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Spontaneous Object Recognition Memory is Maintained Following Transformation of Global Geometric Properties

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Abstract

Studies of spontaneous behaviour to assess memory are widespread, but often the relationships of objects to contexts and spatial locations are poorly defined. We examined whether object-location memory was maintained following global, but not local, changes to the geometric shape of an arena. Rats explored two trial-unique objects in a distinctively shaped arena before being exposed to two identical copies of one of these objects in a different shape in a different physical location. Rats preferentially explored objects that were novel in relation to their local geometric context rather than identifying both locations as novel in the global geometric context.

KEYWORDS: Object location memory, Context, Spatial memory, Geometry.

Author note

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There is considerable evidence that when disoriented animals use the geometric properties of the environment to determine direction. Cheng (1986) was the first to demonstrate this by training rats to locate food in one corner of a rectangular arena. During a retention interval the arena was rotated to ensure the rats had to reorient themselves when they were reintroduced to the arena and allowed to search for the food. Despite the presence of visual or odor cues that could have been used to disambiguate geometrically equivalent corners, the rats consistently made rotational errors, searching in the corner that was featurally distinct from the correct corner, but which shared the same geometric properties. These results have been interpreted to support the notion of an encapsulated module for encoding a representation of environmental geometry that is processed independently of learning based on non-geometric features (Cheng, 1986; Gallistel, 1990; Hayward, McGregor, Good, & Pearce, 2003; McGregor, Horne, Esber, & Pearce, 2009).

Whilst Cheng's (1986) task required rats to reorient with respect to geometric cues after only a single exposure to the environment (see also Margules & Gallistel, 1988), many subsequent studies have explored the use of geometric cues through tasks that involved extensive training to a hidden goal. These have often shown that animals are able to integrate geometric and featural information to avoid making errors to geometrically equivalent but featurally incorrect locations (e.g., Cheng, 1986; Gouteux, Thinus-Blanc, & Vauclair, 2001; Sovrano, Bisazza, & Vallortigara, 2002; Vallortigara, Zanforlin, & Pasti, 1990; Vargas, Petruso, & Bingman, 2004). Indeed, a number of these studies have eroded a central prediction of the geometric module hypothesis that

learning based on geometry should progress independently of learning based on features when the two cue types are presented in compound (e.g., Graham, Good, McGregor, & Pearce, 2006; Horne & Pearce, 2009; Pearce, Graham, Good, Jones, & McGregor, 2006; Rhodes, Creighton, Killcross, Good, & Honey, 2009). However, a number of authors (Cheng & Newcombe, 2005; Gallistel & Matzel, 2012; Sutton, 2009) have suggested that these cue competition studies fail to test the process that the geometric module is responsible for – using geometric cues for reorientation. Reorientation is best studied in circumstances similar to Cheng's (1986) experiment, in which animals returned to a location following a single exposure to the geometric and non-geometric cues near the goal location. The purpose of the current study was to develop a task in which effective reorientation, following a single exposure to the environment, could be achieved only by integrating non-geometric features with the shape of the environment. To achieve this, we adapted an object-location memory task with 'location' information provided only by cues forming the shape of the arena.

The object-location task enabled a second prediction from the geometric module hypothesis to be tested. Cheng and Spetch (1998) and Gallistel (1990) both proposed that in their initial exposure to the arena, rats formed a representation of its overall, or global, shape. Although Pearce, Good, Jones, & McGregor (2004) and Tommasi and Polli (2004) provided evidence that was consistent with animals basing their search behavior on local cues derived from the metric properties of the walls near the goal location (e.g., rats could learn to approach a corner with a particular arrangement of long and short walls), those studies also involved the use

