



# Spatio-temporal organization during group formation in rats

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## Abstract

In the present study, the dynamic process of group formation in eight unfamiliar rats was followed in order to reveal how the group becomes oriented together in time and space, in light of the complexity that accompanies grouping. The focus was on who, where, and when joined together. We found that rats preferred to be in companionship over remaining alone, with all the rats gradually shifting to share the same location as a resting place. Group formation can be viewed as a tri-phasic process, with some rats gradually becoming more social than others, and thus playing a key role in group formation. Starting with seemingly independent traveling, the rats gradually converged to share the same location as a terminal (home base) for roundtrips in the arena. Because such a terminal is considered as the organizer of an individual's spatial behavior, the shared home-base location may be viewed as the organizer of spatial behavior of the entire group. Despite huddling together, the rats continued to travel alone or in duos throughout the 3 h of testing. We suggest that resting together and traveling alone or in duos enabled the maintenance of communal relationship while reducing the complexity involved in traveling in relatively large groups. Taken together, the present results demonstrate the dynamic process during which unfamiliar rats shift from independent to group spatial behavior.

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

“Coming together is a beginning; keeping together is a progress; working together is a success”—Henry Ford

## Introduction

Representation of the living space was termed ‘cognitive map’ by Tolman (1932, 1948), who suggested that rats, and by analogy humans, construct an internal representation of the environment. A few decades later, this abstract representation was extended to the neural mechanisms that control

spatial behavior, with the suggestion that during exploration, spatial information is encoded in 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, discovering place cells (O’Keefe and Dostrovsky 1971), grid cells (Hafting et al. 2005), head-direction cells (Taube et al. 1990a, b), border cells (Solstad et al. 2008) and speed cells (Kropff et al. 2015) as the building blocks of spatial representation. The above process of transforming an abstract behavioral concept to its controlling neural mechanism, however, focused on lone animals. The present study focused on the spatial behavior of groups of rats, with the hope that it will attract the attention to changes that might occur in the activity of the controlling mechanisms once companions are present.

Focusing on the behavior of lone individuals overlooks the impact of the social environment. Clearly, solitary animals usually avoid conspecifics whereas social animals are attracted to their neighbors for staying or traveling together with them (Partridge et al. 1980; Krause and Ruxton 2002; Couzin et al. 2002). Moreover, considering the major costs and benefits of a spatial position within a group (Krause

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Omri Weiss and Anat Levi equally contributed in all phases of this study.

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1994), individuals in groups must orient in relation to both the social and physical environments. For example, a high-ranking individual may exert a major impact on the spatial behavior of other individuals. In line with the theoretical perspective of ‘embodied cognition’ (Varela et al. 1991), further studies have revealed that spatial representation extends to the social space by mapping social relations (Tavares et al. 2015; Eichenbaum 2015); and that by integrating declarative and spatial information, meaningful representations of experiences are created (Chidambaram and Bostrom 1997). Spatial social information is therefore an integral part of spatial representation and, when traveling, one may follow, avoid, or move independently of companions.

When an individual rodent is introduced into an unfamiliar environment it soon chooses a home base, a location from which it takes almost exclusively roundtrips throughout the area. The outbound segments of roundtrips are slow and interrupted, while the inbound segments are fast and continuous (Eilam and Golani 1989). The home base is thus the organizer of the spatio-temporal behavior of individual rodents. When a dyad of rodents is tested in an open field, they establish a shared home base in which they rest together and from which they take solo or duo roundtrips. Interestingly, when traveling together, rat dyads continuously interact and move almost as if they are connected by a string (Weiss et al. 2015). Likewise, the spatial behavior of individuals when tested in dyads was revealed as more complex compared to the spatial behavior of the same individuals when tested alone. Indeed, when traveling alone a rat has to organize its spatial behavior only in relation to the physical environment, whereas in dyads it has to organize it in relation to both the physical and social environments (Dorfman et al. 2016). Thus, the addition of a moving focal component presumably imposes an elevated complexity (Bar-Yam 1997) on spatial behavior compared to that of lone rats. Theoretically, adding more partners should further increase the social complexity with which an animal needs to deal when orienting in time and space. Altogether, individuals in a group must become organized in time and space according to both the social and physical environment, and more and more studies are being published on this perspective of spatial behavior (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; Wang et al. 2015; Dorfman et al. 2016; Weiss et al. 2017a, b). Nevertheless, these past studies have mostly been limited to dyads or very small groups. In the present study, groups of eight unfamiliar rats were tested in an open field, in order to understand how individuals become organized in time and space as part of a group, with the high socio-spatial complexity that accompanies being in a group.

In light of the above, our working hypothesis was that unfamiliar rats, which are social animals, will be attracted

to one another and consequently have to adjust their spatial behavior and coordinate it with their group-mates. They are expected to share their resting places, as found in the aforementioned studies with dyads, triads, and quartets. However, it is not clear whether they will travel together, since in the studies with triads and quartets they mostly traveled alone or in dyads. More specifically, this study presented four aims: (1) understanding how individuals become organized in time and space as part of a large group of eight rats, in terms of sharing the area and traveling together. (2) Characterizing the social dynamics among members of the group by measuring their proximity to each other. (3) Identifying whether some individuals are more sociable than others and, if so, examining how this is reflected in their activity levels. (4) Describing the process of group formation.

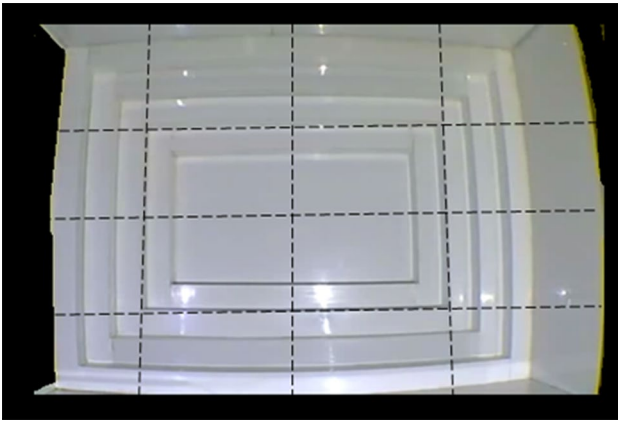
## Methods

### Animals

Male Sprague–Dawley rats ( $n = 64$ ; age 2–3 months; weight 250–300 g) were housed in a temperature-controlled room ( $22 \pm 1$  °C), under a 12/12 h dark/light cycle (dark phase: 8:00–20:00). Rats were held in rodent cages ( $50 \times 35 \times 20$  cm; four rats per cage) with sawdust bedding, and were provided with ad libitum access to fresh water and standard rodent chow. In each cage, each rat was marked on its tail with 1–4 stripes with a black waterproof marker (Artline, AU) and acclimated to handling 15 min a day for 1 week.

### Apparatus

Rats were tested in a  $180 \times 135$  cm stadium-like arena made of white Plexiglas (Fig. 1). The rectangular  $100 \times 55$  cm floor of the apparatus was delimited with five levels of concentric stairs, each 10 cm wide and 10 cm high. This unique structure provided 20 corners and a total circumference of 23.5 m of walls to travel along, all enclosed within  $180 \times 135$  cm. Since rats prefer to travel along walls (“thigmotaxis”; Valle 1971) and tend to rest in corners (Walsh and Cummins 1976), this kind of arena maximized for the rats the possibility to explore the area without imposing on them the need to rest or travel with partners. The arena was located in a light-proofed, air-conditioned room ( $22 \pm 1$  °C), illuminated with two LED projectors (20 W each) positioned 270 cm above the arena together with a color CCTV camera (Provision ISR BX-380IP) that provided a top view of the arena. The video signal was recorded and then tracked for X, Y, T coordinates of the eight rats (Ethovision XT 11.5, by Noldus Information Technologies, NL) at a rate of five frames per second.



**Fig. 1** Top view of the ‘stadium’ apparatus. The apparatus is made of white Plexiglas, comprising a central open space of 100×55 cm, enclosed with 5 concentric 10-cm benches, each bench fenced with 10-cm walls, except for the top level that has 50-cm walls (removable left wall is not shown in this picture). This provides the rodents with 23.5-m-long walls and 20 corners encapsulated in 180×135 m apparatus. This way, each individual has at least one free corner (where rodents like to crouch), and free wall space to travel along. During analysis, the area was divided into 16 equal zones (dashed line)

## Procedure

The 64 rats were assigned to eight octets of unfamiliar members. One week prior to testing the rats were exposed to the apparatus for 1 h, without their designated octet mates, in order to reduce the novelty of the environment and emphasize the social component in the subsequent test. On the day of the experiment, the fur of each rat was gently brushed with a semi-permanent color marker (Chalk Ink Marker®, TX, USA). Each rat was marked with a different color, enabling the tracking system and the experimenters to discriminate among them. The rats were not attracted or sidetracked by specific colors, because for the eight groups, a comparison of the time that each color (rat) spent with each of the other colors (rats) at a distance of less than 25 cm between their center of mass, revealed no significant difference (one-way analysis of variance ANOVA with repeated measures,  $F_{7,72} = 0.629$ ;  $p = 0.731$ ). All eight rats were gently placed together by the experimenter in the center of the apparatus and tracking commenced when the experimenter left the room and continued for 180 min. At the end of the trial, rats were returned to their cages and the arena was mopped with soap and water in order to neutralize odors.

