

# Social spatial cognition in rat tetrads: how they select their partners and their gathering places

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Received: 15 August 2016/Revised: 23 November 2016/Accepted: 3 December 2016/Published online: 17 December 2016  
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**Abstract** Spatial organization is an extensively studied field, in which most of the research has been on how the physical environment is perceived and conceived. There is a consensus that physical attributes such as environment geometry and landmarks are key factors in shaping spatial cognition. Nevertheless, the numerous studies of spatial behavior have usually been carried out on individuals, thereby overlooking the possible impact of the social environment. In the present study, rats were exposed to an unfamiliar open-field, first alone and then in tetrads of unfamiliar individuals, in order to monitor and analyze when and how their individual spatial behavior converged to a group spatial behavior. We found that the unfamiliar rats spent most of their time in companionship, first with preferred partners and ultimately as a quartet. Specifically, group formation was dynamic and gradual, with the rats first forming duos, then trios, and ultimately a quartet. Trios and quartets mostly huddled in the same specific corner that became a shared home base, from which they took solo or duo roundtrips to the arena. The present study unveils how, by means of gradual interactions among self, place, and conspecifics, four unfamiliar rats organized together their social spatial behavior.

**Keywords** Spatial representation · Exploration · Social environment · Social cognition · Group formation

## Introduction

The notion that there is a mental representation of space in the brain (“cognitive map”; Tolman 1948) has been thoroughly investigated. The process by which individuals gather spatial information on the environment and construct its internal representation is that of exploration, which in rodents is composed of frequent returns to specific locales and retracing of recently traveled paths (Eilam and Golani 1989; Eilam 2014). Locales and paths are usually established by referring to physical attributes of the environment, such as geometry (Cheng 1986, 2005, 2008; Gouteux et al. 2001; Cheng and Newcombe 2005; Yaski and Eilam 2008; Ben-Yehoshua et al. 2011; Portugali et al. 2011), landmarks (Collett 1996; Etienne et al. 1996, 2000; Cheng and Spetch 1998; Sovrano et al. 2005), and beacons (Collett 1996; Pearce et al. 2001; Gallistel and Matzel 2013; Eilam 2014). Soon after being introduced into an unfamiliar environment, rodents establish a “home base,” which constitutes a terminal for roundtrips of exploration in the environment (Eilam and Golani 1989). Thus, spatial behavior in rodents is organized in reference to the home base (Eilam and Golani 1989), which is frequently established near a salient landmark (Hines and Whishaw 2005; Clark et al. 2006; Yaski and Eilam 2008). Similarly, in humans, the home constitutes a hub of spatiotemporal behavior, with over 50% of daily trips being home base generated (Golledge 1999). Indeed, data from 50,000 mobile phone users over a 3-month period revealed that “despite our deep-rooted desire for change and spontaneity, our daily mobility is, in fact, characterized by a deep-rooted regularity” (Song et al. 2010). Such regularities reflect the mental representation of the environment, which is constructed by means of exploration when encountering an unfamiliar environment.

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Despite the extensive research, spatial behavior has been studied mostly in lone animals, scrutinizing the impact of the physical environment on spatial behavior of individuals while overlooking the impact of its counterpart—the social environment. In the last few years, however, the latter perspective of spatial cognition has been gaining ground, in studies of multiple individuals (e.g., Maaswinkel et al. 1997; Mintz et al. 2005; Keller and Brown 2011; Ohayon et al. 2013; Weissbrod et al. 2013; Shemesh et al. 2013; Shi et al. 2013, 2015; Weiss et al. 2015; Wang et al. 2015; Dorfman et al. 2016). In dyads of rats, it was suggested that individuals organize their spatial behavior according to both their physical and social environment, with the social environment being as important as the physical environment in shaping spatial cognition (Weiss et al. 2015; Dorfman et al. 2016). While most of the above studies dealt with the basic form of a group—a dyad, the present study focused on a more complex social environment—exploration in a tetrad of rats.

Along with the discovery of place cells (O'Keefe and Dostrovsky 1971), which are neurons that fire according to the animal's position, O'Keefe and Nadel (1978) suggested that the cognitive map is encoded in the hippocampus. This stimulated extensive research into the role of the hippocampus in spatial navigation of lone animals, revealing how additional spatial information is encoded in the brain by head-direction cells (Taube et al. 1990a, b), grid cells (Hafting et al. 2005); border cells (Solstad et al. 2008), and speed cells (Kropff et al. 2015). While these were described in lone rats, it was recently suggested that the social space too is encoded in the hippocampus and that the cognitive map comprises an integrated representation of both the physical and social environments (Eichenbaum 2015; Schiller et al. 2015; Tavares et al. 2015). This is in line with a previous study, suggesting that social skills and spatial skills in human navigation are linked (Shelton et al. 2012). Notably, compared to lone exploration and navigation, traveling with companions is more demanding, requiring the organization of spatial behavior in reference to both the physical and the social environments (Dorfman et al. 2016). Moreover, the perception and conception of these two environments are arguably different. The physical environment is suggested to be perceived in allocentric and Cartesian spatial frames of reference, whereas the social environment is considered to be perceived in egocentric and polar frames of reference (Eichenbaum 2015; Tavares et al. 2015). Individuals thus confront a higher complexity when they need to organize spatial behavior according to both the location of physical attributes of the surrounding and the location of other individuals. Indeed, it was also suggested that social and spatial factors were both important in primate cognitive evolution and presumably coevolved (Proulx et al. 2016). This notion emphasizes

