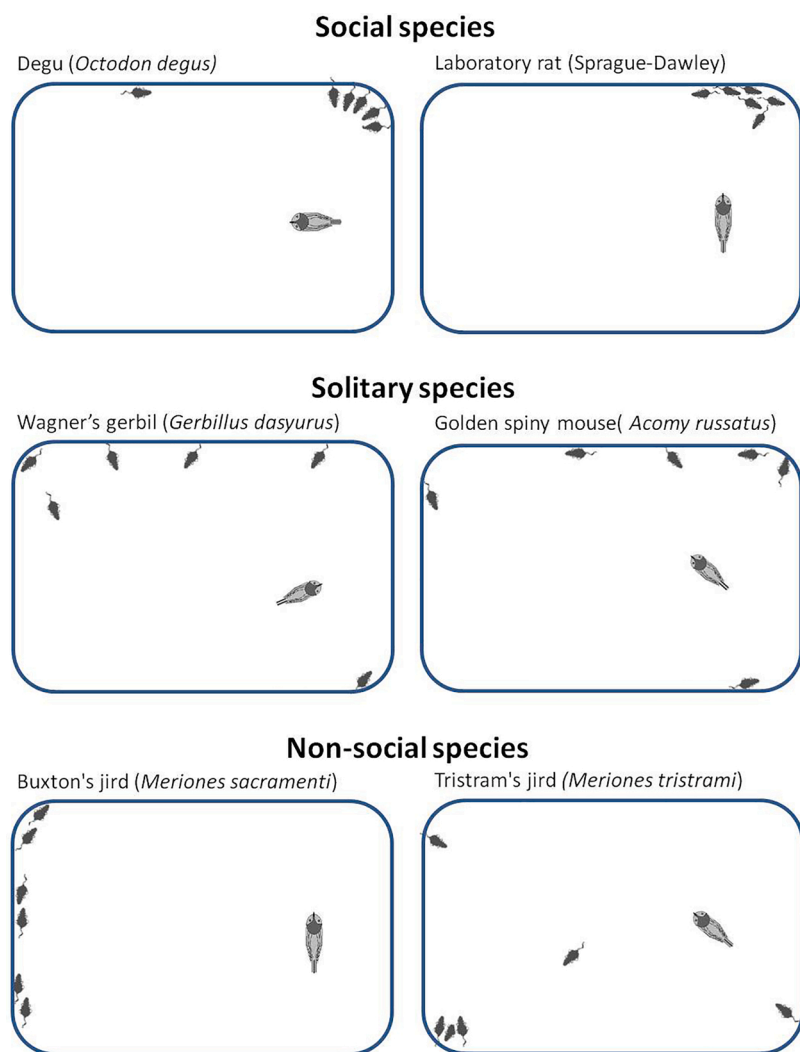
Fig. 4. Spacing of individuals in groups of six, of two social species (top), two solitary species (center), and two species with unclear social structure (bottom). Location and orientation of individuals in each group are depicted according to a snapshot taken during owl attack through a barrier (see Fig. 3), when all rodents were immobile. As shown, the social species (top) huddled together, whereas the solitary species scattered along the perimeter (center). Species with unclear social structure displayed a mixed spacing of the above two responses. (Figure taken from Rabi et al., 2017).
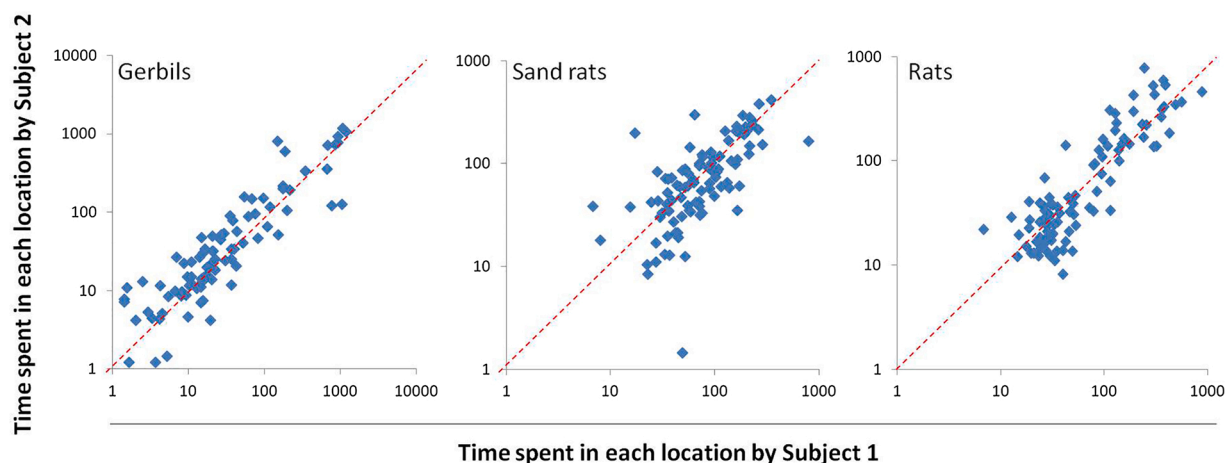
Fig. 5. The correlation between the times spent in each location by each dyad partner in three rodent species. Duration (sec) in the 10 top-validated ranked locations (in terms of the time spent in each location) is depicted in one vs. the other subject of 10 dyads in each of the three rodent species. Each data point represents the time spent by partner 1 (abscissa) vs. the time spent by partner 2 in the same location (ordinate). As shown, there was a significant correlation among locations, demonstrating that the two partners allocated matching times to the various locations.

nearby conspecifics. Specifically, in tests that ranged from 20 min in dyads to up to three hours in octads, each rat spent an average of ~65 % of the time within a distance of 20 cm (about a rat's body-length) or less

to one or more rats (distance was measured between the two rats' center of mass); while for ~35 % of the time, a rat was distant from any other rat, regardless of group size (Fig. 7). In other words, the rats appeared to
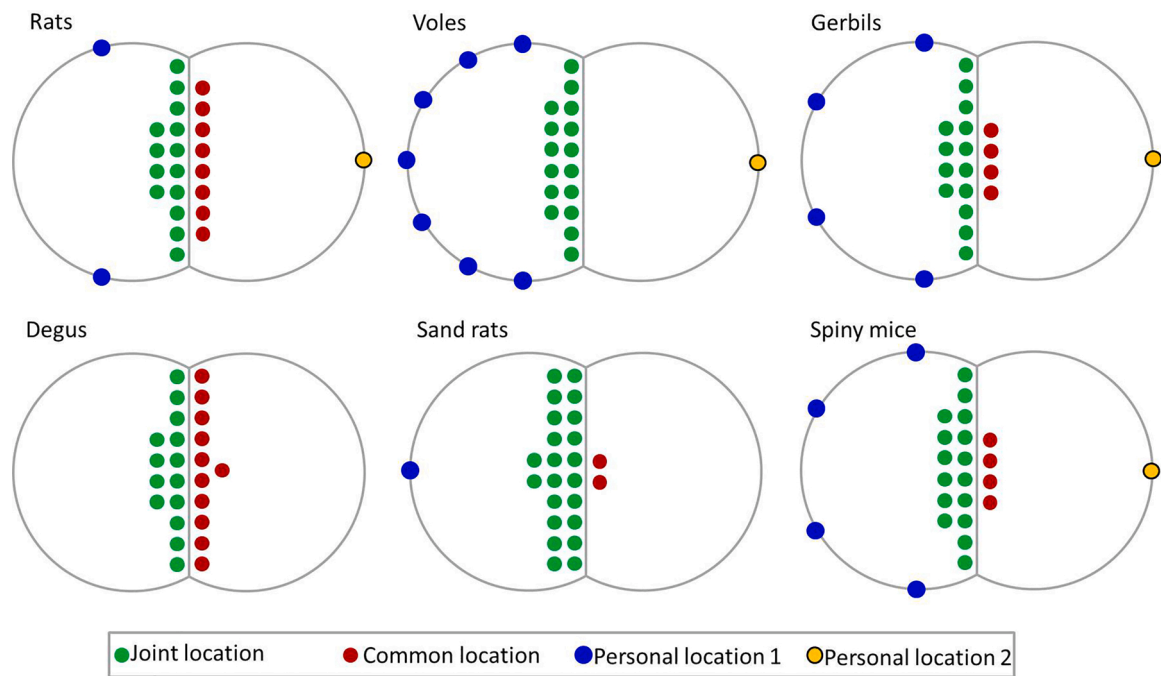
Fig. 6. Four types of locations are depicted for one dyad of six rodent species. Each dot represents one of 25 predefined locations in a 2 × 2 m open field. In each dyad (species), green dots (●) represent joint locations that were visited by both partners at the same time. Red dots (●) represent common locations visited by both partners alone (at separate times). Personal locations are depicted for each dyad partner on the large lateral circles. As shown, all species had many joint places; however, this could be a reflection of the limited open-filed area (2 × 2 m) and the social nature of the species. In voles, there were no common locations, and one of the partners had seven personal locations (●). Degus had no personal locations and shared all locations either together or alone. Sand rats jointly visited most of the locations, indicating that they tended to travel mostly together. This division of locations coincides with place fields as recorded in social situations (see Table 1).
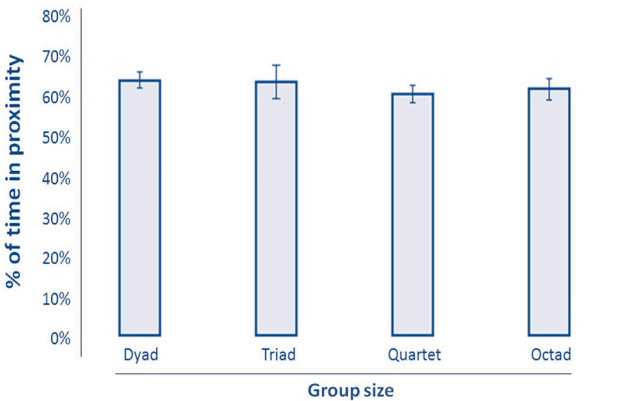
Table 1

A proposed similarity between hippocampal neuronal activity reflecting social place (Danjo et al., 2018; Omer et al., 2018a) and the type of location in the social spatial behavior of dyads in various rodent species (Hagbi, 2018).

