



Research report

Spatial reorientation in rats (*Rattus norvegicus*): Use of geometric and featural information as a function of arena size and feature locationJoseph H.R. Maes^a, Laura Fontanari^{b,*}, Lucia Regolin^c^a Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, 6500 HE Nijmegen, The Netherlands^b CIMeC Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, 38068 Rovereto, Trento, Italy^c Department of General Psychology, University of Padova, Via Venezia 8, 35131 Padova, Italy

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ABSTRACT

Rats were used in a spatial reorientation task to assess their ability to use geometric and non-geometric, featural, information. Experimental conditions differed in the size of the arena (small, medium, or large) and whether the food-baited corner was near or far from a visual feature. The main measure was the percentage of trials with first-choice visits to the baited corner (Corner C) and the geometric equivalent corner (Corner R). Regardless of arena size, only the rats in the near-feature condition learned to make more first-choice visits to Corner C than Corner R. However, in this condition, there was a significant trend suggesting an increasing and decreasing use of, respectively, featural and geometric information with increasing arena size. Continued training with the feature removed caused all rats to primarily visit Corners C and R, reflecting the exclusive use of geometric information. However, again, there was a significant trend suggesting a decreasing use of this type of information with increasing arena size. These results were discussed in the framework of data from previous studies assessing reorientation in other species and of an associative-learning model.

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1. Introduction

Spatial representations enable animals to orient in their own environment. A spatial reorientation paradigm helps us to understand the nature of the environmental features serving as the constitutive elements of spatial representations, allowing spatial mapping processes. The ability to reorient is the result of one's capacity of identifying a location and of establishing a heading by reference to the characteristics of the external environment [6]. Thus, animals in the absence of (very) distant external reference cues, such as the sun, must resort to more local spatial information. Experiments with several animal species, such as fishes (*Xenotoca eiseni*, *Carassius auratus*), chicks (*Gallus gallus*), pigeons (*Columba livia*), rats (*Rattus norvegicus*), rhesus monkeys (*Macaca mulatta*), and humans have been performed in order to assess which kind of spatial information disoriented animals use for reorienting, both from a comparative and a developmental perspective (see for a review [3]). All these studies focused on the encoding of geometric and non-geometric environmental information.

A typical example of an experimental set-up used in the corresponding research is shown in Fig. 1a. Specifically, one corner of a rectangular enclosure is defined as the 'correct' Corner (C),

either by instruction or by providing a reward for visits to it. In one experimental version, in a so-called reference-memory paradigm, the location of the correct corner remains the same from trial to trial and the subject is required to remember and relocate this corner after disorientation. Disorientation may involve rotation of the experimental subject or removal from the enclosure, followed by replacement in a randomly chosen location. In case the arena does not contain any specific 'featural' information, that is, when in Fig. 1a all walls have the same colour, a reliable finding is that, upon replacement into the enclosure, experimental subjects visit Corner C, and the corner that is geometrically identical to this corner, namely Corner R (at 180° rotation), an equal number of times. Moreover, the subjects visit each of these corners significantly more than either the corner nearest to Corner C (Corner NC), or the corner that is nearest to Corner R (Corner NR). This pattern of results is suggestive of the use of geometrical information to reorient. The ability to use this type of information seems to be widespread among vertebrates.

Correct relocation of Corner C may be possible on the basis of additional non-geometric or 'featural' information. This type of information may be provided by a specific landmark located near Corner C, such as when the short wall adjacent to such corner is of a different colour compared to the other walls (see Fig. 1a). Corner C can now be unequivocally distinguished from Corner R.

Results of studies examining the ability of various species to successfully locate Corner C in an experimental set-up as

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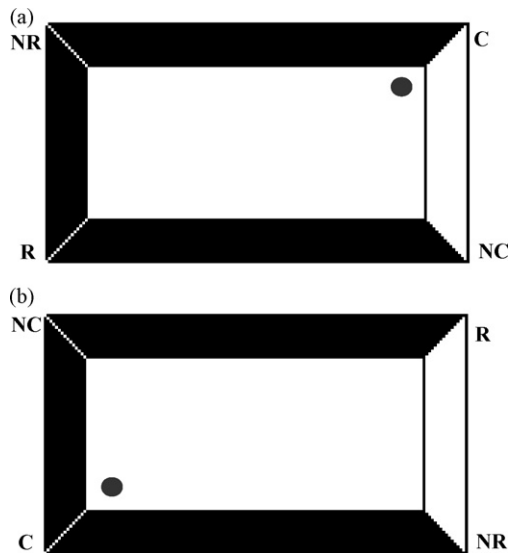