of extensive training to locate a hidden goal. It is possible that the use of extensive training by Pearce et al. (2004) and Tommasi and Polli (2004) altered the way in which animals used geometric cues, compared with the way in which geometry was used by rats in Cheng's (1986) study. Support for such an assertion comes from analyses of where rats swam following release from different locations in the arenas. Pearce et al. (2004) and Jones, Pearce, Davies, Good, and McGregor (2007) showed that following training, rats were more likely to swim directly to the corner containing a hidden platform when released from short walls than from long. They concluded that rats developed a habit (such as a stimulus-response association) of swimming in a particular direction following their release from some walls. In experiments examining whether rats formed a global representation of the geometric properties of the environment, it is possible that these habits formed the basis for the pattern of behavior observed. For example, Pearce et al. (2004) and Esber, McGregor, Good, Hayward, and Pearce (2005) trained rats to locate a platform in one arena before testing them in another with the overall shape transformed but in which some of the local geometric cues were common to both. They found that despite the change in overall shape, the rats continued to search in locations consistent with the platform's position relative to the local geometry of the training environment.

To determine whether rats can recognise an object based on its location relative to the local geometric context after only a single exposure to the environment, we utilised a spontaneous object recognition task in two arenas with different global shapes. The spontaneous object recognition task is frequently used to examine recognition memory in

rodents. Ennaceur and Delacour (1988) first developed the task to take advantage of the natural tendency of rats to explore novel over familiar objects (Cowan, 1976). Typically, in a sample phase rats are presented with identical copies of an object, A, in a familiar open-field arena. In a test phase one copy of A is presented together with a novel object, B, and this is explored in preference to object A. Variants on the task have been used to examine the rat's spatial memory by presenting familiar objects in novel locations (Ennaceur, Neave, & Aggleton, 1997), and the role of spatial context has been examined by swapping a familiar object's location with that of another (e.g., Dix & Aggleton, 1999; Good, Barnes, Staal, McGregor, & Honey, 2007) or by presenting novel object-location combinations in featurally distinctive environments (e.g., Eacott & Norman, 2004). The current study provides us with an opportunity to better understand the mechanisms underlying spontaneous recognition of object-location combinations by testing whether animals can use the local geometric properties of the environment for this recognition or whether maintenance of the global geometric context or distal spatial information is necessary. In Experiment 1 rats were exposed in a sample phase to an object, A, in one right-angled corner of an arena with a distinctive shape (e.g., the corner was made up of a long wall to the right of a short wall), with a second object, B, in another corner that was also right-angled but which was the mirror-opposite of the corner containing object A (e.g., the corner was made up of a long wall to the left of a short wall; see Figure 1). Following a retention interval rats were placed in a new arena in a different room. The second arena was a different overall shape to the first, but the local geometric properties of the right-angled

corners in the two arenas were identical. A new copy of object A was placed in the corner with the same local geometric properties as in the sample phase, together with another copy in the mirror-opposite of that corner. Should rats exhibit a preference for exploring the copy of object A in the novel geometric location then it would indicate that they are capable of remembering the location of an object with reference to the local contextual cues provided by an arena's shape, and that object-location memory is not dependent on the global shape of the arena, the absolute position of the object in a room, or its position relative to other objects. In Experiment 2 we extended the generality of the findings from Experiment 1 by using different shapes for the sample and test phases.

An additional benefit to conducting the study using an object-location task is the possibility that the aversive nature of the water maze tasks described above altered the strategy used by rats to learn the location of the platform. Differences in reorientation strategies can occur between appetitive and aversive tasks (Dudchenko, Goodridge, Seiterle, & Taube, 1997; Golob & Taube, 2002; Whyte, Martin, & Skinner, 2009), possibly due to the disparity in training, motivation, visual cues and proprioception (see Hodges, 1996, for review). Given the foregoing discussion, the primary purpose of the experiments described in the current article was to assess whether rats transfer their spatial behaviour between differently shaped arenas based on the memory of an object's location in a *non-aversive, untrained* task. As such, the experiments remove two inherent problems with previous studies claiming rats learn a location based on local geometric cues: training, and the nature of the reinforcement. In our task the ability of

rats to detect the object in the novel geometric location following transfer between arenas would indicate that in a single exposure to the environment the rat combined the identity of the object and its location relative to the geometric properties of the arena. To our knowledge this would be the first demonstration of such a finding in the rat.