spatial cognition and social cognitions as strongly associated, and therefore, spatial behavior needs also to be studied in a social context—in a group of animals. Accordingly, the scope of the present study encompassed spatial social cognition in tetrads of rats (interactions among self, place, and group).

A group is defined as a social organization of two or more individuals that are interconnected through social relationships (Forsyth 2006). Group formation is a gradual process, which was suggested to be based on four stages: “forming,” “storming,” “norming,” and “performing” (Tuckman 1965). In forming, individuals are focused mostly on themselves; in storming, they interact in order to establish the character and leadership of the group; in norming, conflicts are resolved and subgroups begin to emerge; and in performing, the group is united and focused on a main common goal (Tuckman 1965). Group formation is thus a gradual process, in which time is a major factor (Ancona et al. 2001; Arrow et al. 2004; Ballard et al. 2008). Notably, the hippocampus also maps the temporal organization in allocentric space, indicating that the sense of time is another dimension of encoding spatial information (Eichenbaum 2014). Even more, the two magnitudes, time and space, might share a cognitive and/or neural basis (Walsh 2003). Group formation is dynamic not only in the temporal aspect but also in the sense that it may be reversible. For this, the term “fission–fusion dynamics” is used in order to describe the formation and deformation of groups and subgroups (Bernstein and Mason 1963), as described in social primates (Symington 1990; van Schaik 1999; Amici et al. 2008; Ramos-Fernandez and Morales 2014), in many social carnivores (Popa-Lisseanu et al. 2008; Smith et al. 2008) and herbivores (Cross et al. 2005; Couzin 2006; Sundaresan et al. 2007). Understanding the dynamics of group formation by a tetrad of stranger rats comprised an additional aim of the present study. Specifically, we sought to decipher their group dynamics and to understand how being part of a group affects the spatial cognition and organization of individuals.

## Materials and methods

### Animals

Male Sprague–Dawley rats ( $n = 52$ ; age 3–4 months; weight 300–400 g) were housed in a temperature-controlled room ( $22 \pm 1$  °C) under a 12-/12-h light/dark cycle (dark phase 8:00 to 20:00). Rats were held in standard rodent cages ( $40 \times 25 \times 20$  cm; two rats per cage) with sawdust bedding and ad libitum access to fresh water and standard rodent chow. Each rat was marked with a

waterproof marker on its tail and acclimated to handling—15 min a day, for 1 week.

### Apparatus

Rats were tested in a  $6 \times 5.6$  m open-field, painted light gray, and illuminated with four cool white-toned LED projectors (65 W each), which were sufficient to enable automated color-based tracking (by Ethovision XT 10, Noldus Information Technologies, NL), but also subtle enough to avoid discomfort to the rats. Trials were recorded by four equispaced Mintron MTV-73S85H color CCTV cameras, placed 2.5 m above the open-field, each providing a top view of a different quarter of the arena. The four images were integrated into one video image of the entire arena, from which rats were tracked at a rate of five frames per second.

### Procedure

Forty minutes before testing, rats were brought to a room adjacent to the test room, and their backs were dyed in orange, yellow, turquoise, or red (by “Manic Panic,” NYC vegan hair dyes), enabling the tracking system to discriminate among them.

Testing was carried out in an illuminated open-field (see “Apparatus”) during the dark phase of the rats’ dark/light cycle. The rationale was to test the rats when they are more active, while also allowing enough light to enable the tracking system to distinguish among the four rats, as this was a prerequisite for the present study. Forty rats formed the test group (ten tetrads of cross-caged mates). Each rat first underwent a 30-min trial alone (“pre-tetrad” trial) and a week later was tested again, this time with three other rats from different cages (“tetrad” 30-min trial). The tetrad trial thus comprised ten sets of four rats that were strangers to each other. Another 12 control rats were each tested alone in two repeated trials (at 1-week interval) in order to eliminate a possible effect of repeated exposure to the open-field, thereby isolating the mere impact of the group. Rats were gently placed by the experimenter in the center of the open-field, and tracking began when the experimenter left the arena. At the end of the trial, rats were returned to their cages and the open-field was mopped with soap and water in order to neutralize odors.