## Data acquisition and analysis

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

1. *Distance traveled* The cumulative metric distance (m) traveled over 180 min.
2. *Time in proximity* Proximity was recently suggested as a predictor for social behavior in rats (Bonuti and Morato 2017), and was measured as an estimate of social affiliation and mutual influence among rats. In the present study, the time in proximity was defined as the duration of time (s) that rats spent at a distance of 25 cm or less between their centers of mass. The 25-cm criterion was decided, since it is roughly the body length of an adult rat (excluding the tail). Implicit in this criterion is that when in greater distances, there is no body contact between the rats. While rats may also affect the behavior of one another at greater distances (Weiss et al. 2017b), we applied here a strict criterion according to which rats are likely to be in physical contact with one another.

In accordance with the number of partners in proximity, eight social states were defined: solo, duo, trio, quartet, quintet, sextet, septet and octet. For these, the following parameters were calculated from the  $X$ – $Y$ – $T$  coordinates of ‘Ethovision’:

1. Time lapsed to the first formation of each social state for at least 1 s.
2. *Time in companionship* The total time (s) that each rat spent in the proximity of any other rat was calculated for each social state.
3. *Time in zone* The arena was virtually divided into 16 rectangular zones (approximately 40×50 cm each) and the total duration (s) spent in each zone was calculated for each rat in each social state.
4. *Home-base behavior* For each rat, the zone where it stayed for the longest cumulative time (regardless of its social state) was defined as its home base (Eilam and Golani 1989).
5. *Resting and traveling* a rat was considered resting when traveling less than 5 cm/s, whereas greater speeds were classified as traveling. Speed was measured automatically by the tracking system.

## Network analysis

Based on the *proximity* parameter extracted from Ethovision, the social networks in octets of rats were generated utilizing Gephi software for exploring and manipulating networks (Bastian et al. 2009). Specifically, the total time that each rat spent in proximity to each of its conspecifics was calculated. Then, for each octet, a weighted social network was generated, with each network node representing a rat, and each edge representing a bond between two rats. The following parameters were extracted from Gephi:

1. *Weight* The accumulated duration (s) that a rat spent in proximity to any conspecific.
2. *Degree* The total number of edges that a rat shared with its conspecifics.
3. *Weighted degree* An index calculated from the *degree* that rats scored and the total *weight* that they accumulated. Specifically, this is the sum of the weights of all the bonds attached to each rat.

## Statistical analysis

Unless noted differently, one-way or two-way analysis of variance (ANOVA) with repeated measures, where applied. The above tests were followed by Tukey's HSD or Fisher LSD post hoc tests. The link between sociality and activity was tested by Pearson's correlation test. In all tests Alpha level was set to 0.05.

## Results

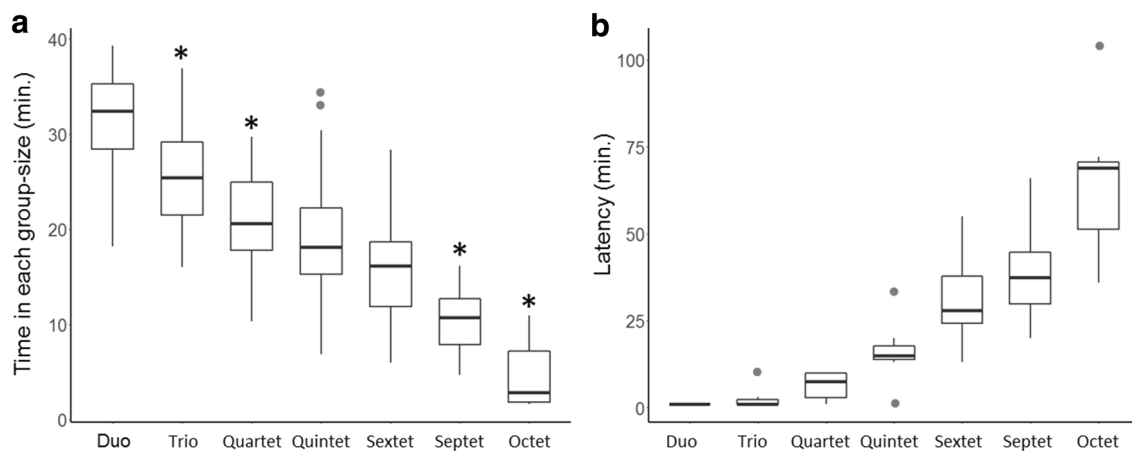
### Rats prefer to be with companions

When tested in octets, rats could either spend their time alone or with other rats. A two-tailed *t* test for dependent samples revealed that rats spent significantly more time in companionship than alone ( $7687.17 \pm 809.44$  s with companions,  $3059.73 \pm 809.09$  s alone;  $t_{63} = 22.87$ ,  $p < 0.001$ ). Dissecting the time-sharing into duos, trios, quartets, quintets, sextets, septets, or octet revealed that the percentage of time spent in each group size decreased with the increase in group size. A one-way ANOVA with repeated measures

revealed a significant difference in time allocations between the seven possible social states (duos, trios, etc.;  $F_{6,384} = 214.85$ ,  $p < 0.001$ ). A Tukey HSD post hoc test revealed that the mean proportion of time spent in almost every group size was significantly shorter than in the preceding group size (Fig. 2a). Notably, this is merely a reflection of the combinations available in each social state. In other words, the rat can socialize with seven different partners in duos but with only one octet. Figure 2b depicts the latency to the formation of each group size for at least 1 s. We set this 1-s margin to eliminate instances in which rats coincidentally encounter one another, with each then continuing to walk. As shown, group size increased gradually and on average was completed within about 60 min, when an octet was formed (Friedman ANOVA; ANOVA  $\chi_{(6)}^2 = 44.097$ ;  $p < 0.0001$ ).

### Group size differed between resting and traveling

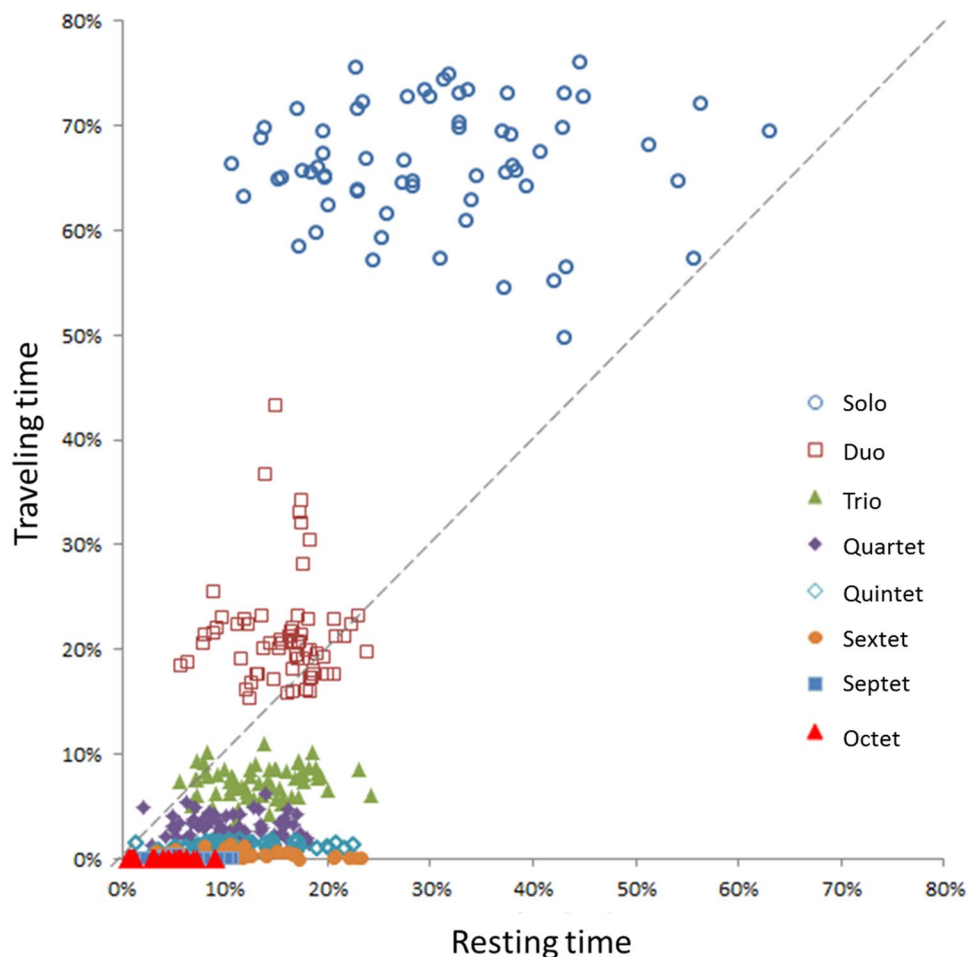
When resting, rats tended to huddle in relatively large groups, but they usually traveled alone or with one companion. Figure 3 depicts for each rat the proportion of traveling time for each group size (ordinate) compared to the proportion of resting time for each group size (abscissa). The diagonal dashed line represents equivalence between the proportions of traveling and resting times. As shown, groups of one rat (solo) and two rats (duo) spent a greater proportion of time in traveling than in resting. Conversely, groups of 3–8 rats (trio, quartet, quintet, sextet, septet, and octet) spent a greater proportion of time resting vs. almost a nil proportion of traveling. Explicit in this figure is that rats typically traveled alone or in dyads, but tended to rest in larger groups of 3–8 rats. Indeed, a two-way ANOVA with