Fig. 1. Example of the experimental arena used in relocation tasks. Corner C is the baited corner and Corner NC is the corner closest to Corner C. Corner R is the geometrically equivalent to Corner C; Corner NR is the corner nearest to Corner R. (a) In the 'near-feature condition', the distinctive featural information provided by a coloured wall is positioned near the target Corner C. (b) In the 'far-feature condition', the feature (coloured wall) is on the opposite side of the arena, near Corners R and NR.

described above, implying the capacity to conjoin geometric and non-geometric (featural) information, are mixed. Three fish species have been shown to be able to combine geometric information and featural information provided by a coloured wall (referring to Fig. 1a: either the top long wall or the right short wall; retdail splitfins: [16,18]; goldfish: [23]; convict fish: [1]). The fish is also able to use featural information consisting of panels located in the corners. However, when these panels are only present far from the target, the animals fail to combine the information provided by the remaining features and the geometry [17].

Chicks have also been found able to conjoin geometric and featural information provided by visually distinct panels located in the corners. However, as in fish, this capacity seems to be lost when the featural information solely consists of panels in Corners NC and NR [20,21].

Pigeons were shown able to conjointly use geometric and non-geometric information even when the latter (i.e., distinctive panels located in the corners) is presented far, rather than near, the target corner [10].

Rhesus monkeys have also been found able to combine the two types of information under certain conditions, that is, both when the featural information consisted of a coloured short wall near the target Corner C (see Fig. 1a) and when the short coloured wall was on the opposite side of the arena (i.e., near Corners R and NR in Fig. 1b). However, monkeys systematically make rotational errors (i.e., visits to Corner R) in both such conditions, and were not able to combine the two types of information when the distant feature consisted of distinctive panels [8].

Human children less than 5 years of age have been reported to be both able [11,12] and unable (i.e., visiting Corners C and R equally often; [9,11]) to use featural information provided by a coloured short wall (right wall as in Fig. 1a). This discrepancy may be related to differences in size of the environment. Specifically, use of non-geometric cues may be restricted to relatively large environments [11]. However, as in the monkey studies [8], even in large environments the children still made systematic rotational errors, visiting Corner R more often than each of the other incorrect corners.

Data for human adults largely correspond with those of older children: they are able to combine the two types of information

regardless of the size of the environment and they make relatively few rotational errors (see Ref. [3] for reviews).

Overall, it seems clear that the spatial scale of the environment plays a crucial role in animals' ability to conjoin geometric and non-geometric information (see for a review [5]). Fishes reoriented by conjoining geometric and non-geometric information independently of the size of the enclosure [18]. Moreover, they were able to reorient when relocated from a large to a small experimental space and vice versa. But an effect of the size was observed with respect to the type of errors fishes made [18,20]: when a generalization occurred from the small to the large tank, they committed relatively more geometric errors, whereas when a generalization occurred from the large to the small tank, fishes committed relatively more non-geometric errors.

Also domestic chicks (*Gallus gallus*) conjoin geometric and non-geometric information in small and large enclosures [22]. Moreover, they reorient immediately when displaced from a large to a small space. Unlike fishes and toddlers, they did not show any differences in the amount of errors. With chicks, the effect of size emerged only when geometric and non-geometric cues provided contradictory information. This was experimentally obtained with transformations altering the geometric relation between the target and the shape of the environment. In such condition, when tested in a small enclosure, chicks relied on geometry, whereas, in the large enclosure, they relied on local features [22]. The claim that chicks encode both types of information in large as well as in small enclosures is further supported by more recent experiments [4]. In these experiments, differences were observed as a function of the size of the experimental space. After removal of the featural cue, chicks searched at the two geometrically equivalent corners, after removal of the geometrical cue they searched at the corner identified by the correct feature; use of residual geometrical information was stronger in small than large arenas whereas use of residual non-geometric information was stronger in large than in small arenas.