### Data acquisition and analysis

The following parameters were extracted directly from “Ethovision” for further analysis with “Microsoft Excel 2010”:

1. *Distance traveled* The cumulative metric distance (m) traveled over 30 min.
2. *Proximity* The duration of time (s) that rats spent at a distance of 0.5 m or less in proximity to each other. In the case of three or four rats, each rat was within proximity of  $<0.5$  m to at least one other rat, and a “sequential” quartet could spread out over a length of 1.5 m. The threshold was set to 0.5 m since this is twice the approximate length of a rat, including its tail. Based on this parameter, the social networks in tetrads of rats were generated utilizing Gephi software for exploring and manipulating networks (Bastian et al. 2009).

In addition, the following parameters were calculated with “Microsoft Excel 2010” from the  $X$ – $Y$ – $T$  coordinates of “Ethovision”:

1. *Time in zone* The arena was virtually subdivided into 100 equal squares (approximately  $0.6 \times 0.6$  m each), and the accumulated duration (s) in each square was calculated for each rat, in four different social states (solo, duo, trio, or quartet). Since rats traveled mostly along the 36 perimeter squares (including four corner squares), the statistical analysis was performed for these squares only, particularly for the top ten perimeter squares at which rats spent the longest accumulated time.
2. *Home base behavior* For each rat, the zone where it stayed for the longest cumulative duration was defined as its home base.

### Statistics

In order to uncover the impact of the presence of companions on spatial behavior, data were compared by means of a two-way analysis of variance (ANOVA) with repeated measures, where the between-group factor was test group versus control group, and the within-group factor was the trials (lone vs. tetrad trials in the test group and first vs. second lone trials in the control group). These tests were followed by an Unequal-N HSD post hoc test. To analyze the differences in the time that rats in the tetrad trial spent in proximity to each other, data were compared by means of a one-way ANOVA with repeated measures, followed by a Tukey HSD post hoc test. None of the tested parameters deviated significantly from normal distribution. In comparing proportions, data were converted using arc sinus of square root transformation. Alpha level was set to 0.05. All statistical analyses were performed in “STATISTICA 8” (Statsoft, UK).

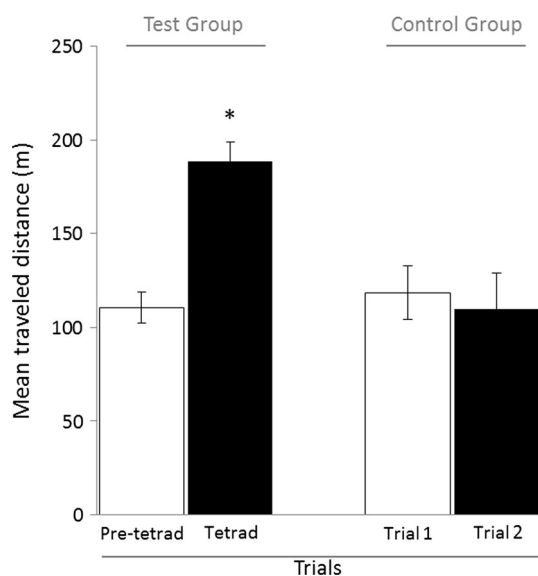
## Results

### Rats were more active in the tetrad trials than in the lone trials

Figure 1 depicts the mean traveled distance that rats accumulated in each trial (pre-tetrad, tetrad, and the two repeated control trials). A two-way ANOVA with repeated measures revealed a significant difference in the accumulated traveled distance between groups (test/control;  $F_{1,50} = 4.22$ ,  $p = 0.045$ ), within group–between trials (first trial/repeated trial;  $F_{1,50} = 17.27$ ,  $p < 0.001$ ), and a significant trial  $\times$  group interaction ( $F_{1,50} = 27.22$ ,  $p < 0.001$ ). An Unequal-N HSD post hoc test confirmed that, when tested in tetrads, rats were more active than when tested as individuals, implying that the presence of other rats facilitated activity.

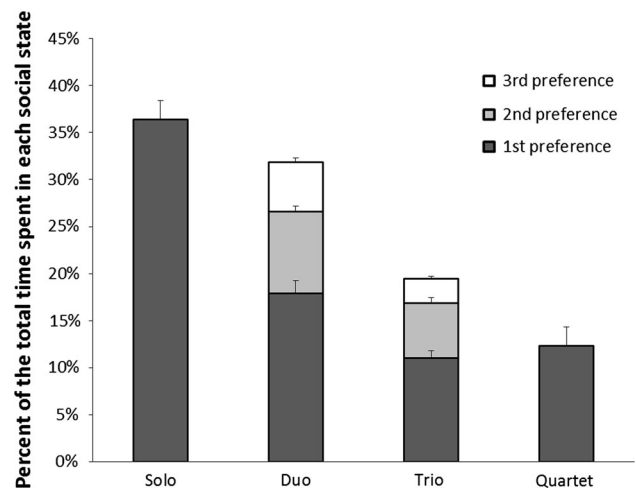
### Rats mostly maintained companionship with specific partners

When tested in a tetrad, a rat could choose either to stay alone or with conspecifics (one or more). We found that rats spent significantly more time in a proximity of up to 0.5 m with at least one conspecific, than alone