Neurons in the hippocampus	Locations in the arena
Joint place fields	Locations in which both partners stay together at the same time
Common place fields	Locations in which both partners stay, but at different times
Own place fields	Personal locations of one partner
Other's place fields	Personal locations of the other partner

Fig. 7. The mean (± SEM) percentage of the total time that individual rats in dyads, triads, quartets, and octads spent in the vicinity (social distance of less than 25 cm) of any other rat. Testing time in each group varied from 20 min in dyads, to 180 min in octads. As shown, all rats spent about 65 % of the time resting or traveling with at least one other rat, regardless of group-size and test duration; and about 35 % of the time resting or traveling alone. (Data collected from Weiss et al., 2015, 2017a, 2017b, 2018).

devote a consistent share of their time to socializing, regardless of test duration and group size.

4.3. Traveling together

A different picture regarding the time spent in the proximity of conspecifics arose when the above data on rats were broken down into resting and traveling. Dyads or triads of rats displayed a strong preference to travel together. Even when the rats were food-deprived and introduced together into an apparatus in which they were familiar with the location of a palatable food, they did not compete for the food. Instead, they traveled together, with one of them collecting more food items than the others. However, in each trial with the same rats, a different individual collected more food items, so that over repeated trials each rat collected on average the same number of baits (Weiss et al., 2017a; see videoclip I). It could be argued that such a strong affinity to foraging together could be due to the heavy application of pesticides used to eradicate rats, based on poisoned favored foods. Accordingly, rats are aware of the food choices of their conspecifics and prefer to feed from the same source (Nagy et al., 2020), thereby reducing

their own chances of being poisoned (Galef and Whiskin, 2008; Galef and White, 1997). Indeed, foraging decisions in rats depend primarily on safety needs, rather than food availability (Arcis and Desor, 2003). However, satiated rats that were free to explore the arena with no food-reward or spatial challenge also tended to travel together (Dorfman and Eilam, 2018; Dorfman et al., 2016). Rats in dyads and triads thus favor to travel together whether foraging or not. In terms of the controlling neuronal mechanism, traveling with 1–2 partners seems reasonable in light of the results found in 'observer' bats, which briefly memorize the flight of a 'demonstrator' bat (Omer et al., 2018a). The
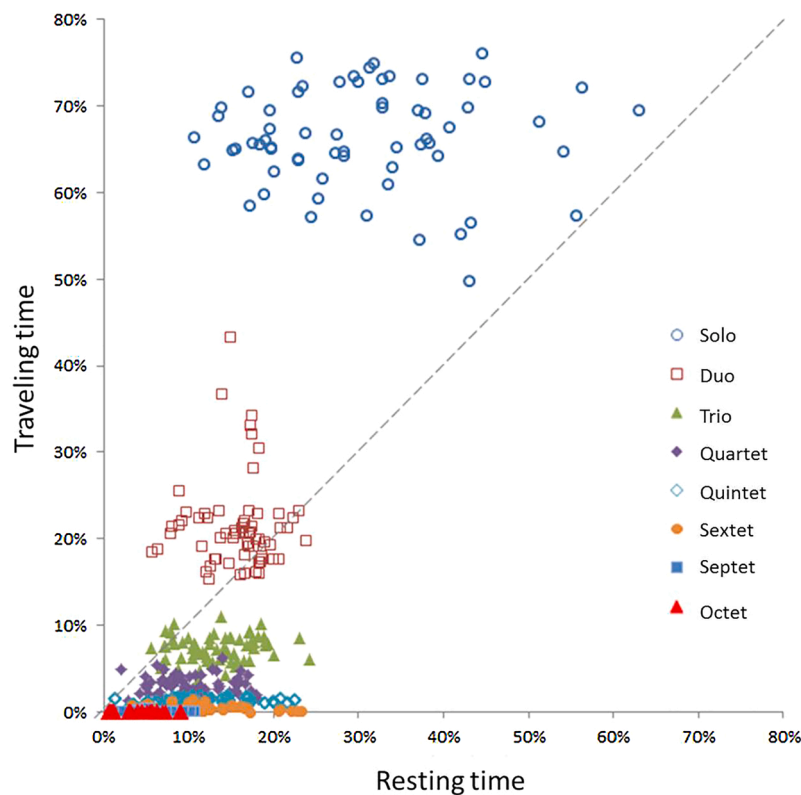
Fig. 8. The percentage of time that each rat traveled (ordinate) against the time it spent resting (abscissa) in each group size for eight groups of eight unfamiliar rats. Each colored symbol represents a social state (solo, duo trio) for the 64 rats (eight groups of eight individuals). For each social state, each of the 64 data points represents for each rat the proportion of time (out of three hours) it was resting (abscissa) or traveling (ordinate). The diagonal dashed line represents a similar resting and traveling proportion of time. As shown, all 64 rats spent a greater proportion of time in solo traveling than in solo resting. Similarly, most of the rats spent more time in duo traveling than in duo resting. In contrast, almost all rats spent a greater proportion of time resting than traveling in social states of trios or more, as evident in the aggregation of their scores below the diagonal line of equivalence. (Figure taken from Weiss et al., 2018).

rule of 'follow your nearest neighbor' (Lemasson et al., 2009) could therefore explain how various animals travel in larger groups.

As shown above, although rats tend to huddle and crouch together in large groups (Barnett, 1963; Ewer, 1971; Schweinfurth, 2020; Weiss et al., 2018), when traveling they tend to travel alone or with just one partner (Weiss et al., 2018). Indeed, as shown in Fig. 8, the rats did not crouch solo or in a duo, but only traveled in these configurations. In contrast, groups of five to eight rats mostly remained stationary. Note that the high tendency to travel alone constitutes part of the relatively short time spent alone compared to the time spent with conspecifics (Fig. 7). It therefore does not contradict the findings of the above studies regarding the preference of rats to travel together; but, rather, indicates their avoidance of being alone when stationary. In humans, moving crowds are in the main composed of friends, couples, or families walking together. At low crowd density they walk side-by-side, and when crowd density increases they switch to a V-shaped pattern (Moussaïd et al., 2010; see also Ahmed et al., 2019; Alahi et al., 2014; Cheng et al., 2019). Moreover, individuals or small groups in human crowds maintain the same distance and typical offset angles among them, and travel at the same speed (Fu et al., 2019). Similarly, animal aggregations could also be perceived as constituting sub-groups with social affiliations. For example, a flock of jackdaws comprises pairs with lifelong bonds (Ling et al., 2019); and groups of eight unfamiliar laboratory male rats soon display affiliation between specific partners (Weiss et al., 2018); Norway rat (*Rattus norvegicus*) colonies usually comprise subgroups of pairs, harems, unisexual groups, and single males and females (Schweinfurth, 2020); and a similar social structure also characterizes the black house rat *Rattus rattus* (Ewer, 1971).

5. When, where, and why to travel in small or large groups?

5.1. The ecological perspective

Wild rats also inhabit complex human environments, and in such habitats food is less scarce and foraging in large groups is not more beneficial than foraging in small ones (Stacey, 1986). Moreover, in such complex environments prey are apparently less salient and less likely to be detected when alone or as part of a small group (Fortin et al., 2009). Consequently, social spatial behavior of resting together but traveling alone or with a few companions is more appropriate for survival than traveling in larger groups. In contrast, foraging in large groups is more common in open environments (Fortin et al., 2009) where, by means of local enhancement, individuals can increase their chances of finding food (Buckley, 1996; Morrison et al., 2019; Poysa, 1992) along with gaining safety in numbers (Burger et al., 2000; Creel et al., 2014; Hebblewhite and Pletscher, 2002). In contrast, predators that hunt in the open, like wolves (*Canis lupus*) and painted wild African dogs (Lycaon pictus), display limited pack size since a large pack requires greater coordination among its members and this can impede hunting success (Creel and Creel, 1995; MacNulty et al., 2012, 2014). Nevertheless, a large pack may provide greater support for other tasks, like pup-guarding (Courchamp et al., 2002); and, indeed, large wild dog packs split between a few that hunt and others that guard the offspring. Rats are renowned for avoiding open areas (Valle, 1971) and, even in small test environments, laboratory rats that for many generations have never experienced a predatory threat nonetheless cling to the safety of the walls and avoid the center (Eilam, 2010; Whishaw et al., 2006). Altogether, whereas animals in structured habitats may rest together in large groups, when traveling they seem to benefit more from being in small groups. In contrast, prey species that forage in open spaces aggregate in large herds, whereas their predators have a limited pack size.