Finally, another animal species that has been examined, which is also the focus of attention in the present experiment, is the rat. Rats are able to combine geometric and non-geometric information (provided by landmarks) in a reference-memory task but not in a working-memory task [2], in an escape task but not in search task [7], although rotational errors are made relatively frequently. Moreover, when only 'distant' featural information is present in the form of landmarks in Corners NC and NR, rats make as many visits to Corner C as to Corner R [2].

These comparative data suggest two factors that may play a role in the ability to conjoin geometric and non-geometric information. The first factor is the location of the featural cue. Using only landmarks that were relatively remote from the target Corner C (namely in Corners NC and NR), fish, chicks, and rats appeared to be unable to use the featural information provided by these landmarks, whereas pigeons could use non-geometric information both when this was placed near or far from the target corner.

However, rats were able to do so when a feature was present near the target corner using as landmarks both distinctive panels located in the corners and a continuous surface (such as a coloured wall; see Fig. 1b). The second relevant factor, as mentioned above, is the size of the enclosure. At least in young human children (but not older children and adults), the featural information appears to be only used when the experimental room is relatively large [11]. In fishes and chicks, arena-size manipulations did not affect the ability to use featural information provided by a coloured wall even though subjects made different types of errors as a function of arena size, showing a preferential use of geometric information in small enclosures and non-geometrical information in large enclosures. It remains to be seen whether this is also true for rats.

The purpose of the present study was to further assess the conditions under which rats are able to use the information provided by

geometric and featural cues. Specifically, rats were trained in experimental conditions that differed in arena size and/or in the location of featural information that was provided by the colour of a short wall (either the short wall near Corners C and NC or Corners NR and R). If size of the enclosure is an important determinant of the ability to use the featural information, as it appears to be the case in human children, rats should only be able to distinguish between Corners C and R in relatively large enclosures. However, even in such a large arena, this ability may be restricted to the condition in which the feature is located near the target corner.

2. Methods

2.1. Subjects

The subjects were 12 male *Wistar* rats, bred and reared at the Radboud University Nijmegen, The Netherlands. The animals were experimentally naïve and had a mean body weight of 396 g prior to the experiment. The rats were housed in Plexiglas cages with a bedding of wood chips. They had free access to water, whereas availability of food was restricted, to maintain the animals at 85% of their free-feeding weight. The rats were maintained on a 12/12-h dark/light cycle, with all experimental sessions conducted in the dark phase. Sessions were run during week days.

2.2. Apparatus

Three different-sized experimental rectangular enclosures were used. One enclosure (small arena) consisted of a Plexiglas box, measuring 50 cm × 25 cm × 38 cm (length × depth × height). The second (medium) and third (large) arena measured, respectively, 100 cm × 50 cm × 38 cm and 200 cm × 100 cm × 38 cm. The dimensions of the medium arena are close to those of the arena used in previous research (e.g. in Ref. [2]: 120 cm × 60 cm × 38 cm). The dimensions of the small and large arena are chosen so as to create relatively large differences in size but to preserve the short/long wall ratio. Each box had black walls and a black floor that was covered with a layer of wood chips. Except during the second training phase (see below), a piece of white board was placed in front of one short wall, to provide a distinct visual cue. The boxes were located in an experimental room that was illuminated by two white 36-W fluorescent tubes located centrally in the ceiling above the box. To record the rat's behaviour inside the box for off-line scoring, a video camera was fixed to the ceiling at a distance of 2.5 m above the box. The camera was connected to a video recorder located behind a curtain in the experimental room. Each box contained four Petri dishes (diameter: 9 cm), one in each corner. Each dish was filled with 45-mg sucrose pellets. Three dishes were covered by an aluminum grid, which enabled the rat to smell the pellets, while preventing it from eating them. An uncovered dish was located in Corner C. For the rats in the 'near-feature' condition, this corner was located in the top right (i.e., Corner C in Fig. 1a), in front of the short white wall. For the subjects in the 'far-feature condition', this dish was positioned in the bottom left corner, in front of the short black wall (i.e., Corner C in Fig. 1b).