**Fig. 2** Inset a depicts the median time (min), including outliers (marked as dots), that rats spent in each group size (duo, trio, quartet, sextet, septet, and octet). As shown, rats spent a decreased duration in each social state as group size rose (each \* indicates a significant difference between the box and its predecessor). Inset b depicts the

median latency (min) to forming groups. As shown, the increase in group size was gradual. First duos and trios were formed, then quartets, quintets, sextets, septets (in this order), and eventually octets, which were typically formed after about 60 min of experimentation

**Fig. 3** The percentage of time that each rat traveled (ordinate) against the time it spent resting (abscissa) in each group size. 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

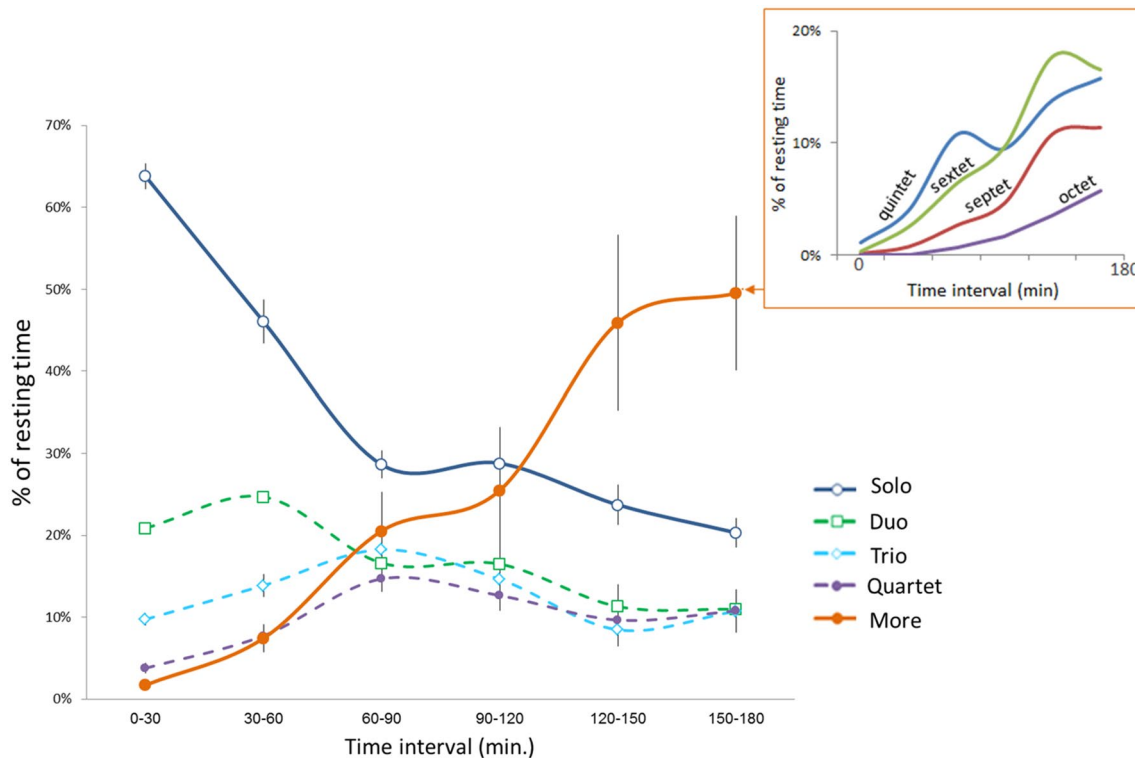


repeated measures revealed a significant difference between the resting and traveling time ( $F_{1,126} = 876.71, p < 0.001$ ), a significant difference among group sizes ( $F_{7,882} = 366.056, p < 0.001$ ), and a significant interaction between mobility (resting or traveling)  $\times$  time in each group size ( $F_{7,882} = 12.85, p < 0.001$ ). In the same context, we found that in the course of the 3-h trial, the rats shifted from their initial tendency to rest alone to resting in larger groups. To illustrate this, the trial was divided into consecutive 30-min intervals and the resting time in each group size is depicted in Fig. 4. As shown, solo resting sharply declined during the first hour while, in contrast, resting in large groups of 5–8 rats increased over time.

### Network analysis

In order to analyze the social organization, the total time that each rat spent in proximity to each of the other rats was calculated. A weighted social network was then generated, with each node representing a rat and each edge (connecting line) representing a bond between two rats. In each octet, rats were ranked according to their sociality

level, as reflected in the accumulated time that they spent in proximity to others (“weight”). Networks of each octet are shown and described in Online Resource 1. From these data, the mean of each rank in the eight networks was calculated, and a social network representing the average ranks of all eight octets was formed and is depicted in Fig. 5. In this representation, the higher the rank the larger and bolder are the nodes. Line width and boldness represent the weight of the bonds, as reflected in the accumulated time that the two rats spent in proximity to one another. This network reveals that some of the rats were more social (as reflected in their greater circles) than others, and the social connections (as reflected in their thicker lines) between specific rats were favored over connections with other rats. Indeed, a one-way ANOVA with repeated measures revealed a significant difference between the ranks ( $F_{7,49} = 21.323, p < 0.001$ ), implying that some rats were socializing more than others. A Tukey HSD post hoc test revealed the top four ranks to differ from the three lowest ranks, but there was no significant difference within these sets of ranks. It should be noted that each line represents the cumulative time that a rat of this rank spent with



**Fig. 4** The percentage of resting time that each rat spent in each group size for each 30-min interval. Resting alone (blue) dropped steeply during the first hour, whereas resting in groups of five or more (orange) increased with time. The inset in the upper right corner

depicts the time resting (min) in each of the groups comprising the orange line, all following the same increasing trend. Resting in duos, trios or quartets was at a steady and overlapping level across the 3 h

one other rat or more (the time that the ranked rat was in a duo, trio, quartet, quintet, sextet, septet and octet).

### The gradual formation of a social network

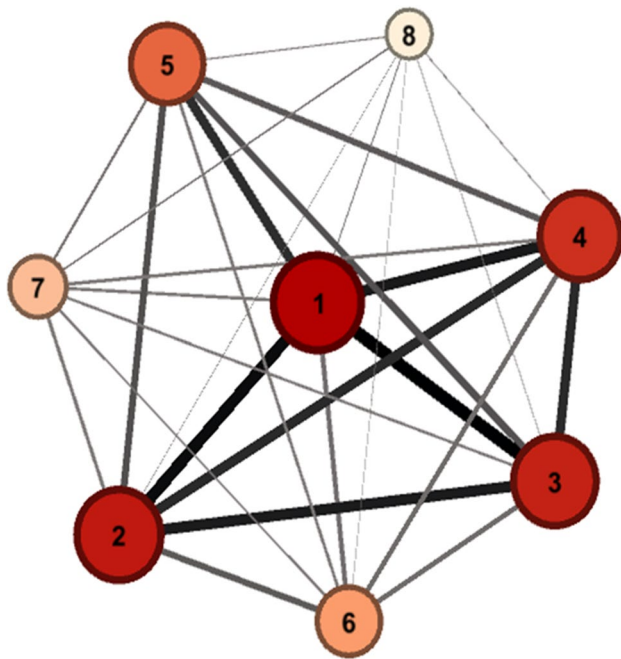
In order to monitor the temporal dynamics of group formation during the 3-h observation, the social network of each octet was divided into six consecutive 30-min intervals. A social network was then generated for each time interval based on rat ranking, representing the dynamic changes in the ranks over 3 h, starting with eight unfamiliar rats (Fig. 6). As shown, the initial state of unfamiliarity (0–30 min interval) is represented by small nodes and almost invisible connecting lines. As time progressed, the nodes expanded and the connecting lines became thicker, indicating that rats spent more time in the proximity of some other rats, with some demonstrating greater social bonding than others.