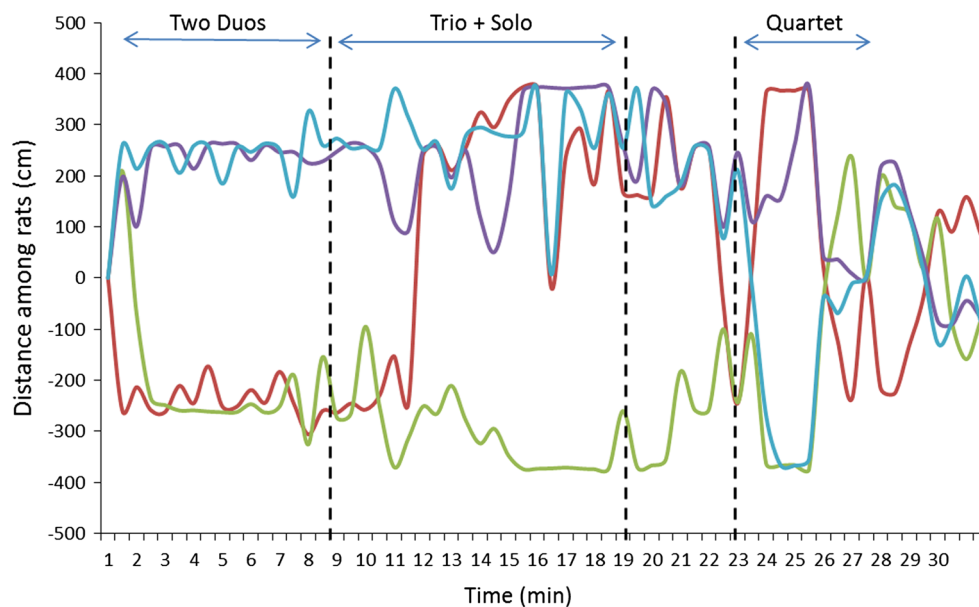


**Fig. 1** Mean ( $\pm$ SEM) traveling distance that rats accumulated during each trial. As shown, rats traveled longer distance when tested in tetrads (left black bar), compared to their previous lone trial (“pre-tetrad” trial; leftmost white bar). In other words, rats were more active when tested as part of a group than when tested alone. To confirm that this was an effect of socialization rather than of repeated testing, a control group (right inset) of rats was tested in two subsequent lone trials. These rats maintained a similar level of activity in both trials, which validated that the increased activity in the tetrad trial was a result of socializing

(1146  $\pm$  39 s vs. 653  $\pm$  39 s; paired  $t$  test:  $t_{40} = 6.45$ ,  $p < 0.001$ ). Moreover, as depicted in Fig. 2, rats spent significantly more time in duos than in trios, and in trios more than in quartets (one-way ANOVA with repeated measures:  $F_{7,273} = 69.28$ ;  $p < 0.001$ ). Notably, socializing was dynamic, as illustrated for one representative tetrad in Fig. 3. As shown, when introduced into the arena, the rats immediately split into two duos. After 8 min, one rat abandoned its mate and joined the other duo to form a trio. During an additional 10 min, the four rats became spatially separated into a trio and a solo rat, and later on (26 min after the beginning of the trial), a quartet was formed. Overall, rats first formed duos, then trios, and ultimately a quartet, while a solo state was either the initial outcome of trio formation or a solo trip away from and back to the partner(s). Indeed, a one-way ANOVA with repeated measures for the ten tetrads revealed a significant difference between the latencies to forming a duo, trio, or quartets (25  $\pm$  6 s, 123  $\pm$  57 s, and 586  $\pm$  180 s, respectively;  $F_{2,20} = 9.22$ ;  $p < 0.001$ ). Four unfamiliar rats thus tended to stay together with one or more partners and to gradually form a quartet.



**Fig. 2** Mean ( $\pm$ SEM) percent of trial time that rats spent in proximity to one another (all bars except the leftmost one) as opposed to staying alone (the leftmost bar). As shown, rats spent more time in proximity to at least one partner, than alone (64% in proximity vs. 36% alone). Moreover, a Tukey HSD test revealed that rats spent more time in duos than in trios, and more time in trios than in tetrads. Scrutiny of the duo and trio states revealed that rats preferred specific partners with which to form duos and trios. This is shown by the stacked bars that depict the most preferred partners (bottom, dark gray bar), the second most preferred partners (central, light gray), and the least preferred partners (upper, white bar). In each, there were significantly favorite partners (first preference) compared with the others (one-way ANOVA with repeated measures;  $F_{2,78} = 61.51$ ;  $p < 0.001$ ; and  $F_{2,78} = 54.99$ ;  $p < 0.001$  for duo and trio, respectively)