2.3. Procedure

The experiment was run in two replications with 6 animals in each. Each animal was assigned to one of three groups ($n=4$). The groups were matched on the basis of body weight. One group was trained in the small arena, a second group in the medium arena, and a third in the large arena. For one half of the rats in each condition, Corner C was always to the left in front of the short white wall; for the other half it consistently was to the left in front of the short black wall. During the training phase, each animal received 8 trials a day, 5 days a week. On each trial, a rat was placed in the middle of the arena, with the location of its head facing the middle of one of the four walls. The choice of the corresponding wall was randomized across sessions. For a maximum of 10 min, the rat was allowed to find the food in Corner C and to eat two pellets. After 10 min or after eating two pellets (whichever came first), the animal was taken out of the arena and placed back into the home cage. The animal was placed back into the arena after a delay of 10–30 s (inter-trial interval, ITI). In the ITI, the arena was rotated 90° or 180°, with the direction of the rotation (to the left or to the right, implying four different positions of the arena) being randomized across trials. Randomization of location of the rat and the arena ensured that the rat could not rely on compass, inertial, or extra-maze cues to locate Corner C. Training continued for a total of 16 days.

In the next phase, training was continued with 8 trials on each of 5 days. The trials were as in the previous training phase except that the short white wall was removed from each of the three arenas. A black wall, identical in colour as the other walls, became visible as a consequence of this manipulation. Hence, the animals could only rely on geometric information to reorient.

2.4. Dependent measure and data analysis

The main dependent measure was based on the type of corner (Corner C, R, NC, or NR) that was visited first on each trial. A visit was defined as 'touching the

Petri dish (or the grid covering it) with whatever part of the rat's body'. For each session, the percentage of trials on which the corner was visited first was computed for each corner, on the basis of the 8 trials within the session. This measure was used as the dependent variable in repeated measures analyses of variance (ANOVAs). Overall ANOVAs were followed by ANOVAs examining specific contrasts. Specifically, for training phase, the percentage of first-choice visits to Corner C was contrasted with that to Corner R, to assess the ability of the rats to distinguish between these two corners. This was used as a test for the ability to combine geometrical and feature information, because such an ability would result in significantly more visits to Corner C than to Corner R. Also, the contrast between the sum of the percentages for Corners C + R and the sum of the percentages for Corners NR + NC was examined to assess the use of geometrical information. The difference between percentage first-choice visits to Corners NC and NR (Difference Score 1) was used as an index of the 'attention-drawing' capacity of the feature: the larger the (positive) difference, the more attraction by the feature. Finally, as a further measure of the ability to specifically use geometrical information, we examined the difference between the percentage first-choice visits to Corner R and the mean of the percentages first-choice visits to the two other non-geometrically correct corners, Corners NR and NC (Difference Score 2). The larger this difference score, the more use of geometrical information is presumed to have been made by the subject. Specifically examined was whether each of these scores showed a linear decreasing or increasing trend as a function of arena size. The level of significance was set at $p < .05$ in all statistical tests.

3. Results

3.1. Training with feature

The rats in each arena-size and feature-location condition showed a gradual decrease across sessions in the mean number of corners visited before eating two pellets. The overall mean number of visits on each trial, pooled across arena size and feature location, decreased from 4.38 to 2.25 from Session 1 to Session 16. Arena (arena size: 3 levels) × Feature Location (2 levels: near or far from target corner) × Session (16 levels) ANOVA using the mean number of visits only revealed a significant main effect of Session, $F(15, 90) = 8.40, p < .001$. Moreover, a similar analysis using the data from the last 5 days of training revealed main effects of Feature Location, $F(1, 6) = 7.15, p = .04$ and Arena, $F(2, 6) = 5.1, p = .05$. The main Feature Location effect reflects the fact that the animals in the near-feature condition needed less visits to eat the two pellets (mean: 1.98 visits) than did those in the far-feature condition (mean 2.54). The Arena effect was due to the rats trained in the large arena needing more visits (mean: 2.71) than the animals trained in the small arena (mean: 1.90). The mean number of visits in the medium arena was in between that of the other two arenas (mean: 2.16).

The rats in all conditions gradually came to emit differences in the percentage of first-choice visits as a function of corner type. Fig. 2 displays, for each arena-size and feature-location condition, the mean percentage of trials on which each corner was visited first. This mean is based on the last five training sessions.