### Social behavior was gradually altered along time

In some of the intervals (especially the first 0–30 min interval), rats did not necessarily interact with all other rats. This is evident in the “weighted degree” parameter, which was extracted for each rat from the dynamic networks. This

parameter combines the degree (number of interacting rats) and the time spent in proximity to these rats (“weight”). As shown in Fig. 7a, rats scored higher weighted degrees as the trial progressed, implying that with time they established stronger social bonds, spending a longer duration in the proximity of others. Indeed, a one-way ANOVA with repeated measures revealed a significant difference in weighted degree among time intervals ( $F_{5,315} = 116.332$ ,  $p < 0.001$ ). A Fisher LSD post hoc test revealed that the increase in socializing occurred in three significant steps: at 30–60, at 60–90, and at 120–150 min. In these intervals, the weighted degree was significantly greater than in the preceding interval. Overall, there seemed to be four stages in socializing: the first half hour, the second half hour, the second hour, and the third hour.

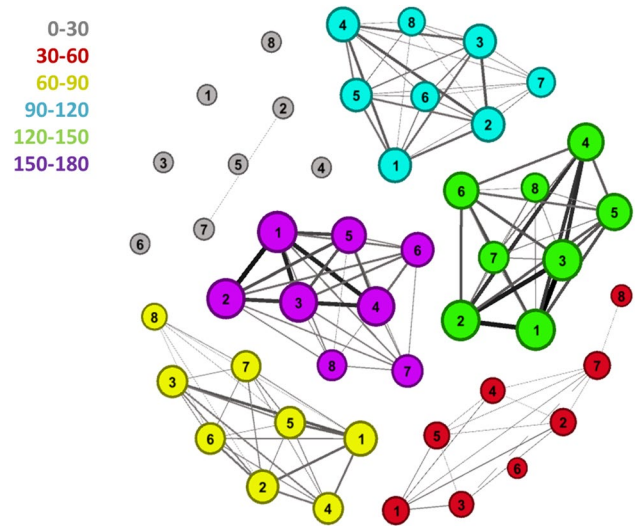
Among each octet of rats there were 28 possible duos. For each of the eight octets, duos were ranked from high to low according to the time that a duo spent in proximity. The mean duration in proximity for each rank in the eight octets is depicted in Fig. 7b at 30 min intervals. The four stages of socializing presented in Fig. 7a are also apparent in Fig. 7b. As shown, the ranks for two intervals of the second hour overlap, as do the ranks of the two intervals of the third hour, resulting in the four stages. Another implication



**Fig. 5** A network analysis of the social interactions among all 64 rats in the eight tested octets. In order to generate a mean network for all eight octets, the rats in each octet were ranked according to the total time they spent in proximity to other rats. Each node (circle) represents a rank (1 is the top rank with the greatest time spent with others; 8 is the lowest rank). The color tone and diameter of the node reflect sociality level (the larger and more reddish the node, the more social the rat). The edges (lines) depict the intensity (‘weight’) of bonds between the ranks, with bolder lines indicating stronger bonds. It should be noted that each line represents the cumulative time that the rats of this rank spent with one rat (duo) or more (trio, quartet, quintet, sextet, septet and octet). The difference between the ranks indicates that some rats were more social than others, as reflected in the size and color of the nodes representing them, and the width of the bonds connecting them to the other rats. This average network reliably represents the social connection in the various octets, as detailed in Online Resource 1

of duo ranking is the increase in the time that certain duos spent in proximity compared with other duos. Particularly, in the first time interval (0–30), the duo ranks slightly diverged from a horizontal line. In the subsequent time intervals the ranks gradually became more inclined, indicating that duos of the higher ranks spent increasing time together compared with the duos of the lower ranks. The rats thus became more social with specific individuals as time progressed, with some rats spending more time together than with other rats.

In contrast to the increase in sociality, rat activity, as reflected in their total traveled distance (Fig. 7c), decreased along the trial. A one-way ANOVA with repeated measures revealed a significant difference in activity among the 30-min intervals ( $F_{5,315} = 200.727, p < 0.001$ ). A Tukey HSD post hoc test confirmed that the decrease in activity occurred successively during the phases shown in Fig. 7a, b. That is, the traveled distance successively decreased from

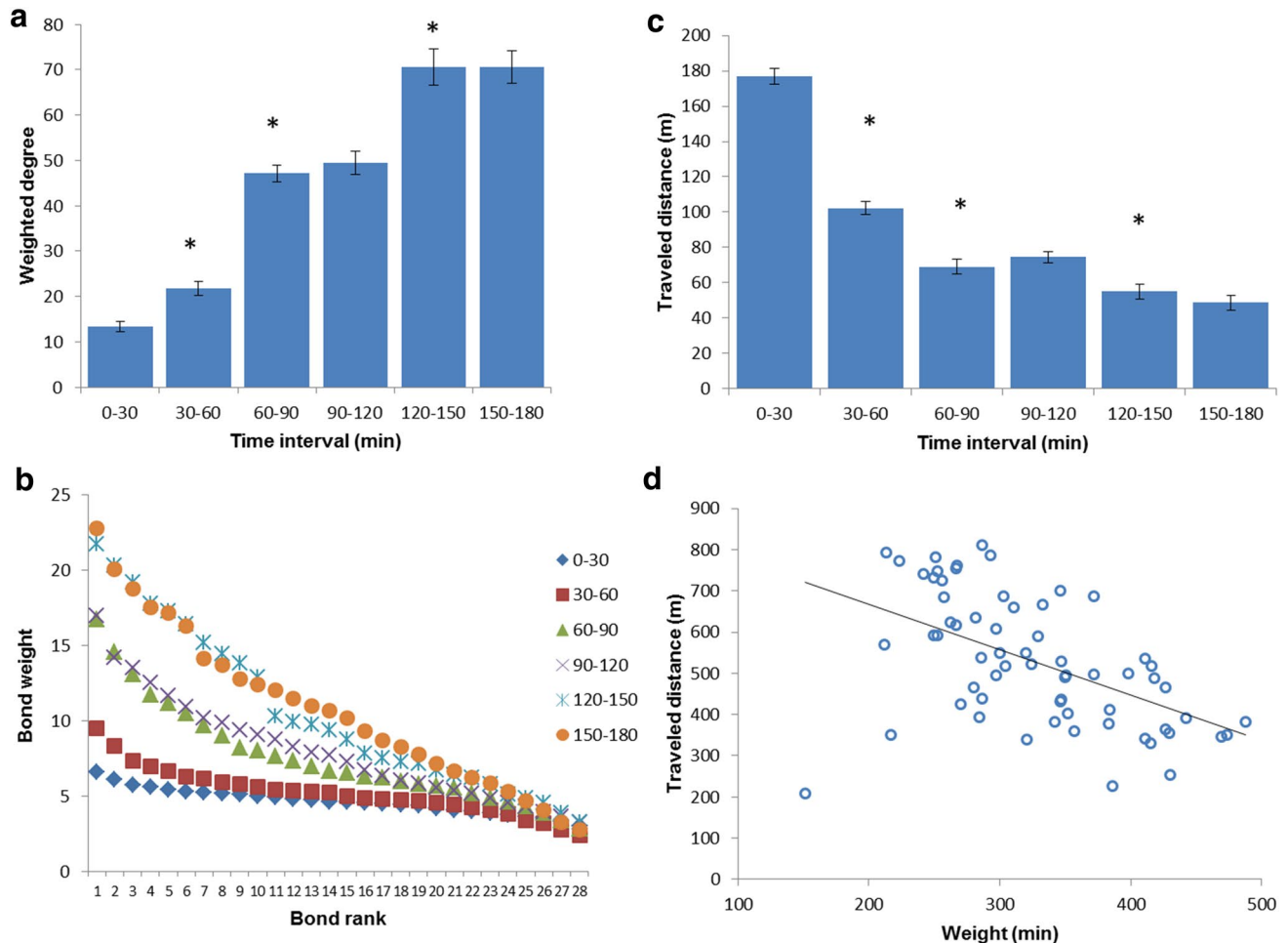


**Fig. 6** Group formation in the mean octet of unfamiliar rats, as reflected in the social networks for six successive 30-min intervals. Each circle represents one rat-rank for each time interval, and its diameter represents the time spent by that rat-rank in the proximity of others. The thickness of the lines connecting each two rat-ranks represents time in proximity (bond) between rats of these two ranks. Numerals represent the ranking of the rat according to total time it spent in proximity to any other rat. As shown, during 0–30 min interval (gray network) social connections were weak and connections were hardly discernible. In the 30–60 min interval (red network) connections emerge, and become stronger between 60 and 90 min (yellow network). At the end (purple network) there were still some “outsider” rats (ranks 7, 8) with weak social connections compared with the higher 1–6 ranks