**Fig. 3** Group formation in an exemplary tetrad. In order to represent the continuous distance alternations among the rats, we set an imaginary reference point, which was the average distance among the four rats (the momentary “group center mass” of the four rats) at 1-min intervals. Since the rats traveled almost exclusively along the walls, we considered a rat located counterclockwise to the reference point as being in a “negative” distance from the reference point and a rat located clockwise away from the reference point as being in a “positive” distance. In this figure, we depicted the distance between

the reference point and each of the rats for each time interval. Accordingly, the representation is of the distance among the four rats regardless of their location in the arena. As shown, group formation was a gradual process: first two duos were formed, as seen in the adjacency of *blue* and *purple*, and the *green* and *red* rats, while the two duos stayed at approximately 4 m away of each other. Approximately 10 min after the beginning of the trial, a trio was formed, and ultimately, approximately 16 min later, the quartet was formed

### Social networking: behavioral traits and grouping

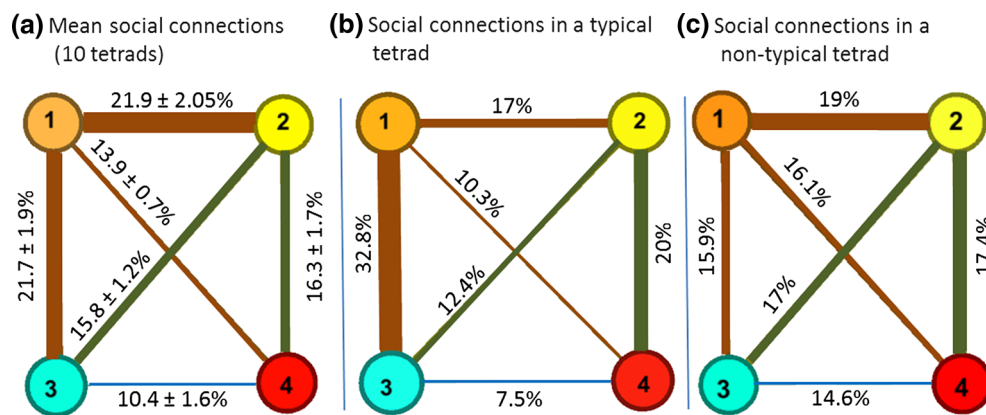
As implicit in the preference for specific partners (Fig. 2), one rat could display intensive social interactions with other rats, whereas another rat could display fewer interactions. To highlight this aspect of the tetrad, the time that each rat spent with each of the other rats, along its 30-min trial, is represented graphically as a social network. Each of the four rats is depicted as a circle, and the proportion of time spent with each partner is depicted along the line connecting the partners (Fig. 4). As shown, there was one rat (“1”) that spent a large percentage of the time with the two other rats (“2” and “3”), while these two rats did not spend as much percentage of the time with each other. The fourth rat (“4”) was a “solo rider,” spending a lower percentage of the time with the other three rats. Overall, the social network of all ten tetrads displays the form of three rats with strong connections and one with weak connections (as also illustrated in the exemplary tetrad in Fig. 3). Scrutinizing the social network of all tetrads revealed variants of this general schema, as illustrated in Fig. 4b, c. Nevertheless, while the variation was in the strength of connection between specific rats, the general pattern in most tetrads was of three linked rats and one that was less connected.

### How they shared the arena

In order to generalize the spatial sharing of the arena by all the different tetrads, the arena was virtually subdivided into a grid of 100 equal zones, and the time spent in each zone by rats when traveling solo, in duos, in trios, and in quartets was calculated. The mean duration for each social state is depicted in Fig. 5 for all tetrads. As shown, in all social states, rats traveled mostly along the perimeter of the open-field. Since the time spent in center zones was infinitesimal, the following analysis focused only on the perimeter zones. As shown, while solo rats spent some time at the entire perimeter zones, spatial behavior of duos began to converge to three of the four corners, with one corner (and the nearby zones) dominating the other two. This trend was further augmented in trios and quartet, with the quartet spending most of the time in the same corner (Fig. 5).

To demonstrate the manifestation of common place preference for each social state, we ranked from high to low the time spent at the top ten perimeter zones and compared the results with the same ranking in the second control trial of lone rats (Fig. 6). The second control trial was specifically chosen, since in this way both these rats and the tetrad rats were already familiar with the arena. A two-way ANOVA with repeated measures revealed a