Method

Thirty adult male Lister Hooded rats were used in Experiment 1, twenty of which were experimentally naïve and ten with experience in an unrelated water maze task. The prior experience of the latter ten animals was counterbalanced. For Experiment 2, twenty experimentally naïve adult male Lister Hooded rats were used. All animals were supplied by Harlan Olac (Bicester, UK). They were housed in pairs in a light-proof room in which the lights were turned on at 0700 hours and off at 2100. Testing was conducted during the light phase. Two medium-density fibreboard arenas each occupying separate testing rooms were used. The two testing rooms were of similar dimensions (approximately 290 cm x 185 cm x 260 cm high) with a speaker for white noise positioned on the wall and a table in the corner of each room on which rats were held. One arena was rectangular and the other was kite-shaped; both were made up of two long walls and two short walls. The dimensions of the long and short walls were identical in each arena (100 cm or 50 cm long x 50 cm high), as shown in Figure 1. Each arena could be positioned in one of four possible orientations along a north-south or east-west axis. On each of four habituation days, rats were exposed to one of the arenas for five minutes before being transferred to the other testing room where they were exposed to the second arena for five minutes. The interval

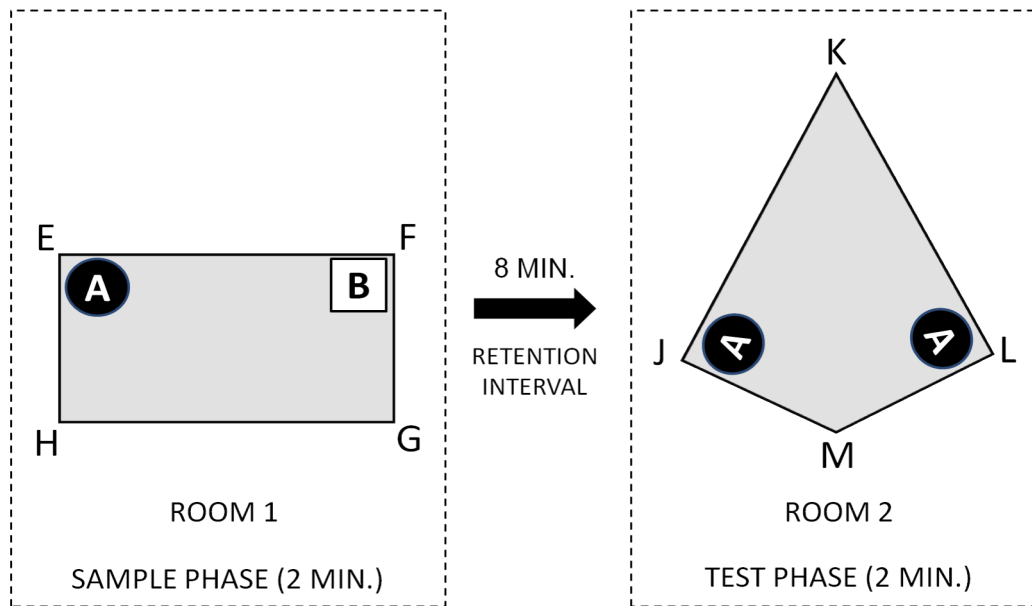


Figure 1. Schematic representation of sample and test phases in Experiment 1. Objects A and B are represented by black circular and white square symbols, respectively. Preferential exploration of the object located in corner L of the kite indicates the animal's detection of its novelty with respect to the local geometric properties provided by the walls of the arena. In Experiment 2 the same procedure was used as that in Experiment 1 but the shapes of the arenas in the sample and test phases were reversed.

between habituation to each arena was eight minutes and the order they encountered the arenas remained the same across all days including those days in the subsequent test phase. Between each habituation day both arenas were rotated 90° anti-clockwise to ensure each rat received five minutes of habituation to each empty arena in all four orientations. The right-angled corners E and G in the rectangle are geometrically equivalent, with the long side to the right of the short side. Equally, corner J of the kite shaped arena is the geometric equivalent of corners E and G in the rectangle.