the first to the second half hour, and then during the second and third hours of the trial, presenting a sort of mirror image of the increase in sociality. Indeed, there was a significant negative correlation between the traveled distance and sociality, as measured by the network weight ( $r = -0.518, p < 0.001$ ; Fig. 7d). In other words, highly social rats were less active than less social rats, and rat activity decreased along the trial with the increase in sociality. Altogether, by the end of the first hour of the trial, all the rats in the eight tested octets had created a full social network in which each rat had accumulated at least 5 min of being with each of the other seven rats. The only exceptions were two (out of 64) rats for which the bond between them was only 4.6 min.

**Spatial organization of group behavior**

As detailed in the “Introduction”, rats in an open field organize their behavior in relation to a ‘home base’ at which they stay for relatively extended periods and from which they set out to roundtrips in the arena. When the eight rats were placed in the arena, they first used several locations as bases, with only a few sharing the same location as a home base. Gradually, however, their home bases converged to the same



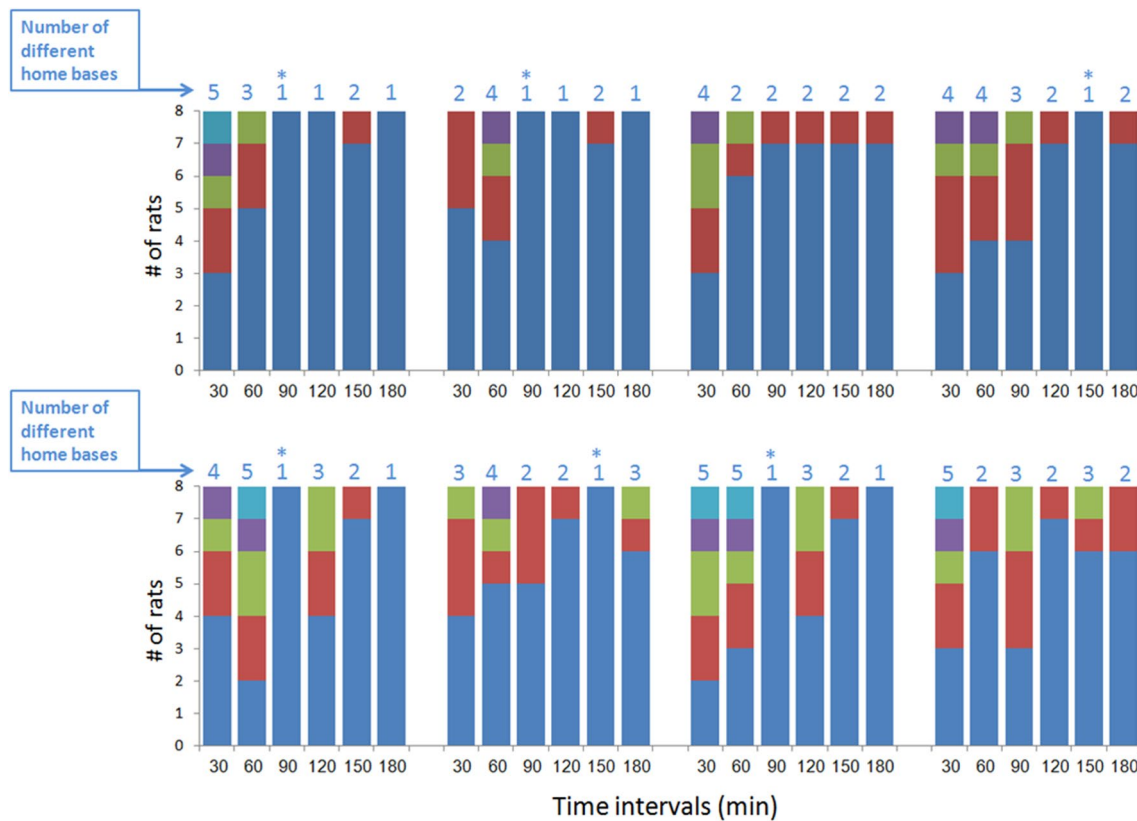
**Fig. 7** Parameters that reflect gradual group formation. Inset a depicts the mean  $\pm$  SEM weighted degree that rats scored along the six time intervals, reflecting the sociality level of the rats for each time interval. As shown, rat sociality levels rose in three steps with trial progression. In particular, rats were more social in the second interval than in the first; in the third more than in the preceding two; and in the fifth and sixth more than in all the preceding intervals. Inset b depicts the weight of each of the 28 bonds of the mean octet for the six time intervals (0–30: blue rhombus; 30–60: red square; 60–90: green triangle; 90–120: purple cross; 120–150: blue asterisk; 150–180: orange circle). As shown, all bonds began with a similar

weight. In the second hour, some bonds became stronger than others, and in the third hour, this trend maximized itself. Inset c depicts the mean  $\pm$  SEM distance that rats traveled along the six time intervals. As shown, rat activity decreased in three steps with trial progression. In particular, rats were less active in the second interval (30–60) than in the first (0–30); in the third (60–90) more than in the preceding two; and in the fifth and sixth (120–150 and 150–180, respectively) more than in all the preceding intervals. Inset d illustrates the correlation between traveled distance (ordinate) and weight (abscissa). Each dot represents one rat. The significant negative correlation indicates that the least active rats socialized more with the other rats

location and almost all rats spent extended periods at that location, where they huddled for resting and from which they set out, either alone or with a partner, to roundtrips in the arena. Figure 8 depicts for each octet (each inset) the number of bases by the numerals at the top of each bar, with each bar in each inset representing a 30-min interval. As shown, all the octets started with several bases, and over time most of the rats converged to the one home base. In four octets all the eight rats ultimately shared the same location as a home base; in another two octets seven rats shared the same base; and in yet another two octets, six rats ultimately shared the same location as a home base.

The organization of traveling in relation to the home base, with the home base serving as a terminal for round trips in the arena, is illustrated in Fig. 9 for the eight rats of one octet. The trajectories of traveling are depicted for the first 5 min and the last 5 min. As shown, during the first 5 min there were four different home bases, each shared by two rats. This, together with the higher activity, resulted in round trips that extended over the entire arena. In the last 5 min, the location of the home base was the same for all eight rats and the trajectories of the rats represent their lower activity, with all the roundtrips anchored at the same home base (top right corner).





**Fig. 8** The convergence of home bases of the eight rats to the same zone. Each of the insets accounts for one group of eight rats, and is divided into six 30 min intervals (six bars). The number of different colors that comprise each bar indicates the number of different locations of home bases in that bar, as depicted at the top of the bar. The length of each colored segment in each bar represents the number of rats sharing that specific zone as a home base. For example, in the top leftmost group, in the first time interval of 30 min, there were five dif-

ferent home-base zones (five different colors). From the bottom to the top of that bar it is shown that three rats shared one zone, two others shared another zone, whereas the remaining three rats has each a different home-base zone. The first bar, (time interval) in which all rats first shared the same home base, is marked with asterisk. As shown, in all octet groups the number of home-base zones decline with time (the numerals above the bars in each octet), with many rats sharing the same home base already during the second hour