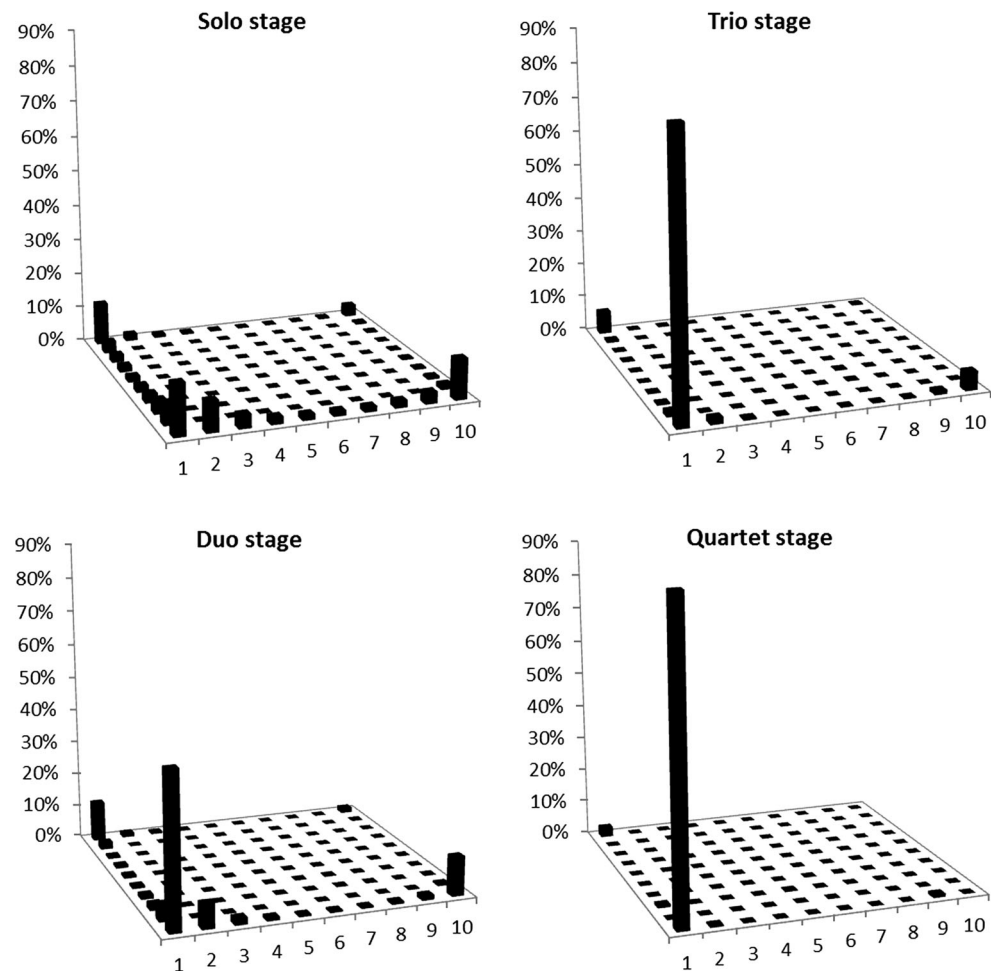




**Fig. 4** **a** Mean connections in the ten tetrads, with the rats in each tetrad ranked from high to low according to the cumulative time spent with others. Accordingly, rat “1” spent the longest duration with others, whereas rat “4” spent the shortest time with others. It should be noted that each connection between two rats consists of all the interactions between them, including triadic and tetradic interactions. As shown, the general pattern of all tetrads was that rat “1” had a

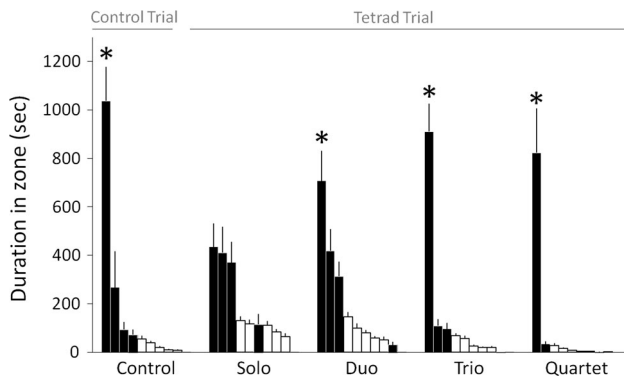
strong social affiliation with rats “2” and “3,” whereas rat “4” had a weak social affiliation with all other three rats. This implies that the general social pattern of the tetrads was of three rats socializing and one “solo rider.” Indeed, this was the pattern in eight out of the ten tetrads. **b** Exemplary social network pattern that characterized specific tetrad which followed the general pattern. **c** Exemplary social network pattern of a tetrad in which all rats were almost equally connected

**Fig. 5** Mean duration (as a percent of the duration in each social state) of the time spent in each zone in each social state (solo, duo, trio, quartet). In eight out of the ten tetrads, rats spent the longest duration at the same corner. Two other tetrads inhabited another corner, and their data were therefore rotated to match that of the other eight tetrads. Then, the mean duration of staying at each zone was calculated as percent of the total duration that the rats spent in each social state (solo, duo, etc.). As shown, rats spent their entire time along the walls, especially in the corners (each corner constitutes one  $0.6 \times 0.6$  m). Furthermore, the group was formed mainly in one specific corner, culminating in a huddle of four rats in that favorite corner



significant difference in the time that rats spent in each social state (solo, duo, trio, quartet, and control individuals;  $F_{4,167} = 7.15$ ;  $p < 0.001$ ), a significant difference in the

time spent by each social state in each zone ( $F_{9,1503} = 54.92$ ;  $p < 0.001$ ), and a significant interaction between these social states and ranked zones