The figure suggests that, irrespective of arena size, the rats with the white wall as near feature were able to distinguish between Corners C and R, whereas those with the white wall as far feature were not. In the latter condition, the rats seemed to primarily rely on geometrical information. Within the near-feature condition, there appeared to be a trend for the Difference Score 1 (indexing 'attraction' by the feature) to increase with increasing arena size. Finally, there seemed to be a tendency for the rats in the near-feature condition to make less rotational errors (visits to Corner R) and more visits to the un-baited corner near the feature (Corner NC), with increasing arena size.

This description of the data was supported by statistical analyses. Arena × Feature Location × Contrast (Corner C vs. Corner R) ANOVA on the data displayed in Fig. 2 only revealed a near-significant Location × Contrast effect, $F(1, 6) = 4.49, p = .078$. Despite the fact that the Location × Contrast effect was only marginally significant, the analysis clearly suggests a trend towards a difference in first-choice visits between the near- and far-conditions. Because of this result, and on the basis of our hypothesis and visual

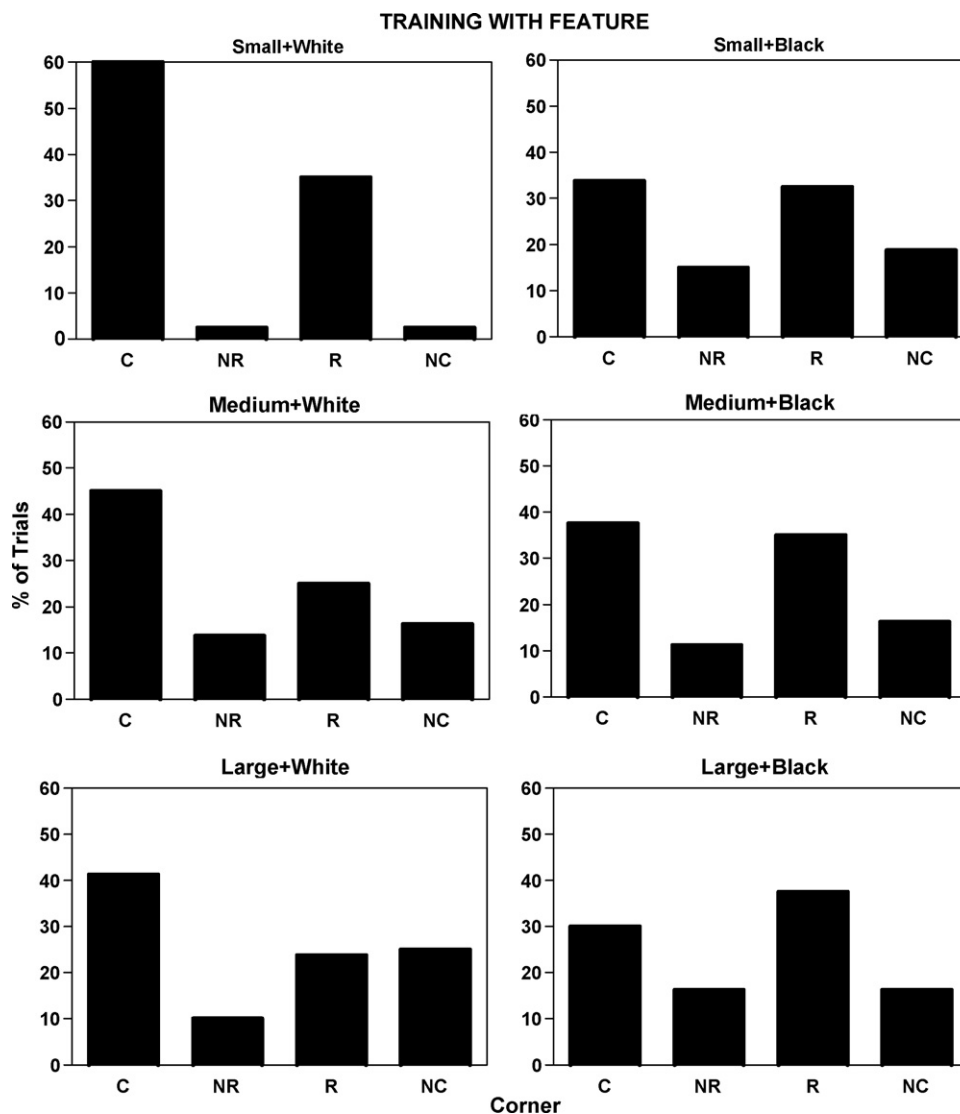


Fig. 2. Mean percentage of trials on which the rats first visited each of the different corners after being released in the arena. The data are based on the last five training sessions. Experimental conditions differed with respect to the size of the rectangular arena (small, medium, or large) and whether the short wall near the baited corner was white or black. See Fig. 1 for an explanation of the corner indices.