5.2. The socio-cognitive perspective

A constraint on group-size when traveling could be the result of socio-cognitive complexity. The behavior of lone rats is well organized in time and space, perhaps because they orient only in reference to the physical environment. The behavior of the same rats when in dyads is more chaotic when assessed in relation to the physical environment,
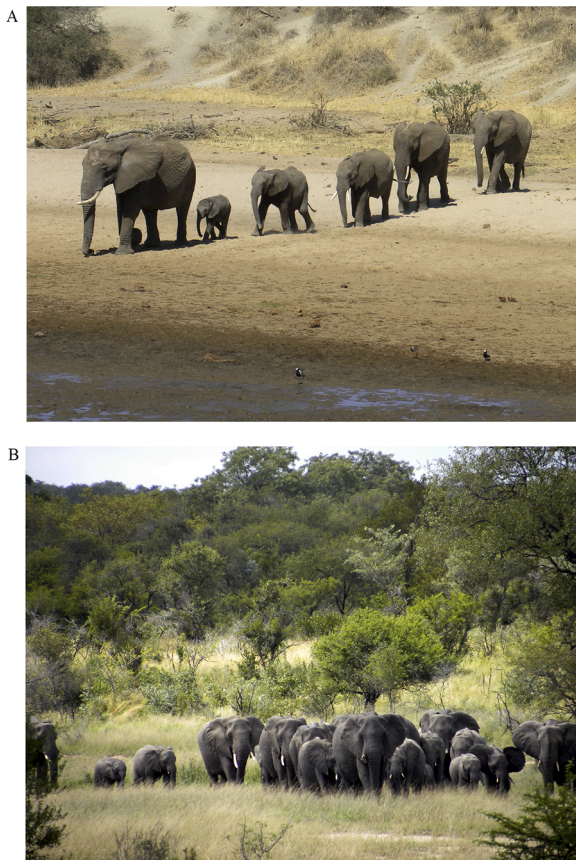
Fig. 9. African elephants (*Loxodonta Africana*). A: Individuals of a family follow the leading matriarch in a tandem arranged from young to old. B: A large herd of around 80 elephants (only part of the herd is shown), comprising several families that travel together, following one of the matriarchs.

since the rats now need to orient in reference to both the physical environment and to their partner (a moving point of reference; Ahuja et al., 2020; Dorfman et al., 2016). Explicit in this addition of a moving focal component is the aspect of elevated complexity (Bar-Yam, 1997) imposed on their spatial behavior compared to that of lone rats. Theoretically, adding more partners should further increase the social complexity encountered by animals when orienting in time and space. Additional complexity is caused by the need to map both the physical and the social environment according to their different frames of reference: Cartesian and allocentric for the physical space; polar and egocentric for the social space (Eichenbaum, 2015; Tavares et al., 2015). While such constraints can act to confine travel in some species to only small groups, there are other species that travel in very large groups; and, despite the expected higher complexity, their spatial behavior does not seem chaotic but, rather, well-coordinated, indicating that there are mechanisms that generate order and overcome the increased complexity. Indeed, animals may travel in groups of dozens, hundreds, or thousands and still behave collectively, such as herds of migrating buffalo (Molszewski, 1983), hunting packs of wolves (Schmidt and Mech, 1997), flocks of aerobatic birds (Davis, 1980), and schools of swimming fish (Parrish et al., 2002). The benefits of such mass-gathering could include transmitting information and protecting resources, as well as promoting foraging, enhancing mate choice, and reducing predation risk (Brown et al., 1988; Creel and Creel, 1995; Hamilton, 1971). A massive aggregation usually appears as a unit acting together with self-organized functioning. Travel in large aggregations is referred to as **collective behavior**, which involves limited and short-lived social interactions with no clear social boundaries, so that anyone can be a member of the aggregation. The present discussion focuses, however,

on **group behavior**, in which individuals tend to remain together for longer time and membership in the group is usually more discriminating (e.g. – based on family ties).

A simple mechanism of group spatial coordination is that of "follow the leader", which in the case of a dyad could be one rat following the other and maintaining the social bond, while the leader (merely in terms of progression) keeps track of the travel. Indeed, as shown in Fig. 9a, an African elephant matriarch is leading the family in tandem to a water source familiar to her, while the others need only to follow. Leading can be extended to include several social ranks and/or massive groups of thousands. For example, larger elephant herds can comprise several families, each led by a matriarch, with all the families following one leader, usually the most experienced and oldest matriarch (Fig. 9b). Similarly, when exposed to a life-threat, young Güenther's vole individuals (*Microtus güentheri*) adopt the behavior of the high body-mass males. Since high body-mass characterizes older and more experienced individuals, these "old and wise" individuals direct the behavior of the group (Bodek and Eilam, 2015).

Large groups, however, do not necessarily present an organized spatial behavior. For example, impalas (*Aepyceros melampus*) that do not belong to a harem tend to forage together in large herds (Schenkel, 1966). In the herd they benefit from safety in numbers and a reduced need for individual vigilance, but otherwise there is no connection among herd members and perhaps also no cognitive component in such gathering. In contrast, African buffalos (*Syncerus caffer*) tend to migrate in a large herd led by "pathfinders" – mature bulls that have experienced previous migrations and know the way. The pathfinders are followed by a column-shaped large herd of hundreds or several thousand, in which the cows and their calves are in the center, surrounded on the perimeter by fierce bulls (Molszewski, 1983).

There are several models for the way that groups can become spatially organized even without social hierarchy. For example, a simple way could be "follow your nearest neighbor" (Lemasson et al., 2009). Another model suggests that an individual with the lowest reserves determines when its group forages, with the follower individuals likely to benefit from the safety of a joint activity, along with the possibility of foraging (Rands et al., 2003). In this case, group coordination emerges spontaneously with a simple rule of thumb: "*I forage if either my reserves have fallen below a certain threshold value, or when my partner chooses to forage*" (Rands et al., 2003). This tactic of spontaneous collective travel requires only the ability to react to changes in partners' behavior (Couzin and Krause, 2003). In other words, the simple rule of "follow the individual that moves first" automatically produces leaders and followers (Price and van Vugt, 2014; van Vugt, 2006). This rule may also apply to an animal that moves first for another reason (e.g. "leader" or "forerunner"), and explains how large groups move together without increased complexity. This model may also explain why resting groups settle around the least active individuals (Fig. 2), according to the simple rule of thumb: "settle with the one that settles first".

A detailed analysis of social spatial interactions suggests viewing these interactions as a set of excursions that originate and end at the ongoing location of another individual(s). By measuring the momentary social distance between individuals, eight possible types of '**social excursions**' have been defined, referring to the travel of one animal in relation to another (Dorfman and Eilam, 2020). In other words, an excursion consists in the time interval in which partners start to become distant from one another and ends when they get together again. Such analysis has revealed that the individuals in normally-behaving rodent duos usually follow one another, albeit frequently exchanging leadership. In contrast, rat duos that displayed drug-induced stereotypy mostly travel independently of one another (Dorfman et al., 2019). Notably, such elaborate and dynamic social interactions are derived from one measurable parameter - social distance (Dorfman and Eilam, 2020). Altogether, the aforementioned studies conclusively demonstrate that the social environment predominates over the physical one in the structure of spatial behavior.
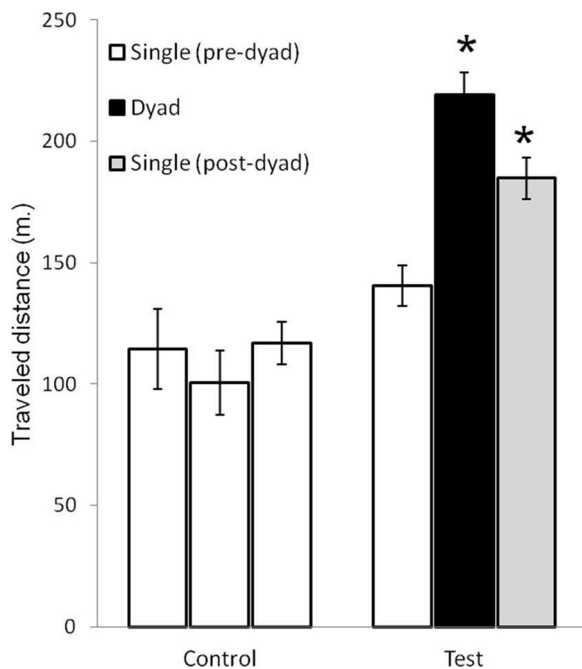
Fig. 10. Mean (± SEM) total traveled distance in the open field. On the right, the white bar represents the mean traveled distance of individuals when tested as singles (pre-dyad trial); the black bar represents the same individuals when tested in dyads (dyad trial); and the gray bar represents the same individuals when retested as singles (post-dyad trial). On the left, control individuals are depicted by three consecutive white bars, representing repeated testing of these individuals as singles. Asterisk marks a significant difference compared to all other bars. As shown, there was a significant effect of testing in dyads (black bar) on the traveled distance of rats. Despite a significant decrease in distance compared with the dyad trial, the effect was also preserved in the post-dyad trial (gray bar), in which traveled distance was significantly greater than in the pre-dyad trial and all control trials (white bars). (Figure taken from Weiss et al., 2015).

## 6. Mental aspects in social spatial behavior

6.1. Social influence: facilitation and loafing

One of the aims of social psychology is to understand how a person's behavior is influenced by others. In this respect, social influence is defined as "the myriad ways that people impact one another, including changes in attitudes, beliefs, feelings, and behavior, that result from the comments, actions, or even the mere presence of others" (Gilovich et al., 2011). Indeed, the partner effect plays an important role in social interactions and perception processes (Ervin and Bonito, 2014). One common social influence is **social facilitation**, in which performance is enhanced by the mere presence of others. Specifically, the presence of observers or partners has been shown to improve an individual's performance in easy or well-practiced tasks (Zajonc, 1965); for a recent review see (Neider et al., 2019). Social psychologists suggest that the mechanism behind social facilitation is that of the audience elevating attention to the task (Belletier et al., 2019; Tricoche et al., 2020) and/or arousal (Davidson and Keene, 2019; Neider et al., 2019). Social facilitation is manifested in a large variety of activities in humans and other animals; for example, crowd noise has a strong impact on professional sports people and on sports referees (Nevill et al., 2002; Sors et al., 2019; Wann and Hackathorn, 2019); in humans, the choice and quantity of the food chosen to eat can result from the desire to make a positive impression on others (Herman et al., 2019); cleaner fish (e.g. wrasses) make fewer mistakes of biting their "clients" when other fishes are watching them (Pinto et al., 2011; Triki et al., 2019; Truskanov et al., 2020; Wismer et al., 2019); rats and fish display facilitated exploration

in the presence of conspecifics (Hughes, 1969; Ward, 2012); and pro-social behavior in marmoset monkeys is augmented in the presence of an audience (Burkart and van Schaik, 2020). Since access to cognition is limited in non-human animals compared to in humans, social facilitation in the former is usually regarded as a consequence of elevated arousal (Rasmussen et al., 2017). This could explain the findings in our studies on dyads, triads, tetrads, and octads of rats, in which these rats were more active in exploring an unfamiliar environment compared with their behavior when alone (Fig. 10). Socially-facilitated exploration could also result from an elevated sense of security rendered by the presence of a conspecific, as discussed above. Animals in groups are more active, display lower neophobia, and explore new objects more thoroughly than individuals do (Beck and Chow, 1984; Clayton et al., 2008; Magurran and Pitcher, 1983; Menzel, 1971). Similarly, a novel object has been shown to be explored faster by a partner in raven dyads (*Corvus corax*) in various social combinations of male and female dyads (Stöwe et al., 2006). Indeed, animals in groups may benefit from an increased probability of detecting a predator ("the many eyes theory" - Lima, 1995; Roberts, 1996; and "safety in numbers" - Hamilton, 1971), and thus be able to reduce individual vigilance (Elgar and Catterall, 1981; Pulliam, 1973) and modify their spatial behavior by spending more time in foraging or other activities.