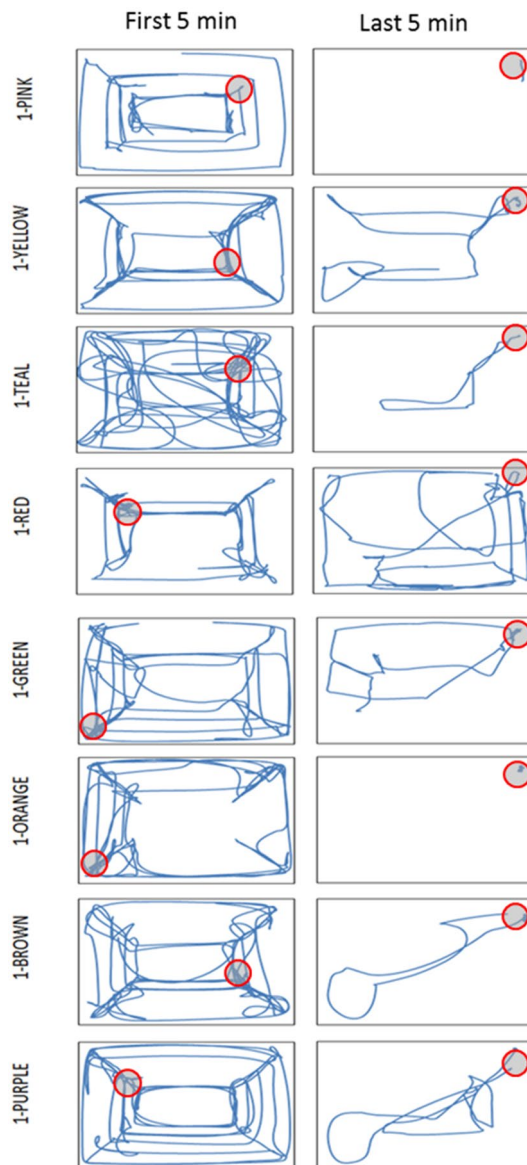
**Put it all together: group formation in time and space**

The above findings reveal that the octets of unfamiliar rats gradually formed a social network, with some having stronger bonds than others. They rested together in relatively large groups, while typically traveling alone or with one partner. In the beginning, the unfamiliar rats seemed to travel relatively independently from one another, and accordingly the behavior of the eight rats was initially organized in relation to several home-base locations. Later, all rats converged to the same home-base location, from which they all took roundtrips in the arena. Finally, the least active rats were shown to be those with the strongest social bonds. In order to illustrate the formation of the group, we depict in Fig. 10 two exemplary octets. For each octet, we depicted for each group size (duo, trio, and so on from top to bottom) the individuals that spent the longest duration together in that group size. The arrows at the top mark the rat with the

highest connectivity that accordingly spent most time with others. As shown, the group was formed around these rats, which were involved in each group size that spent the longest time compared to other combinations of individuals in the same group size.

**Discussion**

In this study, we examined how eight unfamiliar laboratory rats, which are social rodents, gradually established a group and coordinated their spatial behavior. As hypothesized, the unfamiliar rats adjusted their spatial behavior and coordinated it with their group-mates. They shared their main resting place—the home base, but mostly traveled along or in dyads. During the first few minutes the rats mainly traveled alone, exploring the arena and briefly interacting with one another. Their initial high activity gradually declined through the first hour, during which the rats spent about 90%



**Fig. 9** The organization of traveling in relation to the home base. In order to illustrate the spatial organization in relation to the home base (marked with red circles), the trajectories of the first 5 min (left column) and last 5 min (right column) of experimentation were plotted for the eight rats (each row represents one rat) in an exemplary octet. As shown, during the first 5 min there were four different home bases, each shared by two rats. This, together with the higher activity, resulted in round trips that extended over the entire arena. In the last 5 min, however, the location of the home base was the same for all the rats (the top right corner) and the trajectories of the rats represent the lower activity, with all the roundtrips anchored at the same home base

of their resting time in small groups of 1–3 rats. Activity (traveling time) further decreased in the second hour and still decreased in the third hour, with the rats gradually spending more time in larger and larger groups. Despite the decreased activity and the larger resting groups, the rats continued to

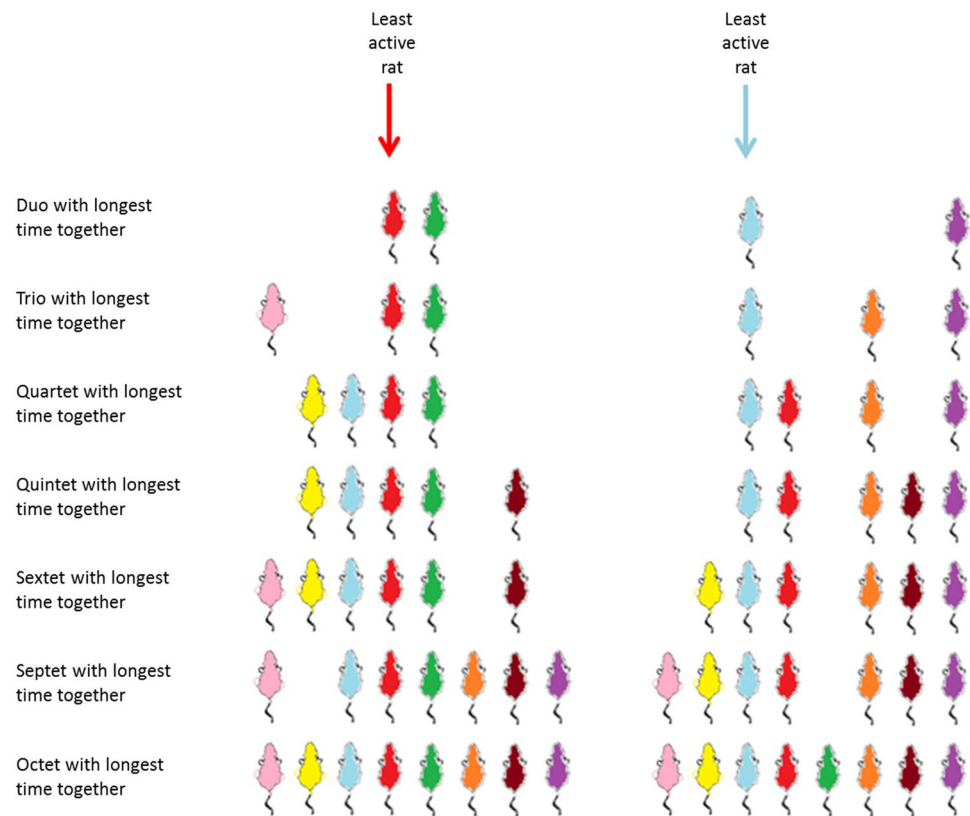
travel either alone or with only one partner throughout the 3 h. In the group, certain individuals had stronger bonds with some members compared to others, and the least active rats were those with the strongest social bonds. In the course of group formation, the rats gradually coordinated their spatial behavior. Specifically, in the beginning, different rats used different locations as a home base, which is a terminal for roundtrips in the arena. Gradually, they switched to share the same location as a home base and ultimately all the rats huddled at the same home-base location, with rats taking solo or duo roundtrips out and back to that location. In the following discussion, we suggest that the dichotomy to resting in larger groups and traveling in small groups is a common trait in animals, and offer a functional rationale for this dichotomy. We then describe the dynamics of group formation and the emergence of group spatial behavior.

### The impact of the social environment

It could be argued that most of the present results are not the outcome of the social environment. Specifically, huddling together in the same location could occur by chance or due to certain physical properties of a specific location. Huddling could be also the result of the rats “bumping” into a resting rat and joining it. These possibilities were ruled out by comparing the present results with those obtained in two other procedures: (1) a computerized simulation; and (2) the behavior of eight rats that were each tested alone in the stadium-like arena (see Online Resource 1). The computerized simulation of group exploration revealed that the eight virtual rats had 4–5 home bases throughout the 3 h of simulated exploration (Figure S4 in Online Resource 1) whereas rats in the groups typically converged to one and the same home base during the second hour (Fig. 8). Rats in the other reference group, which were each tested alone and grouped virtually into one group, also had five different home-base locations. Moreover, the above two reference groups did not form groups of 6 or more rats (Figure S2 and Figure S3 in Online Resource 1) as did the rats in the tested octets. Thus, the huddling of all the rats in the same home base, as revealed in the present study, was not random but a result of the presence of conspecifics.

The location of the home base in individual rats is usually set next to a salient landmark (Nemati and Whishaw 2007; Yaski and Eilam 2008) and it could be argued that accordingly, the grouped rats were all responding to the same environmental cue. There are, however, two arguments against this “unifying” impact of the physical environment. First, rats in octets did not share home base in the first hour, but diverged to 4–5 different locations. This implies that they were not all responding primarily to the same environmental cue. Moreover, this divergence of home bases may reflect an initial avoidance of the other unfamiliar rats. Second,

**Fig. 10** The recruitment of rats into the group around the least mobile rat, but with the greatest social connectivity (marked with ↓) is illustrated for two exemplary octets. Each column (color) represents one rat, and each row represents the combination of rats that spent the greatest time together compared with other possible combinations of rats for this group size. As shown, in both octets the marked rat participated in all group sizes (i.e., duo, trio, quartet, etc.) with the longest total time, as if the group had been formed around it



eight rats that were each tested alone in the same apparatus had 4–5 home-base locations, illustrating again the absence of a landmark that could attract different rats to set their home base in one specific location. “Bumping” into a resting rat and staying along with it is also not likely to be a sole explanation for huddling since the rats bumped into one another throughout the 3 h, but kept traveling alone or with a partner and could rest in any of the 20 arena corners, as occurred in the virtual simulation of a traveling octet (Online Resource 1). Altogether, the convergence of the eight rats to rest together in the same location seems to be a result of social affiliation rather than a random product or a mere response to the physical features of a specific location (see however the following discussion on thermotaxis).