inspection of the data in Fig. 2, we analyzed the data separately for the near- and far-feature conditions. ANOVA comparing first-choice visits to Corners C and R for the near-feature condition (pooled across arena sizes) revealed a significantly higher percentage for Corner C than Corner R, $F(1, 5)=9.33$, $p < .028$, suggesting the combined use of geometrical and feature information. The mean Difference Score 1 was 0.0, 2.5, and 15.0, for the small, medium, and large arena, respectively, and the increasing linear trend was significant, $p = .046$, suggesting increased attraction by the feature with increasing arena size. The Difference Score 2 was 32.5, 10.0, and 6.25 for the small, medium, and large arena, respectively, and the decreasing linear trend was significant, $p = .041$, suggesting less use of geometrical cues with increasing arena size.

Focusing on the data from the far-feature condition depicted on the right side of Fig. 2, a Corner C vs. Corner R comparison clearly revealed no difference, ANOVA with Contrast as main factor, $F < 1$, suggesting the absence of any use of the featural information. The rats clearly relied on geometrical information in each arena size, as suggested by the results of an Arena \times Contrast (sum of Corners C + R vs. sum of Corners NR + NC) ANOVA, which revealed significantly more visits to Corners C and R than to Corners NR and NC in each

arena-size condition, main Contrast effect, $F(1, 3) = 12.27$, $p = .039$, with the interaction effect being insignificant, $F < 1$. An examination of the Difference Scores 1 and 2 clearly failed to reveal significant linear trends, $ps > .92$, as a function of arena size.

3.2. Continued training without feature

Fig. 3 depicts the results of the second training phase. The figure suggests that, without the information provided by the white wall, the rats in all arena-size and previous feature-location conditions relied on geometric information to guide their choices. However, there seemed to be a tendency for the rats to make less use of this type of information with increasing arena size.

An Arena \times Previous Feature Location \times Contrast (Corner C vs. Corner R) ANOVA on the data in Fig. 3 did not reveal any significant main or interaction effects, $ps > .1$, which reflects the absence of any feature information. An Arena \times Previous Feature Location \times Contrast (sum of Corners C + R vs. sum of Corners NR + NC) ANOVA only revealed a highly significant main contrast effect, $F(1, 6)=51.70$, $p < .001$, suggesting the use of geometrical information in each condition. However, ANOVA with arena size