Along with the social facilitation that takes place under easy or well-practiced tasks, it was also noted that when performing difficult or unfamiliar tasks, performance worsened in the presence of others, a phenomenon termed **social loafing** (Zajonc, 1965). Past experience and task complexity, however, are not necessarily the only factors in the dichotomy between loafed and facilitated performance, since both these terms were derived from a scrutiny of task completion, which is not necessarily the ultimate goal of performance. For example, food-deprived rats were individually trained to collect palatable food items from 16 familiar equally-spaced locations. At the end of training, when the rats were familiar with the location of all the food items in the apparatus, three well-trained but unfamiliar rats were introduced together into the apparatus. These rats chose first to socialize, sniffing and huddling with one another, and only then turned to collect the food items, with no overt competition (Weiss et al., 2017a; see videoclip). A preference by food-deprived rodents to first socialize was also demonstrated in rats in which the individuals in one group were trained to find food on one side of an apparatus, and the individuals in a second group were trained to find food on the other side of the apparatus. A dyad comprising one individual from each of the two differently-trained groups was then introduced into the apparatus (Dorfman and Eilam, 2018; Hagbi, 2018). Since both dyad partners had each initially been trained alone and only afterwards performed the same spatial task alongside another individual, the dyads should have displayed an enhanced performance of the well-practiced task, with each rat quickly collecting the baits from its familiar locations. The results, however, were the opposite, with both rats taking more time to collect the baits when in a dyad than when alone. This diversion from the expected pattern of social enhancement is in line with the interpretation that food-deprived rodents attend one another more than they attend to the available food, attesting again to the primacy of socializing over foraging (performance). In humans, the dichotomy between facilitation and loafing is biased by culture. For example, Western cultures are generally individualistic and perceive an importance in self-achievement, which results in high levels of self-sufficiency. This is in contrast to Eastern cultures, which are more collective in nature, with lower levels of self-efficiency resulting from other individuals in the group sharing the burden of task completion (Grundy and Jamieson, 2005; Pulford et al., 2005; Zor et al., 2011). Whether performance is facilitated or loafed by the presence of others, these effects unequivocally demonstrate that the social environment exerts a considerable influence on spatial behavior, and that this effect is more complex than merely facilitation in simple and well-practiced tasks and loafing in complex or unfamiliar spatial tasks.
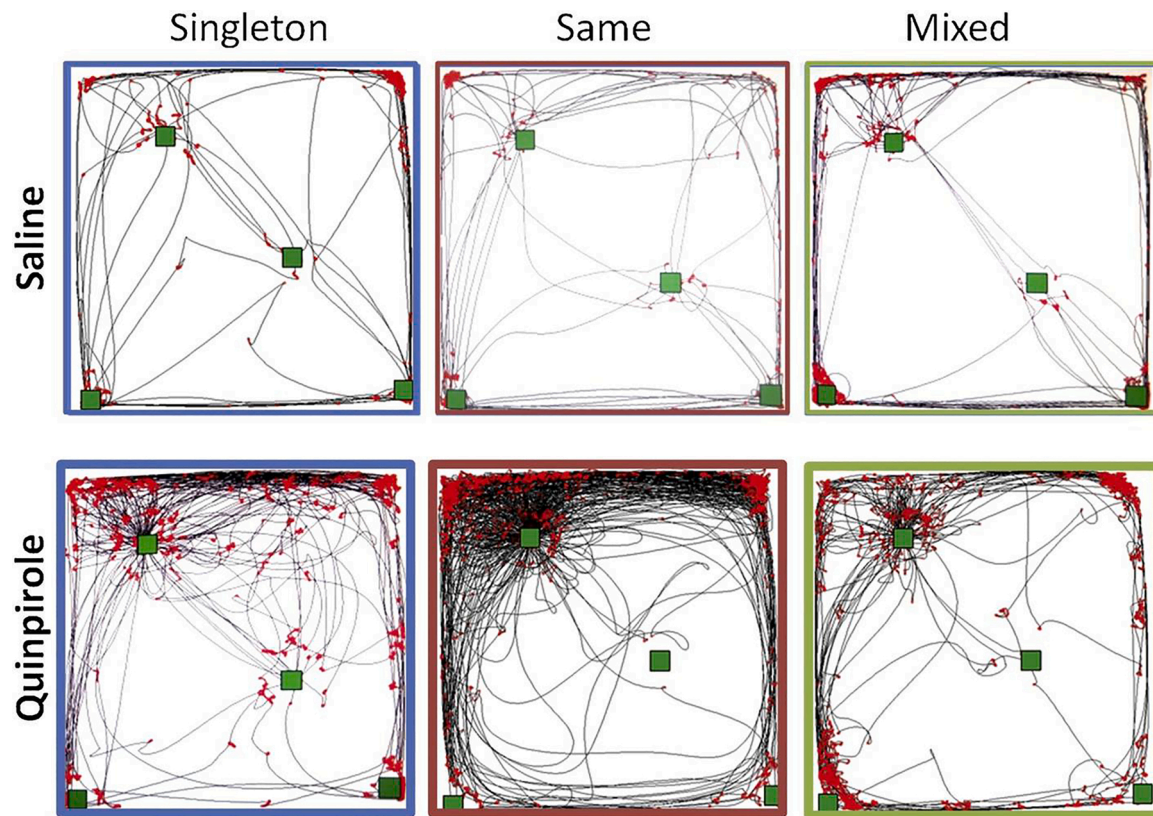
Fig. 11. Effects of social context on the trajectories of travel (black lines) and location of stops (red dots) in rats following the 10th injection of saline or quinpirole. Green squares indicate locations of four objects that were placed in the open field in order to attract the rats. Each inset represents the behavior of one rat, as follows: the trajectories and stops are plotted for two rats tested alone ("Singleton" - left column); a rat from a dyad in which both partners were administered with saline (central column, top); and a rat from a dyad in which both partners were injected with quinpirole (central column, bottom); Finally, a rat injected with saline (right column top) and a rat injected with quinpirole (right column, bottom), both from a dyad in which one rat was administered saline and the other with quinpirole. For each rat, locomotor trajectories during the entire session are shown; the density of trajectory lines corresponds to amount of locomotion. As shown, behavior of saline rats (top row) was hardly affected by the presence or type of partner. In contrast, stereotypy increased in the quinpirole rat tested with another quinpirole rat (bottom center), but was attenuated when the quinpirole rat was tested with a saline-injected partner (bottom right).

## 6.2. Social contagion in spatial behavior: the impact of a stereotyped partner on conspecifics

The effect of the social environment on behavior can take various forms, such as imitation, conformity, pro-sociality, compassion, sympathy, and empathy. In this section we do not refer to each of these specific mechanisms, but to the social transmission of behavior by means of the broader form of social contagion. It has long been noted that people in a group behave differently to how they would have behaved if alone under identical circumstances. Gustave LeBon extremist theory (Le Bon, 2009) suggested that crowd episodes are "irrational reversions to animal emotion". According to LeBon, crowd behavior is the result of a hypnotic influence of the crowd on its members together with an individual feeling of anonymity. Crowd behavior is contagious and therefore feeds upon itself and spreads in the crowd like a disease. Other theories of crowd behavior also exist, such as the convergence theory and the emergent-norm theory (see Raafat et al., 2009 for review), but all concur regarding the contagiousness of behavior in social groups. Indeed, individuals in social groups need to display a certain level of collective behavior and an alignment of behaviors in order to maintain group cohesion (Carere et al., 2009; Conradt and List, 2009); see also a set of articles in *The Philosophical Transactions of the Royal Society*, vol. 364, 2009). A simple mechanism for the occurrence of such an alignment of behavior without any apparent centralized coordination could be that of social contagion, with one individual, sometime unintentionally, copying the behavior of its neighbor(s). This may explain, for example, the tendency of rats to travel together (Nagy et al., 2020).

Moreover, it was suggested that copying just a few specific acts is the key process in the transmission of collective rituals (Eilam, 2015; Keren et al., 2013; Nielbo et al., 2017).