### Social spatial behavior in rats: resting together but traveling alone or with a partner

In the present study, rats preferred to stay in companionship over staying alone, and eventually huddled together in large groups of four conspecifics or more. Nevertheless, rats took mostly solo or duo roundtrips from that huddle. A similar phenomenon was observed in previous laboratory studies in rats (Loewen et al. 2005; Weiss et al. 2017b) and in various wild species that roost communally but forage alone (for example, herons, *Ardea* sp., harriers, *Circus* sp.; Ward and Zahavi 1973; the Gambian epauletted fruit

bat, *Epomophorus gambianus*; Thomas and Fenton 1978; and Bechstein’s bat, *Myotis bechsteinii*; Kerth and Reckardt 2003). However, there are many other species that roost communally and forage in groups, such as the pied wagtail (*Motacilla alba*; Broom et al. 1976), turkey vulture (*Cathartes aura*; Buckley 1996), black vulture (*Coragyps atratus*; Buckley 1996), common starling (*Sturnus vulgaris*; Yom-Tov et al. 1977; Caccamise and Morrison 1986), cattle egret (*Ardeola ibis*; Siegfried 1971), and rook (*Corvus frugilegus*; Swingland 1977). Indeed, many social species roost together, but while individuals in some of these species leave the roost to travel alone, others forage together. This raises the questions of (1) what is the advantage in roosting together, and (2) when is it advantageous to travel alone compared to traveling with companions?

Communal roosting, which in some species can be in large aggregations of thousands, has been considered as a means to reduce energy consumption for thermoregulation since animals that cluster together lose less heat to the environment (Yom-Tov et al. 1977; Swingland 1977; Barclay 1982; du Plessis et al. 1994). Rats are relatively small mammals, and they probably benefit from such a mechanism of thermotaxis. Indeed, Norway rat (*Rattus norvegicus*) pups huddle together throughout their postnatal development for thermoregulation and energy conservation needs (Alberts 1978a, b, 2007; Schank and Alberts 1997). Thermotaxis may therefore account, at least partially, for the aggregation of

the rats in one place. Communal roosting may also reduce predation risk, since there are more individuals that can spot a predator and alert their conspecifics to its presence (Eiserer 1984; Delm 1990). This latter aspect is especially vital in open environments (Delm 1990). Indeed, foraging in large groups is more common in open environments (Fortin et al. 2009), where by means of local enhancement an individual can increase its chances of finding food (Poysa 1992; Buckley 1996). Since wild rats are heavily exposed to predation, such defensive mechanisms may have been preserved in their laboratory descendants. This may explain the present finding that the rats tended to spend most of the time in companionship to rest in huddles. In the same vein, we found in previous studies that rats were more active when tested in groups compared to lone testing, perhaps as a manifestation of an increased sense of security due to the presence of conspecifics (Weiss et al. 2015, 2017b). Communal roosting has also been suggested to serve as an “information center” (Ward and Zahavi 1973) for food abundance, in which starving animals can interact with well-fed conspecifics, and then forage with them (or follow them) the next day (Ward 1965; Weatherhead 1983; Bijleveld et al. 2010). Indeed, in some animals it seems advantageous to roost and travel together for safety.

While traveling in groups characterizes open areas, rats are renowned for avoiding such areas (Valle 1971). Even in small testing environments, laboratory rats cling to the safety of the walls and avoid the center (Whishaw et al. 2006; Eilam 2010). Wild rats are commensal animals that dwell in the complex human environment. In such habitats, food is less scarce, but foraging in large groups is no more beneficial than foraging in small ones (Stacey 1986). In such complex environments, prey are apparently less salient and less likely to be detected when alone or part of a small group (Fortin et al. 2009). The social spatial behavior of resting together but traveling alone or with one companion thus seems more appropriate to survival than traveling in larger groups. However, it should be noted that, unlike the present study with satiated rats, the behavior of food-deprived rats is governed by additional factors. For example, wild rats are susceptible to the pesticides that are being applied to their preferred foods. Accordingly, they are aware of the food choices of their conspecifics and prefer to feed from the same source. By doing so, they reduce their chances of being poisoned (Galef and White 1997). In other words, foraging together in wild rats might be vital for the individual’s survival. Indeed, previous laboratory studies have revealed that food-deprived rats in dyads (or triads) followed one another in foraging tasks (Brown 2011; Dorfman et al. 2016; Weiss et al. 2017a). Altogether, spatial and social behavior are also sensitive to test conditions, which in the present study comprised satiated rats that were free to explore the arena with no food reward or spatial task.

## The temporal dynamics of group spatial behavior

In the present study, four stages were apparent in the various parameters that delineated the formation of groups of eight unfamiliar rats over the course of 3 h. These were the weighted degree (Fig. 7a); the time spent in proximity with specific partners (Fig. 7b); and the traveled distance (Fig. 7c). These phases were also reflected in the percentage of resting time (Fig. 4). Dividing the trial of each group (3 h) into 30-min intervals revealed that there was no difference between these time intervals for the second hour and the third hour. Accordingly, we consider the time interval of 0–30 min as a first stage, the 30–60 min interval as a second stage, the second hour (intervals 60–90 and 90–120 min) as a third stage, and the third hour (120–150 and 150–180 min intervals) as a fourth stage. These stages were manifested in the dynamics of group formation as follows. During the first stage (first half hour) the rats began by exploring the arena for a few minutes, briefly encountering their mates and immediately continuing to travel. After about 5 min, the rats started to interact more with one another, but did not yet establish stable groups and frequently exchanged partners (Fig. 7b). This process resulted in relatively weak connections between the rats that were hardly discernible during the first half hour (Fig. 6). The same trends of a decrease in traveling (Fig. 7c) and increased duration of resting with more and more partners continued in the second stage (30–60 min; Figs. 2, 4). In effect, the first and second stages were continuous and comprised the most dynamic period during which the group was formed. The statistically significant differences between the first and second stage are attributable to the major changes that occurred during the first hour and it is possible to regard the entire first hour (stages 1 and 2) as a single phase of *group formation* (see supplemental Online Resource 1).

The second hour (time intervals 60–90 and 90–120) was the period in which the group had already stabilized. The major changes that occurred in the first hour led to the formation of relatively large resting groups. However, there were still many rats in motion (alone or with one partner). This was also the time when most of the rats shared the same home base (Fig. 8), with emerging bonds between specific individuals (Figs. 6, 7b). These processes, which are illustrated in supplemental Online Resource 2, can be regarded as a phase of *group stabilization*.

The third hour (120–180 min) was the period when the dynamic processes leveled off. Activity decreased further, the rats rested together in one place, and every now and then a few rats, typically alone or with a partner, took roundtrips into the arena (see supplemental Online Resource 3). Rats now showed extensive bonds with specific individuals (Fig. 7b) and the phase can be regarded as *group performance*. The group was thus formed in the course of the first

hour, which involved extensive changes. In the second phase the group became stabilized, with the rats interacting with more and more conspecifics while decreasing their activity. Finally, in the third phase of performance, the rats displayed intensive bonds (time sharing) with specific individuals, sharing a home base and taking solo or duo roundtrips from it into the arena.

### The dynamics of group formation

When eight unfamiliar rats were introduced together into the arena for a 3-h trial they had various possible social options. In order to monitor the dynamics of social bonds, a network analysis (Wey et al. 2008; Ilany et al. 2013) was conducted, depicting the bonds between rats for each of the six 30-min time intervals. This analysis revealed that rats initially did not show a preference for specific individuals and kept changing partners. Bonds with specific partners then began to emerge and extended throughout the entire trial (Online Resource 1 for exemplary octet; Figs. 6, 7b for the mean octet). However, despite the formation of octets, septets, and sextets, there were also one or two “outsider” rats that had weaker bonds than the others (Figs. 5, 6). Such a trait of rats with weaker social bonds was also noted in rat tetrads (Weiss et al. 2017b), and seems to reflect individual differences among rats. Notably, rats that formed the most extensive social bonds were typically the least active rats, and the groups were formed around them. It is as if these rats had settled (not necessarily in the final location of the home base), and the other rats gradually joined them, until the octet group was formed (Fig. 10).