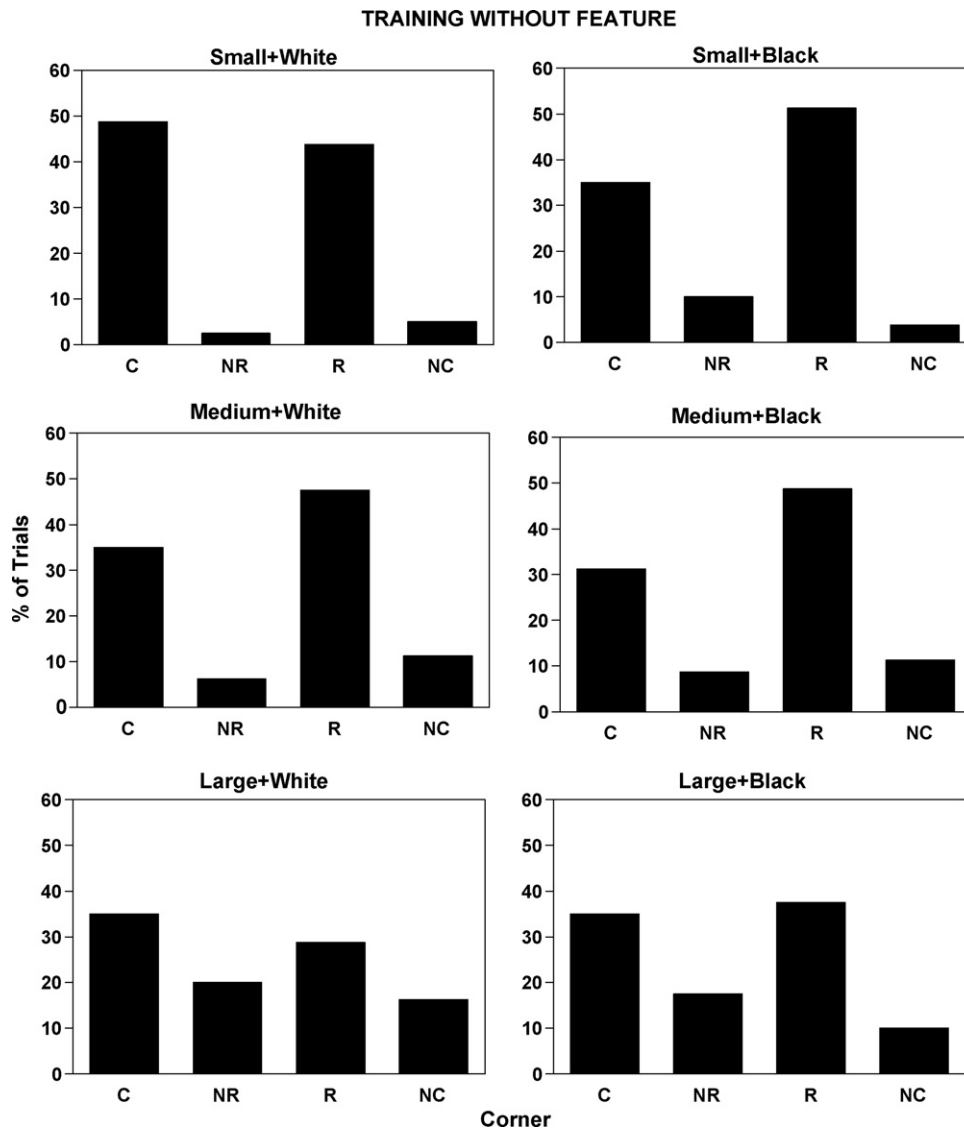


Fig. 3. Mean percentage of trials on which the rats during the second training phase (5 sessions) first visited each of the four corners. The white-wall feature was removed during this training phase, but the different arena-size and feature-type conditions as present during the initial training phase are still indicated above each graph for comparison purposes. See Fig. 1 for an explanation of the corner codes.

as single factor on Difference Score 2 (values: 42.19, 38.75, 17.19, for the small, medium, and large arena, respectively) revealed a significant decreasing linear trend, $p = .044$, suggesting a decreased use of geometrical information with increasing arena size.

4. Discussion

The data of the first training phase suggest that the rats were able to use geometric information and featural information given by a coloured wall, provided the latter is presented near the target location. Moreover, the larger the arena, the more the rats were attracted by the feature cue, and the less they used geometrical information. After removal of the white wall, the rats primarily used geometrical information, supporting the claim that during the first training phase with the feature present, the rats in the near-feature condition were indeed using the featural information and that the ability to distinguish between Corners C and R did not rest upon the use of some other cues, like extra-maze cues. Finally, in the first training phase with feature, the tendency for a reduction in the use of geometrical information with increasing arena size, as indexed

by Difference Score 2, was only present in the near-feature conditions. However, with continued training without the feature, an identical tendency also appeared for the rats that, in the previous training phase, had been trained with the far feature. This finding again supports the suggestion that, generally (i.e., also in the absence of featural information), small and large arenas, respectively, encourage and disfavour the use of this type of information.

The finding that large environments promote the rats' use of featural information is consistent with the data from the study by Learmonth et al. [11] with 3–5 year old children, who only used the featural information provided by a blue curtain when they were in a relatively large room. Next to a relatively large arena size, another factor that proved to be conducive to the rats' use of featural information was a location of the feature that was near to, as opposed to far from, the target corner. This finding is consistent with data from studies on fish, chicks, and rats, in which the featural information was provided by landmarks located near the corners (differently from pigeons).