In the context of social contagion, the emotional and/or mental state of individual(s) may reflect on other individuals (Hatfield et al., 1993; Neumann and Strack, 2000). In other words, emotional contagion in both humans and other animals occurs when the emotions of individual(s) directly trigger similar emotions in others (for a review see Palagi et al., 2020). For example, personality traits in voles are shaped by the structure of their family groups (Lantová et al., 2011). Negative or problematic emotional or mental states can also trigger rejection/alienation by others. Indeed, exorcism, isolation, lobotomy, and asylums were harsh treatments administered in many countries and cultures to people with mental illnesses. Affected humans were hidden away by their families, isolated from the community/society, and it is only in the more recent decades that efforts are being taken to provide mentally-disabled people with a normal social life. In nature, social animals usually abandon or move away from individuals displaying abnormal behavior. This is aptly phrased in Hans Christian Andersen's allegory of the ugly duckling: *"What a queer looking duckling; we don't want him here," and then one flew out and bit him in the neck. "Let him alone," said the mother; "he is not doing any harm." "Yes, but he is so big and ugly," said the spiteful duck, "and therefore he must be turned out".*

Because hippocampal activity is involved in social cognitive mapping, it was suggested that hippocampal dysfunction co-occurs in mental disorders (Shafer and Schiller, 2018). Indeed, animal models of mental disorders usually involve an apparent change in spatial behavior
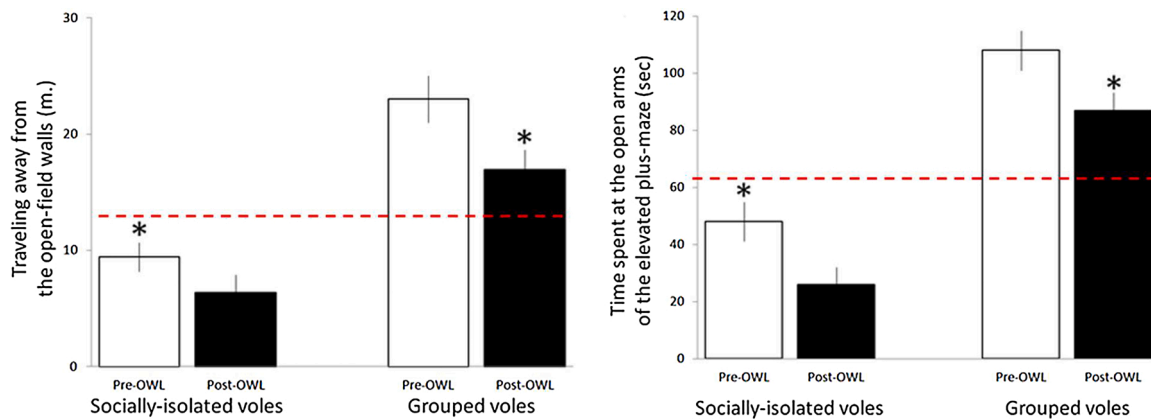
Fig. 12. Behavior of lone compared with grouped voles (*Microtus guentherii*). The means (± SEM) of traveling away from walls (left) and of time spent in the center of the open field (right) are depicted by clear bars for the behavior prior to exposure to owl, and black bars for the behavior following owl attack. As shown isolated voles traveled less away from the open-field wall and spent less time in the center, in both pre- and post-owl attack tests. (Figure modified from Bodek and Eilam, 2015).

(Szechtman and Eilam, 2004; Eilam and Golani, 1994). The question remains as to how the spatial behavior of an individual with abnormal behavior may affect the spatial behavior of its conspecifics, and vice versa. In this context, compelling evidence for the impact of the social environment on drug-induced stereotypy in rats was demonstrated by testing a stereotyped rat together with a normal (saline-injected) rat. Specifically, the behavior of rats chronically injected with the $D_{1,2}$ dopamine-agonist quinpirole presents a solid model of obsessive-compulsive disorder (OCD); a model that has been comprehensively evaluated and validated in numerous studies (Alonso et al., 2015; Camilla d'Angelo et al., 2014; Stuchlik et al., 2016). While this animal model was initially developed in single animals (Szechtman et al., 1998), later testing of rat dyads revealed that the presence of a partner that was also treated with quinpirole or a partner that was treated with saline, modulated the quinpirole-sensitized rat compared to the stereotypy shown by it when tested alone. In other words, the vigor of compulsive behavior was attenuated in the presence of a saline-treated partner and augmented in the presence of a quinpirole-treated partner. Although the behavior of the stereotyped partner was attenuated, the behavior of the normal partner hardly changed (Dorfman et al., 2019; Fig. 11). Such modulation of the expression of stereotyped behavior by means of social interaction indicates the need to study the influence of drugs also in the context of the social environment.

A boost in social contagion can occur during or after a stressful event. Human behavior following a disaster is characterized by individuals adopting a similar behavioral code, which is expressed as solidarity, altruism, loyalty, and volunteering (Lowe and Fothergill, 2003; Poulin et al., 2009; Tierney et al., 2001). For example, after the September 11th attack on the World Trade Center in New York, there emerged more public-mindedness, greater interest in volunteering, stronger feelings toward nation and community, and higher levels of patriotism. Strict behavioral codes also characterize other occasions of stressful events, such as following bereavement (Lehman et al., 1993). These collective responses emerge across a broad scale of age, occupation, income, ethnic background, and gender (Lowe and Fothergill, 2003). The above-noted radical behavioral changes under a life-threatening event are also manifested in spatial behavior.

As previously noted, the large individual variability demonstrated in the rodents' spatial behavior measured prior to owl attack on the groups of social voles, was significantly reduced after the attack, when all the voles in the group displayed a relatively similar pattern of activity (Eilam et al., 2011; Izhar and Eilam, 2010; Fig. 12). This similar response of grouped animals was in contrast to that of isolated voles, of which, when exposed individually to owl calls, some displayed freezing and others frantic fleeing (Eilam et al., 1999). Other studies in rodents have

suggested that exploring unfamiliar areas is governed by the attempt to maximize safety (Gielman et al., 2020; Whishaw et al., 2006). Accordingly, we suggest that the home (or home-base) and familiar paths are perceived as safe havens to which spatial behavior converges under life-threatening events. In humans, home is a hub and an 'organizer' of spatial behavior, and mobility is characterized by deep-rooted regularities (Song et al., 2010) with over 50 % of daily trips being home-generated (Golledge, 1999; p.26). It is suggested here that, whereas normally a person can freely divert from such spatial regularities, under extreme events spatial flexibility diminishes and the deep-rooted regularities dominate spatial behavior. Indeed, after the tragic 2010 earthquake in Haiti, tracking cell-phone usage revealed that people maintained their regular spatial behavior as established in their past experience and social bonds (Lu et al., 2012). Similarly, tracking the exodus from Wuhan, China, after the outbreak of the COVID-19 pandemic, revealed that people mainly continued to maintain their usual social and economic ties (Jia et al., 2020). We therefore suggest that, under extreme events, degrees of freedom in spatial behavior shrink and people revert to their deep-rooted socio-spatial routines. Thus, tracking spatial routines ahead of time could provide a valuable means for controlling the situation following an extreme negative event.

6.3. Social distance (proximity) as a tool in studying the dynamics of group formation

In light of the above survey on the fundamental behavioral impact of the social space, we suggest that the dynamics of a simple measureable parameter - the social distance (or proximity) between individuals (Bonuti and Morato, 2018) present a key for understanding social spatial interactions and cognition (Dorfman and Eilam, 2020). As will be shown below, social distance can reveal the dynamics of social processes such as group formation and social interactions. Indeed, applying this parameter in groups of eight unfamiliar rats revealed three phases in group formation (Weiss et al., 2018). The unfamiliar rats began by exploring the arena independently, "bumping" briefly into their mates, sniffing them, and continuing to travel. After a while, the rats started to interact with one another, while frequently exchanging partners. Social connections then gradually emerged and became stronger, with the rats spending increasingly longer duration in resting with more partners. This change, which occurred in the first hour after introducing the unfamiliar rats together into the arena, led to the **formation** of relatively large resting groups in the following hour, which was the period during which the group underwent **stabilization**. Activity then further decreased, with all the rats resting together in one place, and individuals every now and then taking roundtrips in the arena either alone or with a
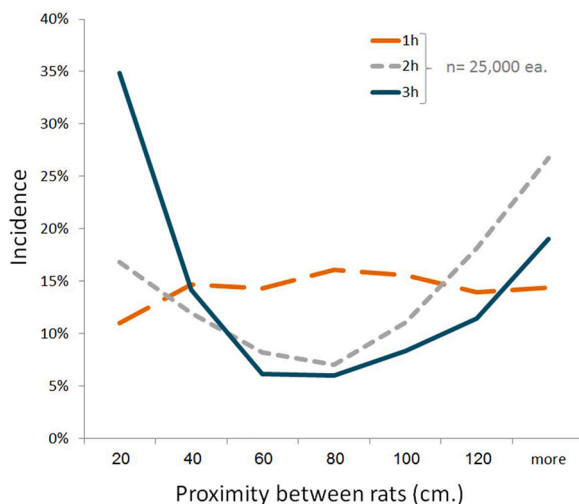
Fig. 13. Change over time in the proximity among unfamiliar rats. Eight groups, each comprising eight unfamiliar male rats, were each introduced together into a large arena and tested for three hours. The proximity among each two rats was extracted 5 times per second for each of the three hours (totaling 25,000 records/hr), and the relative incidence of proximity in 20 min bins is depicted for each hour. As shown, during the first hour (orange dashed line) the rats equally scattered at any distance from one another, reflecting the state of unfamiliarity. By the second hour (dashed grey line) and third hour (solid blue line) they dichotomized to either mainly staying in close vicinity to each other (left side of the curve) or away from each other (right side of the curve). Comparing this with Fig. 3, presenting the social distance as measured in social vs. solitary species, the rats appeared to display solitary-like distribution in the first hour when they were still unfamiliar, and then shifted to a social-like distribution in the third hour when they had become familiar to each other. (Data taken from Weiss et al., 2018).

partner. This was the ***performance*** phase, in which all eight rats displayed the same structure of spatial behavior. Notably, the previously unfamiliar rats formed groups and performed together despite being an ad-hoc group with no shared history. Such a background of unfamiliarity is a major concern and obstacle in group formation in humans (Chidambaram and Bostrom, 1997). In light of the above, using social distance (proximity) as a parameter for assessing social spatial behavior offers a relatively simple method that circumvents the obstacles inherent in studying group formation via task completion and goal achievement.