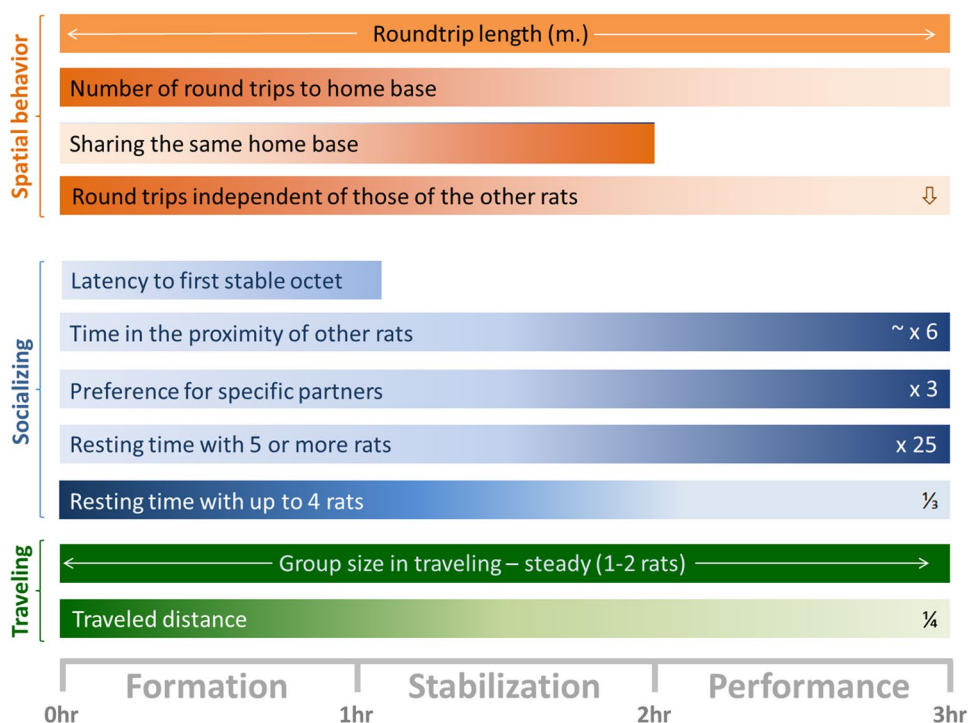
### From individual to social spatial behavior

So far we have focused on group dynamics from the social perspective. However, at the same time the eight rats also underwent a process of coordinating their spatial behavior, a process during which they switched from individual to social spatial behavior. When a lone rat is introduced into an arena (open field), it soon establishes a home base in which it rests for extended periods and from which it takes round trips to explore the arena (Eilam and Golani 1989; Golani et al. 1993; Tchernichovski and Golani 1995; Hines and Whishaw 2005; Whishaw et al. 2006; Wallace et al. 2006; Nemati and Whishaw 2007). Accordingly, exploration is conceived of as a set of round trips that start and end at the home base (Golani et al. 1993), and the home base is defined as the location in which the rat spends the longest duration (Tchernichovski and Golani 1995; Szechtman et al. 1998). The different arena shape in the present study could affect the spatio-temporal structure of behavior. For example, the structure of “stairs” added a 3D component which could modify exploration. Nonetheless,

behavior of the rats was similar to the behavior of lone or smaller groups of rats as revealed in previous aforementioned studies. This accords with previous studies in which the arena size was changed drastically (Eilam 2003; Ben-Yehoshua et al. 2011; Weiss et al. 2015, 2017b) or when switching from square to circular arena (Yaski and Eilam 2008; Weiss et al. 2012). Altogether, the shape and size of the arena in the present study do not seem to alter the usual structure of spatio-temporal behavior in rats.

Several studies have discussed the physical environmental attributes that dictate the selection of the location at which the home base is formed in lone rats (Nemati and Whishaw 2007; Yaski and Eilam 2008; Ben-Yehoshua et al. 2011). Due to this impact of the physical environment, most rats in the former studies set their home base in the same location, and therefore, the tendency of rats in most of the groups to set their home base at the same location is not different from that described in previous studies. Nonetheless, unlike studies with lone rats that all set the home base in the same location, rats in the present study initially set their home base at various locations and it was only later that they all converged to huddle at the same location (Fig. 8). This indicates that it was not only the physical, but also the social structure of the environment that was involved in setting the group’s home-base location. Notably, the home base (as well as ‘home’ in other animals, including humans) is the organizer of behavior in time and space (see Blumenfeld-Lieberthal and Eilam 2016 for review). The behavior of rats is greatly influenced by the presence of conspecifics (Brown 2011; Weiss et al. 2015, 2017a, b; Dorfman et al. 2016). Moreover, the spatial behavior of rats in dyads is more chaotic than their behavior when alone, since a lone rat has to organize its spatial behavior only in relation to the physical environment, whereas when in a dyad it has to organize it also in reference to a moving point of reference—the other rat (Weiss et al. 2015; Dorfman et al. 2016). Explicit in this addition of a moving focal component is elevated complexity (Bar-Yam 1997). Theoretically, adding a third, fourth, or more partners should further increase the social complexity with which animals need to contend when orienting in time and space, and group behavior may become utterly chaotic. This is definitely not the case since animals move in large herds, packs, swarms, flocks and schools (Krause 1993; Grand and Dill 1999; Krause and Ruxton 2002; Couzin et al. 2002; Ward 2011). There are various ways to reduce the theoretical complexity, and here we found that rats rarely traveled in groups of more than one or two, but rested in larger groups. Accordingly, their organization in time and space during travel was manageable, whereas at rest the rats only had to coordinate the location of their home base. In other words, the present study shows that a group of rats comprises a relatively

**Fig. 11** A list of the gradual changes that rats undergo as part of the process of group formation. We suggest that this process is tri-phasic, with each hour starting a new phase. In the first phase (*formation*), rats are most active and less attendant to other rats or to sharing a home base. In the second phase (*stabilization*), rats become less active and begin to settle together. In the third and last phase (*performance*), there is already a shared home base in which all the rats huddle together. From the home base rats take solo or duo roundtrips. The numerals on the right of some parameters indicate the magnitude of the change compared to the beginning of the trial



large number of individuals staying together in one place, but with the group members typically traveling alone or with one partner.

The present results demonstrate that the eight unfamiliar rats began with relatively independent exploration of the physical arena (Fig. 9; Online Resource 1). This was reflected in the finding that during the first 30 min there were four home-base locations for the eight rats. From the second hour on, they converged to one and the same home-base location (Fig. 10; Online Resource 3). The home base is the most prominent and stable feature of spatial behavior in rats, and sharing the same home-base location indicates that the entire group of eight rats similarly organized their behavior in reference to that same location, as reflected in the trajectories of progression of each rat during the last 5 min, compared with their trajectories during the first 5 min (Fig. 9). Indeed, this figure illustrates how spatial behavior of eight unfamiliar rats was initially relatively independent of one another and anchored at various physical locations. With time, home-base behavior of all eight rats converged and became coordinated and anchored in the same physical location.

## Conclusion

While research on socio-spatial cognition has been gaining ground recently, little is still known on how individuals become organized in time and space when in a group.

Furthermore, the process of group formation in the animal world, and rodents in particular, is still unclear. The social environment is a prominent factor in shaping the individual's behavior (Krause 1993; Couzin et al. 2002), and specifically its spatial organization (Loewen et al. 2005; Weiss et al. 2015, 2017b; Dorfman et al. 2016). In the present study we found that time spent traveling with companions decreased as group size rose, with all the rats gradually shifting to share the same location as a home base, but traveling mostly alone or in duos. We suggest that by doing so, rats on the one hand maintain a communal relationship, while on the other hand avoiding the complexity of traveling in large groups. These processes, which characterize group formation, are schematically summarized in Fig. 11. It is possible that some of these processes predominated group formation whereas other processes were a product of the former ones. While the present analysis of group formation could not discern among such processes, it provides a description of group formation from relatively independent three perspectives: social network analysis, activity, and spatial distribution of activity. As shown, group formation can be viewed as a tri-phasic process, with some rats gradually becoming more social than others, and thus playing a key role in group formation. Starting with several home-base locations, the rats gradually converged to share the same location as their home base. Since the home base is considered as the organizer of an individual's spatial behavior (Eilam and Golani 1989), sharing the home base implies that the

spatial behavior of all group members has become organized in relation to the same location, which is now not only the organizer of the individual, but also the organizer of the entire group.

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## Compliance with ethical standards

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

**Ethical approval** 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 # 04-15-061).

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