Following habituation animals received one object recognition trial per day for four days. The objects they encountered in each trial were unique and approximately matched for height, volume and material. In the sample phase of Experiment 1, rats were exposed to two different objects, A and B, in corners E and F of the rectangle, which was situated in room 1, for two minutes. The orientation of the rectangle changed between days

but remained constant for all animals on the same day. Following a retention interval of eight minutes the rats were then transferred to the kite, which was situated in room 2, for the test phase in which two identical copies of one of the objects were presented in the right-angled corners J and L. For this test phase, animals were split into equal groups so that half received object A at test and the remainder object B, and in so doing ensured that the novel location (corner J or L of the kite) was also assigned equally between animals. Only two of the four possible kite orientations were used on any given day and although it was ensured that each orientation was counterbalanced equally between all animals, it was not possible to split each object subgroup ($n = 15$) exactly in half. For each individual rat, the corner housing the novel object changed daily. Therefore any preference for exploration of one object over another could not be explained by the positions of the objects with respect to generalization between

extra-maze cues or by a preference for one right-angled corner over another.

For ease of exposition in the following discussion it will be assumed that the rats were exposed to objects A and B in corners E and F of the rectangle respectively prior to being tested with two copies of object A in corners J and L of the kite, but in reality the identity of the object (A or B), and thus the corner containing the novel object, in the test phase was counterbalanced. With reference to the local geometric cues provided by corner E, in which object A was previously encountered, it was predicted that during the test phase rats would preferentially explore the copy of object A in corner L of the kite, as this was a novel location for object A. The failure of rats to explore preferentially the copy of object A in corner L could be attributed to the object locations, in the sample phase, being remembered with reference to their absolute positions with respect to room cues, or with reference to their relative positions with respect to each other, or with reference to the overall geometric shape formed by the arena walls. However, if the rats were to explore preferentially the copy of object A in corner L, then rats could not have used the absolute positions of the objects with respect to room cues, as the room cues had changed between sample and test phases. Similarly, the relative positions of the objects differed between sample and test phases, as the identity of the objects present in each phase differed. Finally, should the rats have remembered the locations of the objects in the sample phase with reference to an overall geometric representation then they would be expected to explore the two copies of object A in corners J and L of the kite equally, as this representation would be of little use in the rearranged shape. In Experiment 2 we sought to extend the

generality of the findings from Experiment 1 by exposing rats to objects A and B in corners J and L of the kite in room 2 during the sample phase, and testing them with identical copies of A in corners E and F of the rectangle in room 1. Other details of the experiment were identical to those described previously for Experiment 1.

In each experiment performance of rats in the test phase of each trial was measured by recording the time that each animal actively explored or sniffed the objects head on from a distance of no greater than 2 cm. Brief whisking of or climbing on the objects was not recorded. Coding was conducted from video recordings and the scorer was blind to the conditions under which the rat was being tested. In addition a second scorer, also blind, scored a subset of trials (40%) from the experiments. A Pearson product-moment correlation of exploration times between the two scorers was significant ($r = .9, p < .01$).

Results

Performance measures: From the object exploration times described above two measures of discrimination were calculated: d_1 , a discrimination index and d_2 , a discrimination ratio. The d_1 score was calculated for each rat as the difference in exploration between the two objects in the test phase, i.e., time spent exploring the novel object – time spent exploring the familiar object. The d_2 ratio for each rat was calculated by dividing the difference in time exploring the novel and familiar objects by the sum of these times. Chance performance in both cases is zero. These discrimination ratios are commonly presented indicators of preference for the novel object, and are used to control for the natural variation in exploratory activity towards different pairs of objects (Ennaceur & Delacour, 1988).