In the above discussion of proximity among individuals of social compared to non-social rodent species, we showed that social rodents huddled together and, consequently, spent most of the time in a proximity of 20 cm or less. In contrast, the non-social rodents all scattered to various distances (Figs. 3 and 4). In the same vein, a transition from initial scattered proximity to huddling together occurred when groups of eight unfamiliar rats were introduced together into an unfamiliar arena. The eight rats first all scattered to various distances, but after three hours were observed to huddle together in close proximity (Fig. 13). These initially unfamiliar rats had seemingly transformed from a non-social to a social state after remaining together for three hours. Once a group is formed and its individuals avoid further isolation, aligning themselves with their neighbors (Partridge, 1982; Partridge and Pitcher, 1980) by minimizing their distance from them, the transition between behavioral states depends on the previous structure of the group (Couzin et al., 2002). Notably, it has been suggested that social interactions do not depend on the metric distance, unlike the position of most current models and theories, but rather on the topological distance to a fixed number (six to seven on average) of neighbors (Ballerini et al., 2008). We suggest that this is not in conflict with the present emphasis on social distance, but that part of establishing a topological link with specific partners lies in maintaining minimal social distance.

7. Epilogue

The findings from the various studies presented here suggest that the social environment predominates and shapes the structure of spatial behavior, and that the spatial representations of separate individuals converge to form collective spatial behavior. We also present the parallel between social spatial behavior and hippocampal activity. By focusing on social distance (proximity) among individuals as an objective and measurable proxy for socializing, it is possible to uncover how a group of unfamiliar individuals becomes organized or coordinated in time and space when resting or traveling. This has been illustrated here by showing that home (or home-base), which is where humans and other animals anchor their traveling, is established according to the location of conspecifics, and that a shared area within different home ranges reflects the affiliation among individuals. Despite the argument presented here for a predominance of the social environment in shaping spatial behavior, the physical environment too has its share. For example, animals in structured habitats may rest together in large groups but when traveling seem to benefit more from doing so in small groups. In contrast, prey species that forage in open spaces aggregate in large herds, whereas their predators have a limited pack size. Overall, social spatial cognition rests on the individual's knowledge of both the social and the physical environments, but is primarily modulated by the former, as illustrated in the effect of social interactions on drug-induced stereotypy. Accordingly, studies on the biobehavioral mechanisms that control spatial behavior (i.e. - the hippocampal formation, animal models for mental disorders) should also take into account the social environment rather than only studying lone animals.

Acknowledgements

References

Ahmed, S., Johora, F.T., Müller, J.P., 2019. Investigating the role of pedestrian groups in shared spaces through simulation modeling. In: International Workshop on Simulation Science. Springer, Cham, pp. 52–69.

Ahuja, N., Lobellová, V., Stuchlík, A., Kelemen, E., 2020. Navigation in a space with moving objects: rats can avoid specific locations defined with respect to a moving robot. Front. Behav. Neurosci. 14, 576350.

Alahi, A., Ramanathan, V., Fei-Fei, L., 2014. Socially-aware large-scale crowd forecasting. The IEEE Conference on Computer Vision and Pattern Recognition (CVPR) 2203–2210.

Alonso, P., Lopez-Sola, C., Real, E., Segalas, C., Menchon, J.M., 2015. Animal models of obsessive-compulsive disorder: utility and limitations. Neuropsychiatr. Dis. Treat. 11, 1939–1955.

Arcis, V., Desor, D., 2003. Influence of environment structure and food availability on the foraging behaviour of the laboratory rat. Behav. Process. 60, 191–198.

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Viale, M., 2008. Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study. Proc. Nat. Acad. Sci. U. S. A. 105, 1232–1237.

Barnett, S.A., 1963. The Rat. A Study in Behaviour. Aldine Publishing Company, Chicago.

Bar-Yam, Y., 1997. Dynamics of Complex Systems. Addison-Wesley, Reading, MA.

Beck, C.H.M., Chow, H.L., 1984. Solitary and social behavior of male rats in the open-field. Physiol. Behav. 32, 941–944.

Belletier, C., Normand, A., Huguet, P., 2019. Social facilitation and impairment effects: from motivation to cognition and the social brain. Curr. Dir. Psychol. Sci. 28, 260–265.

Blumenfeld-Lieberthal, E., Eilam, D., 2016. Physical, behavioral, and spatiotemporal perspectives of home in humans and other animals. In: Portugali, J., Stolk, E. (Eds.), Complexity, Cognition Urban Planning and Design. Springer, Heidelberg, pp. 127–149.

Bodek, S., Eilam, D., 2015. Revisiting the "visible burrow system": the impact of the group, social rank, and gender on voles under owl attack. Physiol. Behav. 146, 79–85.

Bonuti, R., Morato, S., 2018. Proximity as a predictor of social behavior in rats. J. Neurosci. Methods 293, 37–44.

Brown, M.F., 2011. Social influences on rat spatial choice. Compar. Cogn. Behav. Rev. 6, 5–23.

Brown, J.S., Kotler, B.P., Smith, R.J., Wirtz, W.O., 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76, 408–415.

Burger, J., Safina, C., Gochfeld, M., 2000. Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. Acta Ethol. 2, 97–104.

Burkart, J.M., van Schaik, C.P., 2020. Marmoset prosociality is intentional. Anim. Cogn. 23, 581–594.

Camilla d'Angelo, L.S., Eagle, D.M., Grant, M.A., Fineberg, N.A., Robbins, T.W., Chamberlain, S.R., 2014. Animal models of obsessive-compulsive spectrum disorders. CNS Spectr. 19, 28–49.

Carere, C., Montanino, S., Moreschini, F., Zoratto, F., Chiarotti, F., Santucci, D., Alleva, E., 2009. Aerial flocking patterns of wintering starlings, Sturnus vulgaris, under different predation risk. Anim. Behav. 77, 101–107.

Cheng, H., Li, Y., Sester, M., 2019. Pedestrian group detection in shared space. IEEE Intelligent Vehicles Symposium 1707–1714.

Chidambaram, L., Bostrom, R., 1997. Group development (I): a review and synthesis of development models. Gr. Decis. Negot. 6, 159–187.

Clark, B.J., Hamilton, D.A., Whishaw, I.Q., 2006. Motor activity (exploration) and formation of home bases in mice (C57BL/6) influenced by visual and tactile cues: modification of movement distribution, distance, location, and speed. Physiol. Behav. 87, 805–816.

Clayton, N., Dally, J., Emery, N., 2008. Social influences on foraging by rooks (*Corvus frugilegus*). Behav. Brain Res. 145, 1101–1124.

Conradt, L., List, C., 2009. Group decisions in humans and animals: a survey. Philos. Trans. Royal Soc. Lond. B: Biol. Sci. 27, 719–742.

Courchamp, F., Rasmussen, G.S., Macdonald, D.W., 2002. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. Behav. Ecol. 13, 20–27.

Couzin, I.D., Krause, J., 2003. Self-organization and collective behaviour in vertebrates. Adv. Stud. Behav. 32, 1–75.

Couzin, I.D., Krause, J., James, R., Ruxton, G.D., Franks, N.R., 2002. Collective memory and spatial sorting in animal groups. J. Theor. Biol. 218, 1–12.

Creel, S., Creel, N.M., 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Anim. Behav. 50, 1325–1339.

Creel, S., Schuette, P., Christianson, D., 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behav. Ecol. 25, 773–784.

Danjo, T., Toyoizumi, T., Fujisawa, S., 2018. Spatial representations of self and other in the hippocampus. Science 359, 213–218.

Davidson, A., Keene, J.R., 2019. Alone in a crowded room: the impact of crowd noise in music recordings on social facilitation, mental imagery, and cognitive processing. J. Radio Audio Media 26, 299–317.

Davis, J.M., 1980. The coordinated aerobatics of dunlin flocks. Anim. Behav. 28, 668–673.

Dorfman, A., Eilam, D., 2018. The hierarchy of food, sociality, and experience in spatial decision-making by food-deprived rats. Behav. Process. 157, 1–6.

Dorfman, A., Nielbo, K.L., Eilam, D., 2016. Traveling companions add complexity and hinder performance in the spatial behavior of rats. PLoS One 11, e0146137.

Dorfman, A., Szechtman, H., Eilam, D., 2019. Social interaction modulates the intensity of compulsive checking in a rat model of obsessive-compulsive disorder (OCD). Behav. Brain Res. 359, 156–164.

Eichenbaum, H., 2015. The hippocampus as a cognitive map... of social space. Neuron 87, 10–11.

Eilam, D., 2010. Is it safe? Voles in an unfamiliar dark open-field divert from optimal security by abandoning a familiar shelter and not visiting a central start point. Behav. Brain Res. 206, 88–92.

Eilam, D., 2014. Of mice and men: building blocks in cognitive mapping. Neurosci. Biobehav. Rev. 47, 393–409.

Eilam, D., 2015. The cognitive roles of behavioral variability: idiosyncratic acts as the foundation of identity and as transitional, preparatory, and confirmatory phases. Neurosci. Biobehav. Rev. 49, 55–70.

Eilam, D., Golani, I., 1989. Home base behavior of rats (*Rattus norvegicus*) exploring a novel environment. Behav. Brain Res. 34, 199–211.

Eilam, D., Dayan, T., Ben-Eliyahu, S., Schulman, I., Shefer, G., Hendrie, C.A., 1999. Differential behavioural and hormonal responses of voles and spiny mice to owl calls. Anim. Behav. 58, 1085–1093.

Eilam, D., Izhar, R., Mort, J., 2011. Threat detection: behavioral consequences in animals and humans. Neurosci. Biobehav. Rev. 35, 999–1006.

Elgar, M.A., Catterall, C.P., 1981. Flocking and predator surveillance in house sparrows: test of an hypothesis. Anim. Behav. 29, 868–872.

Ervin, J., Bonito, J.A., 2014. A review and critique of partner effect research in small groups. Small Group Res. 45, 603–632.