Turning now to an explanation of the arena-size effect observed in rats and children, one suggestion is that these species are inclined

to only use featural information relevant for reorienting when the corresponding cues are at some minimal distance [14]. It has been suggested that animals are 'prepared' to treat non-geometric features as orienting cues (landmarks) only when these are perceived as farther away, but not when they are perceived in close proximity. In the light of this explanation, in a small room when the feature is placed at 6 ft (about 183 cm) of distance (i.e., the length of the long wall) it is not treated as a landmark by the children; the same feature in a larger room (located at 12 ft, about 366 cm, of distance) is instead used as a landmark for reorienting. In other words, distance to the feature may be the critical factor. However, another possibility is that the critical factor is feature size (related to its salience). Support for this possibility comes from a monkey study by Gouteux et al. [8]. Specifically, while keeping constant the arena size, the size of the featural information (provided by a coloured panel in the middle of one short wall) was manipulated. The monkeys could only discriminate between Corners C and R when the panel was relatively large. In our present experimental set-up, the two factors are obviously confounded: the size of the feature proportionally increased with the increasing of arena size. Therefore, the present data cannot be used as evidence for one or the other possibility. Perhaps, it is most plausible to assume that both factors interact. There must be some minimal distance from the feature cue in order for it to be used as orientation cue, but the cue must also have a minimal dimension for it to be sufficiently salient to be noted at all.

The most plausible hypothesis for explaining the size effect for using both geometric and non-geometric information was put forward by Sovrano and Vallortigara [19]. They claimed a different linkage of sense information (left–right) with either metric (long vs. short wall) or landmark information depending on the size of the environment. In small spaces animals link sense with metric properties of surfaces, in large spaces animals link sense with local landmark cue. Both chicks and fishes were tested in a transformation altering the geometric relations between the target and the shape of the environment (affine transformation). Chicks tended to make more geometric errors when tested in the small than in the large space [4,22]. In a large enclosure, chicks associate local information with sense information, whereas in a small enclosure they preferentially associate metric properties of the surfaces with sense [19]. In support of this hypothesis, fishes tested in large and small tanks with a displacement of the coloured feature on the adjacent wall chose the corner that maintained the correct metric arrangement of the walls with respect to sense in the large space. In the small environment, fishes chose the corner that maintained the metric arrangement of the walls with respect to sense between the two corners with the coloured feature, and they even chose the corner in the geometric position lacking any featural cue [20]. This would explain why geometric information, although encoded even when not strictly necessary, it is not used in large spaces (see Ref. [3] for a review). This hypothesis would explain the different kinds of errors our rats make as a function of arena size: increasing of non-geometric errors and decreasing of the geometric ones with increasing of arena size. Of course more research is necessary in order to fully extend this hypothesis to rats. It would be interesting to see how rats behave when transferred in arenas of different size and in following an affine transformation of the arena.

Yet another (or perhaps better: complementary) theoretical approach, which may incorporate certain assumptions based on some of the foregoing models, is in terms of an associative-learning model, like the Rescorla-Wagner model [15] (see also Ref. [13] for a conceptually identical approach). Accordingly, such a model may treat corner and colour cues as two separate stimuli that gain or lose associative strength, which in turn may be translated into strength of 'approach' or 'avoidance' tendencies, as a result of being paired with (non-) reinforcement. Specifically, suppose a corner with a

long side to the left and a short wall to the right is perceived as a separate cue, 'Cue A'. A corner with a long wall to the right and a short wall to the left is called 'Cue B'. Moreover, suppose we consider the colour of the wall near each corner as 'Cue X' when it is white and 'Cue Y' when it is black. Therefore, Corner C may be represented as consisting of the stimulus compound AX. Likewise, Corners NR, R, and NC may be represented as, respectively, BY, AY, and BX. Accordingly, for the rats in the near-feature condition, we can describe the training trials as AX+, BY–, AY–, BX– trials, with + and – representing the presence and absence of food-reinforcement, respectively. The corresponding training trials in the far-feature condition are: AY+ (Corner C), BX– (Corner NR), AX– (Corner R), and BY– (Corner NC). These hypothetical stimulus compounds may be used as input in computing associative-strength changes of the constituent elements as a result of training trials. We performed a number of such computations (the results of which will not be presented here for the sake of brevity) and were successful in simulating the main results given certain assumptions concerning the salience of stimulus elements, specifically, that the white wall is more salient than the black wall and that the salience of the feature is larger in a large as opposed to a small arena.

Overall, regardless of these theoretical considerations, the present results allow us to support the claim that, as is the case for other species, in rats small spaces encourage the use of geometric information, whereas large spaces encourage the use of non-geometric information near the goal.

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