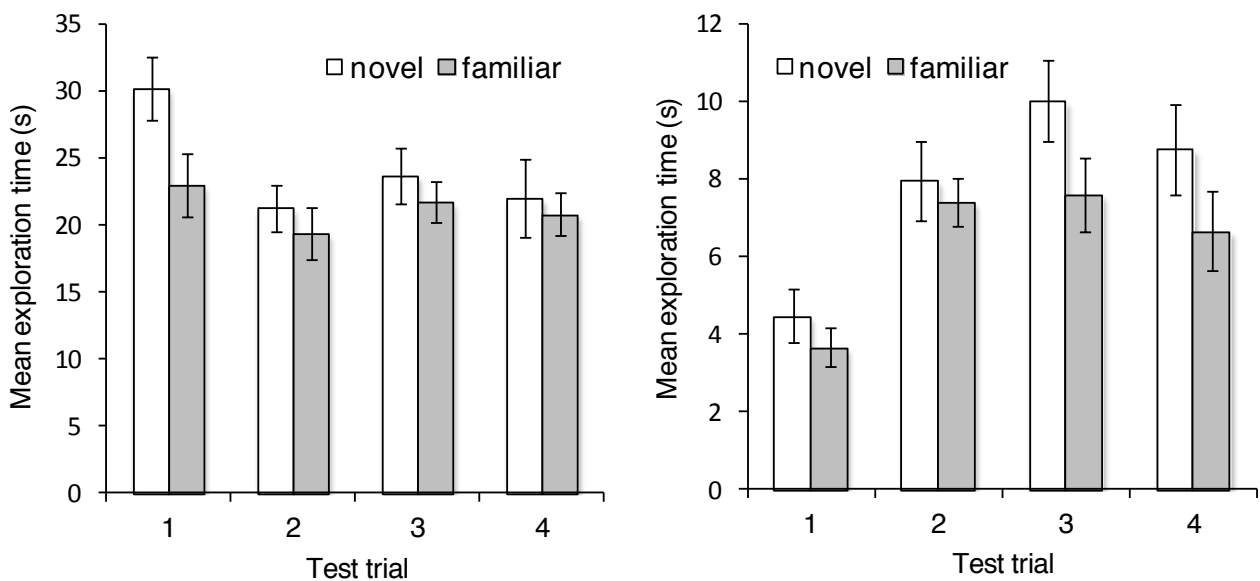


Figure 2. Mean exploration times (+SEM) for both novel (white bars) and familiar (grey bars) object locations across four trials during Experiment 1 (left-hand panel) and Experiment 2 (right-hand panel).

Experiments 1 and 2

For Experiment 1, one-sample t-tests of the four-day means of individual d_1 scores, $M = 2.65$, $SEM = 1.24$, $t(29) = 2.14$, $p < .05$, and d_2 scores, $M = .05$, $SEM = .02$, $t(29) = 2.29$, $p < .05$, revealed that rats spent more time exploring the novel object than expected by chance. In addition, a repeated measures Analysis of Variance (ANOVA) of individual times spent exploring the two objects at test over four trials in Experiment 1 revealed that more time was spent exploring the novel than the familiar object, $F(1,29) = 4.59$, $p < .05$. There was also a significant effect of trial, $F(3,87) = 5.85$, $p < .01$, but no interaction between the main effects, $F < 1$. Pairwise comparisons revealed that the effect of trial was due to significantly higher exploration of objects in trial 1 than in trial 2, while there were no differences among total exploration times for any of the other days. Similarly, for Experiment 2 one-sample t-tests of four-day means of individual d_1 and d_2 scores also revealed that rats explored the novel object for a significantly greater proportion of time

than expected by chance, $M = 1.47$, $SEM = .50$, $t(19) = 2.96$, $p < .01$ and $M = .09$, $SEM = .03$, $t(19) = 2.59$, $p < .02$, respectively. A repeated measures ANOVA of individual times spent exploring the two objects in the test phase over four trials revealed a significant effect of object, $F(1,19) = 8.74$, $p < .01$, with rats exploring the novel object for longer than the familiar object. There was again a significant difference in total exploration times among trials, $F(3,57) = 11.82$, $p < .01$, with pairwise comparisons this time revealing that exploration times were lower on trial 1 than on the other three trials, with no differences among the subsequent trials. There was no trial x object interaction, $F < 1$; see left- and right-hand panels of Figure 2.

Discussion

The data demonstrate that in a spontaneous object recognition task rats are able to remember the location of an object with reference to the geometric context in which it was first encountered. The corner containing the novel object-

geometry combination varied among trials, so the recognition of familiarity with the previously encountered object-location combination occurred from a single exposure to the objects. The results are important both in terms of our understanding of the parameters of recognition memory as measured using spontaneous object recognition tasks, and in terms of the notion of a geometric module.