Ewer, R.F., 1971. The biology and behaviour of a free-living population of black rats (*Rattus rattus*). Anim. Behav. Monogr. 4, 125–174.

Fortin, D., Fortin, M.E., Beyer, H.L., Duchesne, T., Courant, S., Dancose, K., 2009. Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. Ecology 90, 2480–2490.

Fu, L., Cao, S., Shi, Y., Chen, S., Yang, P., Fang, J., 2019. Walking behavior of pedestrian social groups on stairs: a field study. Saf. Sci. 117, 447–457.

Galef, B.G.J., Whiskin, E.E., 2008. 'Conformity'in Norway rats? Anim. Behav. 75, 2035–2039.

Galef, B.G.J., White, D.J., 1997. Socially acquired information reduces Norway rats' latencies to find food. Anim. Behav. 54, 705–714.

Gielman, S., Hagbi, Z., Dulitzky, Y., Blumenfeld-Lieberthal, E., Eilam, D., 2020. How do rodents explore a three-dimensional environment? Habitat-dependent and direction-dependent differences. Behav. Process. 178, 104183.

Gilovich, T., Keltner, D., Nisbett, R.E., 2011. Social Psychology, 2nd ed. WW., Norton & Company, NY.

Golani, I., Benjamini, Y., Eilam, D., 1993. Stopping behavior: constraints on exploration in rats (*Rattus norvegicus*). Behav. Brain Res. 53, 21–33.

Golledge, R.G., 1999. Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes. Johns Hopkins university press.

Grundy, S., Jamieson, L., 2005. Are we all Europeans now? Local, national and supranational identities of young adults. Sociol. Res. Online 10, 169–183.

Hafting, T., Fyhn, M., Molden, S., Moser, M.-B., Moser, E.I., 2005. Microstructure of a spatial map in the entorhinal cortex. Nature 436, 801–806.

Hagbi, Z., 2018. Spatial Behavior in Social and Solitary Rodent Species, Zoology. Tel-Aviv University, Tel-Aviv, Israel.

Hamilton, W., 1971. Geometry for the selfish herd. J. Theor. Biol. 31, 295–311.

Hatfield, E., Cacioppo, J., Rapson, R., 1993. Emotional Contagion (Studies in Emotion and Social Interaction). Cambridge University Press, Cambridge, UK.

Hebblewhite, M., Pletscher, D.H., 2002. Effects of elk group size on predation by wolves. Can. J. Zool. 80, 800–809.

Herman, C.P., Polivy, J., Pliner, P., Vartanian, L.R., 2019. Social facilitation. In: Herman, C.P., Polivy, J., Pliner, P., Vartanian, L.R. (Eds.), Social Influences on Eating. Springer, Cham, pp. 181–200.

Hughes, R.N., 1969. Social facilitation of locomotion and exploration in rats. Br. J. Psychol. 3, 385–388.

Izhar, R., Eilam, D., 2010. Together they stand: a life-threatening event reduces individual behavioral variability in groups of voles. Behav. Brain Res. 208, 282–285.

Jia, J.S., Lu, X., Yuan, Y., Xu, G., Jia, J., Christakis, N.A., 2020. Population flow drives spatio-temporal distribution of COVID-19 in China. Nature 582, 389–394.

Keren, H., Fux, M., Mort, J., Lawson, E.T., Eilam, D., 2013. Are motor collective rituals as rigid as they seem? A test case of a Zulu wedding dance. J. Cogn. Cult. 13, 17–32.

Kropff, E.M., Carmichael, J.E., Moser, M.B., Moser, E.I., 2015. Speed cells in the medial entorhinal cortex. Nat. Commun. 523, 419–424.

Kuipers, B., 1982. The "map in the head" metaphor. Environ. Behav. 14, 202–220.

Lantová, P., Šíchová, K., Sedláček, F., Lanta, V., 2011. Determining behavioural syndromes in voles–the effects of social environment. Ethology 117, 124–132.

Le Bon, G., 2009. Psychology of Crowds. Sparkling Books, Southampton, UK.

Lehman, D.R., Davis, C.G., DeLongis, A., Wortman, C.B., Bluck, S., Mandel, D.R., Ellard, J.H., 1993. Positive and negative life changes following bereavement and their relations to adjustment. J. Soc. Clin. Psychol. 12, 90–112.

Lemasson, B.H., Anderson, J.J., Goodwin, R.A., 2009. Collective motion in animal groups from a neurobiological perspective: the adaptive benefits of dynamic sensory loads and selective attention. J. Theor. Biol. 261, 501–510.

Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., Burgess, N., 2009. Boundary vector cells in the subiculum of the hippocampal formation. J. Neurosci. 29, 9771–9777.

Lima, S.L., 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Anim. Behav. 49, 11–20.

Ling, H., Mclvor, G.E., van der Vaart, K., Vaughan, R.T., Thornton, A., Ouellette, N.T., 2019. Costs and benefits of social relationships in the collective motion of bird flocks. Nat. Ecol. Evol. 3, 943–948.

Loewen, I., Wallace, D.G., Whishaw, I.Q., 2005. The development of spatial capacity in piloting and dead reckoning by infant rats: use of the huddle as a home base for spatial navigation. Dev. Psychobiol. 46, 350–361.

Lowe, S., Fothergill, A., 2003. A need to help: emergent volunteer behavior after September 11th. In: Monday, J.L. (Ed.), Beyond September 11th: An Account of Post-Disaster Research. University of Colorado, Boulder, pp. 293–314.

Lu, X., Bengtsson, L., Holme, P., 2012. Predictability of population displacement after the 2010 haiti earthquake. Proc. Nat. Acad. Sci. U. S. A. 109, 11576–11581.

MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A., Packer, C., 2012. Nonlinear effects of group size on the success of wolves hunting elk. Behav. Ecol. 23, 75–82.

MacNulty, D.R., Tallian, A., Stahler, D.R., Smith, D.W., 2014. Influence of group size on the success of wolves hunting bison. PLoS One 9 e112884.

Magurran, A.E., Pitcher, T.J., 1983. Foraging, timidity and shoal size in minnows and goldfish. Behav. Ecol. Sociobiol. 12, 147–152.

Menzel, E.W., 1971. Communication about the environment in a group of young chimpanzees. Folia Primatol. (Basel) 15, 220–232.

Menzel, E.W., 1973. Chimpanzee spatial memory organization. Science 182, 943–945.

Molszewski, M.J., 1983. The Behavior and Ecology of the African Buffalo. Cambridge University Press, Cambridge.

Monaco, J.D., Rao, G., Roth, E.D., Knierim, J.J., 2014. Attentive scanning behavior drives one-trial potentiation of hippocampal place fields. Nat. Neurosci. 17, 725–731.

Moussaïd, M., Perozo, N., Garnier, S., Helbing, D., Theraulaz, G., 2010. The walking behaviour of pedestrian social groups and its impact on crowd dynamics. PLoS One 5 e10047.

Nagy, M., Horicsányi, A., Kubinyi, E., Couzin, I.D., Vásárhelyi, G., Flack, A., Vicsek, T., 2020. Synergistic benefits of groups search in rats. Curr. Biol. 30, 1–6.

Neider, D.P., Fuse, M., Suri, G., 2019. Cockroaches, performance, and an audience: reexamining social facilitation 50 years later. J. Exp. Soc. Psychol. 85, 103851.

Nemati, F., Whishaw, I., 2007. The point of entry contributes to the organization of exploratory behavior of rats on an open field: an example of spontaneous episodic memory. Behav. Brain Res. 182, 119–128.

Neumann, R., Strack, F., 2000. Mood contagion: the automatic transfer of mood between persons. J. Pers. Soc. Psychol. 79, 211.

Nevill, A.M., Balmer, N.J., Williams, A.M., 2002. The influence of crowd noise and experience upon refereeing decisions in football. Psychol. Sport. Exerc. 3, 261–272.

Nielbo, K.L., Fux, M., Mort, J., Zamir, R., Eilam, D., 2017. Structural differences among individuals, genders and generations as the key for ritual transmission, stereotypy, and flexibility. Behaviour 154, 93–114.

O'Keefe, J., Dostrovsky, J., 1971. Hippocampus as a spatial map - preliminary evidence from unit activity in freely-moving rat. Brain Res. 34, 171. -&.

O'Keefe, J., Nadel, L., 1978. The Hippocampus As a Cognitive Map. Oxford University Press, Oxford.

Okuyama, T., Kitamura, T., Roy, D.S., Itohara, S., Tonegawa, S., 2016. Ventral CA1 neurons store social memory. Science 353, 1536–1541.

Omer, D.B., Maimon, S.R., Las, L., Ulanovsky, N., 2018a. Social place-cells in the bat hippocampus. Science 359, 218–224.

Omer, D.B., Maimon, S.R., Las, L., Ulanovsky, N., 2018b. Social place-cells in the bat hippocampus. Science 359, 218–224.

Palagi, E., Celeghin, A., Tamietto, M., Winkielman, P., Norscia, I., 2020. The neuroethology of spontaneous mimicry and emotional contagion in human and non-human animals. Neurosci. Biobehav. Rev. 111, 149–165.

Parrish, J.K., Viscido, S.V., Grünbaum, D., 2002. Self-organized fish schools: an examination of emergent properties. Biol. Bull. 202, 296–305.

Partridge, B.L., 1982. The structure and function of fish schools. Sci. Am. 246, 114–123.

Partridge, B.L., Pitcher, T.J., 1980. The sensory basis of fish schools: relative role of lateral line and vision. J. Comp. Physiol. 135, 315–325.

Pinto, A., Oates, J., Grutter, A., Bshary, R., 2011. Cleaner wrasses Labroides dimidiatus are more cooperative in the presence of an audience. Curr. Biol. 21, 1140–1144.

Portugali, J., 2005. Cognitive maps are over 60. Lect Notes Comput. Sci. 3693, 251–264.