**Fig. 6** Duration of time spent at the top ten perimeter zones. Since rats spent negligible time in the center zones (see Fig. 5), we ignored them and for each rat ranked the 36 perimeter zones from high to low, according to the time spent in each zone. Since the time spent in many of these zones was almost nil, statistical analysis included only the ten top-ranked zones of each rat. The time spent in each of these zones in each social state (solo, duo, trio, quartet) is depicted in the figure. Data of the control group which is depicted for second lone trial had only the solo state since each control rat was tested alone. Corner zones are depicted as *dark bars* (■) and other perimeter zones as *open bars* (□). Asterisks label zones in which the duration was significantly greater than the time spent in any other zone in this social state. This zone, at which rats spent significantly more time, is considered as a “home base” zone. As shown, in the solo state of the tetrad trial there was no distinct home base, whereas in the duo, trio, and quartet states, a home base was evident as corner zone in which the rats spent more time than in any other zone. This implies that rats were not independently organizing their spatial behavior, but rather coordinating it with at least one partner. In the control lone trial (leftmost set of bars), home base was apparent, emphasizing that the rats in the tetrad trial did not have home base in a solo state since they shared the home base with partners. Therefore, while control lone rats organized their spatial behavior according to physical factors, rats in tetrads also organized their spatial behavior in relation to the social environment

( $F_{36,1503} = 6.04$ ;  $p < 0.001$ ). An Unequal-N HSD post hoc test confirmed that rats had a favorite corner in which duos, trios, and quartets stayed. This corner functioned as a hub (“home base”) from which rats continued to perform solo or duos roundtrips. Notably, however, in the solo state within the tetrad trial, rats had no distinct favorite corner. This differs from the behavior of the control nonsocial trials (see control lone trial in Fig. 6). Thus, while rats in the lone control trial had an apparent home base, rats in the tetrad trial did not exhibit home base behavior when traveling alone. Specifically, they did not spend significantly more time in a specific place than in other places. Nevertheless, home base behavior, as manifested by extended duration of staying in one place compared with other places, was manifested and shared with at least one partner (Fig. 5).

Since the home base is the “organizer” of spatial behavior, rats tested in tetrads were spatially organized according to their mates, whereas lone rats were organized only according to the physical environment. Notably, there

was no systematical order of establishing the home base (home corner) among the tetrads; in four tetrads it was one rat that settled there first, in three tetrads two rats initially settled at the home corner, in two tetrads three rats settled together first, and in one tetrad all four rats settled together from the beginning at one corner. The pioneering rats that were first to settle at the home base did not differ from the others in their traveled distance, time spent in the home corner, and time spent in proximity to any other rat (data not shown).

## Discussion

In the present study, rats were tested in a large open-field, first alone and then in tetrads with unfamiliar partners. We found that the presence of other rats augmented activity (“social facilitation”), as reflected in the greater travel distance that rats accumulated when tested in tetrads compared to their lone trials. Rats in the tetrad trials spent most of their time in companionship with at least one partner. Specifically, rats spent more time in duos than in trios and in trios more than in quartets. The process of group formation was dynamic and gradual: the rats first formed duos, then trios, and ultimately a quartet. Solo travel bouts were either transitional bouts toward the formation of a huddle, or sporadic solo roundtrips from the huddle. Rats showed a preference to stay in proximity to certain specific partners over others. Moreover, in each tetrad there was an “outsider rat” that was less socially involved with the other three rats. Duos, trios, and quartets were formed mostly in a specific corner that functioned as a home base, from which the rats took solo or duos roundtrips into the arena. In other words, when tested in tetrads, the rats’ spatial behavior was also organized according to the location of their mates rather than merely according to the physical environment. Altogether, the present study extends our previous study with dyads by demonstrating when, where, and how small groups (tetrads) are formed, including partner exchanges within groups. In the following discussion, the above processes are referred to in the context of three general questions that underlie social spatial cognition: With whom, when, and where to socialize?

### With whom to socialize?

When tested in tetrads, our rats first formed duos, then trios, and ultimately a quartet. In a previous study, it was found that when exposed to an acute stress, four rats immediately formed a huddle (Bowen et al. 2012). Although huddling is a typical response to threat in social rodents (Rabi and Eilam unpublished data), this was not the

case in our rats, which were not exposed to any particular stressor during testing and were familiar with the apparatus and test conditions other than the social factor. We also found that rats in tetrads had specific partners that they favored over others. Specifically, rats tended to form subgroups of duos and trios with specific partners. However, each social state was transient, and the rats exchanged partners, forming and deforming duos, trios, and quartets (“fission–fusion” dynamics; Kummer 1971). Notably, the fission–fusion dynamics were suggested to be based mainly on dyadic interactions (Ramos-Fernandez and Morales 2014; Smith-Aguilar et al. 2016). Since the acquaintance with new partners is a prerequisite for grouping, we suggest that changing partners among duos constitutes the principal process in the formation of small groups. Moreover, based on the balance theory (Heider 1958), stable duos lead to stable trios and, further on, to the formation of larger groups, since a pair of individuals that are highly attracted to one another tend to be also highly attracted to other individuals by virtue of their similar preferences (Newcomb 1961). Similarly, in order to form a trio, one rat had to temporarily leave its partner and join the other duo. Later on, this rat connected between its original partner and the other duo, resulting in the formation of the quartet. This process was also evident in the social network of tetrads, in which three rats were almost equally connected and one rat was an “outsider,” spending most of its time alone. Altogether, four stranger rats first form duos with a favorite partner, they then form trios, with a significant preference for specific partners in the trio and one outsider rat, and ultimately they form a quartet.