Poulin, M.J., Silver, R.C., Gil-Rivas, V., Holman, E.A., McIntosh, D.N., 2009. Finding social benefits after a collective trauma: perceiving societal changes and wellbeing following 9/11. J. Traum. Stress 22, 81–90.

Price, M.E., van Vugt, M., 2014. The evolution of leader-follower reciprocity: the theory of service-for-prestige. Front. Hum. Neurosci. 8, 363.

Pulford, B.D., Johnson, A.B., Awaida, M., 2005. A cross-cultural study of predictors of self-handicapping in university students. Pers. Individ. Dif. 39, 727–737.

Pulliam, H.R., 1973. On the advantages of flocking. J. Theor. Biol. 38, 419–422.

Raafat, R.M., Chater, N., Frith, C., 2009. Herding in humans. Trends Cogn. Sci. 13, 420–428.

Raam, T., McAvoy, K.M., Besnard, A., Veenema, A.H., Sahay, A., 2017. Hippocampal oxytocin receptors are necessary for discrimination of social stimuli. Nat. Commun. 8, 2001.

Rabi, C., Zadicario, P., Mazon, Y., Wagner, N., Eilam, D., 2017. The response of social and non-social rodents to owl attack. Behav. Ecol. Sociobiol. 71, 131.

Rands, S.A., Cowlishaw, G., Pettifor, R.A., Rowcliffe, J.M., Johnstone, R.A., 2003. Spontaneous emergence of leaders and followers in foraging pairs. Nat. Commun. 423, 432–434.

Rao, R.P., von Heimendahl, M., Bahr, V., Brecht, M., 2019. Neuronal responses to conspecifics in the ventral CA1. Cell Rep. 27, 3460–3472.

Rasmussen, E.E., Keene, J.R., Berke, C.K., Densley, R.L., Loof, T., 2017. Explaining parental coviewing: the role of social facilitation and arousal. Commun. Monogr. 84, 365–384.

Ringelman, K.M., Eadie, J.M., Ackerman, J.T., Sih, A., Loughman, D.L., Yarris, G.S., McLandress, M.R., 2017. Spatiotemporal patterns of duck nest density and predation risk: a multi-scale analysis of 18 years and more than 10 000 nests. Oikos 126, 332–338.

Roberts, G., 1996. Why individual vigilance declines as group size increases. Anim. Behav. 51, 1077–1086.

Sanguinetti-Scheck, J.I., Brecht, M., 2020. Home, head direction stability, and grid cell distortion. J. Neurophysiol. 123, 1392–1406.

Schenkel, R., 1966. On sociology and behaviour in impala (*Aepyceros melampus*) Lichtenstein. Afr. J. Ecol. 4, 99–114.

Schmidt, P.A., Mech, L.D., 1997. Wolf pack size and food acquisition. Am. Nat. 150, 513–517.

Schweinfurth, M.K., 2020. The social life of Norway rats (*Rattus norvegicus*). eLife 9 e54020.

Skinner, M., Miller, N., 2020. Aggregation and social interaction in garter snakes (*Thamnophis sirtalis sirtalis*). Behav. Ecol. Sociobiol. 74, 1–13.

Song, C., Qu, Z., Blumm, N., Barabasi, A., 2010. Limits of predictability in human mobility. Science 327, 1018–1021.

Sors, F., Tomé Lourido, D., Parisi, V., Santoro, I., Galmonte, A., Agostini, T.A., Murgia, M., 2019. Pressing crowd noise impairs the ability of anxious basketball referees to discriminate fouls. Front. Psychol. 10, 2380.

Stacey, P.B., 1986. Group size and foraging efficiency in yellow baboons. Behav. Ecol. Sociobiol. 18, 175–187.

Stöwe, M., Bugnyar, T., Loretto, M.C., Schloegl, C., Range, F., Kotrschal, K., 2006. Novel object exploration in ravens (*Corvus corax*): effects of social relationships. Behav. Process. 73, 68–75.

Stuchlik, A., Radostova, D., Hatalova, H., Vales, K., Nekovarova, T., Koprivova, J., Svoboda, J., Horacek, J., 2016. Validity of quinpirole sensitization rat model of OCD: linking evidence from animal and clinical studies. Front. Behav. Neurosci. 10, 209.

Szechtman, H., Sulis, W., Eilam, D., 1998. Quinpirole induces compulsive checking behavior in rats: a potential animal model of obsessive-compulsive disorder (OCD). Behav. Neurosci. 112, 1475–1485.

Taube, J.S., Muller, R.U., Ranck Jr, J.B., 1990b. Head direction cells recorded from the postsubiculum in freely moving rats. II. Effects of environmental manipulations. J. Neurosci. 10, 436–447.

Tavares, R.M., Mendelsohn, A., Grossman, Y., Hamilton-Williams, C., Shapiro, M., Trope, Y., Schiller, D., 2015. A map for social navigation in the human brain. Neuron 87, 231–243.

Thompson, S.M., Berkowitz, L.E., Clark, B.J., 2018. Behavioral and neural subsystems of rodent exploration. Learn. Motiv. 61, 3–15.

Tierney, K.J., Lindell, M.K., Perry, R.W., 2001. Facing the Unexpected: Disaster Preparedness and Response in the United States. Joseph Henry Press, Washington DC.

Tolman, E.C., 1948. Cognitiva maps in rats and men. Psychol. Rev. 55, 189–208.

Tricoche, L., Ferrand-Verdejo, J., Pélisson, D., Meunier, M., 2020. Peer presence effects on eye movements and attentional performance Front. Behav. Neurosci. 13, 280.

Triki, Z., Wismer, S., Rey, O., Ann Binning, S., Levorato, E., Bshary, R., 2019. Biological market effects predict cleaner fish strategic sophistication. Behav. Ecol. 30, 1548–1557.

Truskanov, N., Emery, Y., Bshary, R., 2020. Juvenile cleaner fish can socially learn the consequences of cheating. Nat. Commun. 11, 1–9.

Valerio, S., Taube, J.S., 2012. Limbic system structures differentially contribute to exploratory trip organization of the rat. Nat. Neurosci. 15, 1445–1453.

Valle, F.P., 1971. Rats' performance on repeated tests in the open field as a function of age. Psychon. Sci. 23, 333–334.

van Vugt, M., 2006. Evolutionary origins of leadership and followership. Pers. Soc. Psychol. Rev. 10, 354–371.

VanderWaal, K.L., Wang, H., McCowan, B., Fushing, H., L.A., I, 2014. Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). Behav. Ecol. 25, 17–26.

Wallace, D.G., Whishaw, I.Q., 2003. NMDA lesions of Ammon's horn and the dentate gyrus disrupt the direct and temporally paced homing displayed by rats exploring a novel environment: evidence for a role of the hippocampus in dead reckoning. Eur. J. Neurosci. 18, 513–523.

Wallace, D.G., Hines, D.J., Pellis, S.M., Whishaw, I.Q., 2002a. Vestibular information is required for dead reckoning in the rat. J. Neurosci. 22, 10009–10017.

Wallace, D.G., Hines, D.J., Whishaw, I.Q., 2002b. Quantification of a single exploratory trip reveals hippocampal formation mediated dead reckoning. J. Neurosci. Methods 113, 131–145.

Wann, D.L., Hackathorn, J., 2019. Audience Effects in Sport: the Reciprocal Flow of Influence Between Athletes and Spectators, APA Handbook of Sport and Exercise Psychology. American Psychological Association, pp. 469–488.

Ward, A.J.W., 2012. Social facilitation of exploration in mosquitofish (*Gambusia holbrooki*). Behav. Ecol. Sociobiol. 66, 223–230.

Weiss, O., Segev, E., Eilam, D., 2015. Shall two walk together except they be agreed?" Spatial behavior in rat dyads. Anim. Cogn. 18, 39–51.

Weiss, O., Dorfman, A., Ram, T., Zadicario, P., Eilam, D., 2017a. Rats do not eat alone in public: food-deprived rats exchange leadership and followership in collecting baits. PLoS One 12, e0173302.

Weiss, O., Segev, E., Eilam, D., 2017b. Social spatial cognition in rat tetrads: how they select their partners and their gathering places. Anim. Cogn. 20, 409–418.

Weiss, O., Levi, A., Segev, E., Simbirsky, M., Eilam, D., 2018. Saptio-temporal organization during group formation in rats. Anim. Cogn. 21, 513–529.

Whishaw, I.Q., Gharbawie, O.M., Clark, B.J., Lehmann, H., 2006. The exploratory behavior of rats in an open environment optimizes security. Behav. Brain Res. 171, 230–239.

Winter, S.S., Koppen, J.R., Ebert, T.B., Wallace, D.G., 2013. Limbic system structures differentially contribute to exploratory trip organization of the rat. Hippocampus 23, 139–152.

Wismer, S., Pinto, A.I., Triki, Z., Grutter, A.S., Roche, D.G., Bshary, R., 2019. Cue-based decision rules of cleaner fish in a biological market task. Anim. Behav. 158, 249–260.

Yadav, C.K., Verma, M.K., Ghosh, S., 2010. Statistical evidence for power law temporal correlations in exploratory behaviour of rats. BioSystems 102, 77–81.

Yaski, O., Eilam, D., 2008. How do global and local geometries shape exploratory behavior in rats? Behav. Brain Res. 187, 334–342.

Zadicario, P., Ronen, S., Eilam, D., 2007. Modulation of quinpirole-induced compulsive-like behavior in rats by environmental changes: implications for OCD rituals and for exploration and navigation. BMC Neurosci. 8.

Zajonc, R.B., 1965. Socialfacilitation. Science 149, 269–274.

Zor, R., Fineberg, N., Eilam, D., Hermesh, H., 2011. Video telemetry and behavioral analysis discriminate between compulsive cleaning and compulsive checking in obsessive-compulsive disorder. Eur. Neuropsychopharmacol. 21, 814–824.