### When to socialize?

The present findings demonstrate that the formation of small groups (quartets) was gradual: the four stranger rats usually began by forming two duos; after about 10 min, they formed a trio; and ultimately, almost at the end of the trial, they formed a quartet. Indeed, time is a key factor in group dynamics (Ancona et al. 2001; Arrow et al. 2004; Ballard et al. 2008). This raises the question of what could be the advantage of the gradual formation of the quartet. In a previous study, we found that rats in dyads coupled their behavior to travel together (Weiss et al. 2015). The coupled spatial behavior turned out to be more complex than the structured spatial behavior of the same rats when tested alone (Dorfman et al. 2016). In other words, while lone rats had to organize their spatial behavior only in reference to the physical environment, when the same rats were tested with a partner, they had to organize their spatial behavior in reference to the physical environment as well as to a moving point of reference—the other rat (the social environment). Explicit in this addition of a moving focal

component is the elevated complexity (Bar-Yam 1997) imposed on social spatial behavior compared to that of lone rats. Theoretically, adding three partners in the present study should have further increased the social complexity with which the rats had to deal when orienting in time and space. Another source of increased complexity in social spatial behavior is that of different frames of reference: Cartesian and allocentric for the physical space; polar and egocentric for the social space (Eichenbaum 2015; Tavares et al. 2015). Notably, despite the presumed higher complexity, spatial behavior of the rat tetrads was not chaotic, but well organized in time, space, and within the group. Accordingly, we suggest that the advantage of the gradual exploration of both the physical and the social environments is reducing the chaos that might otherwise emerge from the more complex social environment that comprises several partners. In other words, gradual socializing, starting with just one partner and then getting more complex from there, could be a means to initially reduce the complexity of social spatial behavior.

### Where to socialize?

Spatial behavior in lone rodents is composed of a set of roundtrips to a home base, which a rat establishes soon after being introduced into an unfamiliar environment (Eilam and Golani 1989; Eilam 2014). The home base is usually established in a corner, or near a salient landmark (Hines and Whishaw 2005; Clark et al. 2006; Yaski and Eilam 2008). Furthermore, it was previously described that rat dyads share a home base (Mintz et al. 2005; Weiss et al. 2015; Dorfman et al. 2016). Similarly, the present study revealed that rats in quartets became spatially organized in relation one of the corners of the open-field. Specifically, soon after being introduced with unfamiliar partners into the arena, the rats split into two duos, with each duo selecting one corner as a temporary home base from which they took either solo or duo roundtrips. Once a trio and then a quartet had been formed, the rats shared the same corner as a home base, from which they took solo, duo, trio, and occasionally even quartet roundtrips. Overall, the present results demonstrate that spatial behavior of rats in tetrads was also organized according to the location of their mates (the social environment) rather than merely according to the physical attributes of the environment, as in lone rodents.

### Conclusion

Groups are considered as an important component of social life, in which a group constitutes “two or more individuals that are connected through social relationships with one another” (Forsyth 2006). In the present study we found that



four stranger rats increased their activity compared to their behavior when alone (“social facilitation”; see Weiss et al. 2015) and gradually formed a group, ultimately huddling together in one corner (home base) and taking roundtrips, typically solo or duo, out of and back to that home corner, thus organizing their spatial behavior in accordance with the location of their partners as well as to the physical environment. This connection between social and spatial behavior could be the behavioral expression of recent studies, which revealed that in addition to mapping the physical environment, the social environment is also encoded onto the hippocampus (Eichenbaum 2015; Tavares et al. 2015). This social spatial information, together with the sense of time, which is another self-generated dimension mapped by the hippocampus (Eichenbaum 2014), reflects the multidimensional and high complexity of social spatial behavior and its importance for life. Indeed, it was suggested that by creating a network of memories, the hippocampus supports our ability to “navigate life” and solve problems in many domains (Eichenbaum 2014). While extensive knowledge and research exist on how the physical environment, but not on how the social environment, shape spatial behavior, the present study offers another small step toward understanding the currently unfamiliar ground of social spatial cognition.

**Acknowledgements** This study was supported by the *Israel Science Foundation* Grant 230/13 to DE. We are grateful to Naomi Paz for language editing. DE is a Visiting Professor at the Department of OTANES, University of South Africa.

#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical standards** This study and the maintenance conditions for the rats were carried out under the regulations and approval of the Institutional Committee for Animal Experimentation at Tel-Aviv University (permit # L-14-026).

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