With respect to recognition memory, the cues necessary to remember an object's location have not been systematically studied. In the spatial context variants of the object recognition tasks described in the Introduction (e.g., Dix & Aggleton, 1999; Good et al., 2007), both the relative positions of the moved objects (with respect to one another or to other objects in the array) and the absolute positions of the objects (with respect to cues outside the arena) could be used to define spatial location. Whether relative or absolute position is a prerequisite for spatial memory has not previously been tested. While context has been shown to be important in object-location memory (e.g., Dellsu, Fauchy, Le Maul, & Simon, 1997) what aspects of a context are necessary to disambiguate occasions is also not clear. Our results demonstrate that despite encountering objects in different rooms and in different arenas (meaning both the absolute and relative positions of the objects changed between phases), our rats were able to detect an object that was novel with reference to some local contextual information provided by the shape of an arena.

The importance of the results of our experiments with respect to the geometric module is two-fold. First, evidence showing that rats are capable of transferring spatial behaviour between differently shaped arenas comes from

tasks in which they are repeatedly reinforced for heading to a particular set of cues that are common to both arenas (Pearce et al., 2004; see also Tommasi & Polli, 2004). As discussed in the Introduction, such findings could be the result of stimulus-response habits that formed over repeated trials, thus weakening the argument that rats in tasks such as Cheng's (1986) reorientation task relied not on an abstracted global representation but instead on a local representation of the cues near the goal location. In our task memory for the object against its geometric context occurred incidentally, without any obvious reinforcement and without repeated trials. The results thus provide support for Pearce et al.'s (2004) claim that transfer between environments is the result of learning based on local cues, and extend those findings by ruling out S-R associations as the sole cause of their results.

Others have used procedures that rely on dishabituation to previously encountered objects to examine animals' spatial representation, but these have tended to use arrays of objects to create a notional shape (e.g., Poucet, Chapuis, Durup, & Thinus-Blanc, 1986). Although animals explored displaced objects more than non-displaced, in each case the absolute position of the object in the room altered, as well as its position relative to the geometry of the array. Skov-Rackette and Shettleworth (2005) cleverly controlled for this problem and found that while rats responded to changes in inter-object distance, they did not detect when an array's shape was changed to its mirror image, suggesting the rats' representation of the object array was limited to local inter-object relations, rather than the global array. Our results support this conclusion, but also extend those findings by requiring the rats

to encode the object locations not with reference to each other, but with reference to the geometry of the arena, a situation arguably closer to Cheng's (1986) original experiments.

It should be noted that our results cannot conclusively rule out the possibility that rats in our experiments made use of global shape parameters other than the overall shape, such as the principal axes of the two arenas. If, in the sample phase, the rat associated an object with a location as defined by the principal axis of the arena, then at test in the transformed arena the same rule may be exploited, thus allowing the rat to detect the novelty of the relocated object. This was Cheng and Gallistel's (2005) criticism of Pearce et al.'s (2004) and Tommasi and Polli's (2004) findings. However, despite experiments aimed at detecting whether rats and chicks are capable of abstracting the principal axis of a geometric shape, the results have been equivocal (Kelly, Chiandetti, & Vallortigara, 2011; McGregor et al., 2006), and as Sutton (2009) points out, in other aspects of animal cognition specialised and prolonged training is required to produce evidence of an animal's ability to form an abstract representation (e.g., Wright, 1997). We would argue that our demonstration of rats' ability to use the geometric properties of the environment in object-location memory provides a platform for new experiments aimed at examining this question further.

Our second result of note relates to Cheng's (1986) conclusion that rats rely primarily on the geometric properties of their environment to navigate, but that over time non-geometric cues could be 'glued on' to this metric frame (p.174). Cheng and Newcombe (2005) subsequently suggested that two processes should be considered in studies that involve learning about geometric

cues: one used when reorienting, which is entirely geometric, and another, which may include non-geometric cues, used to locate a particular target location (see also Sutton, 2009). However, in each of the above descriptions of how geometry may come to have primacy in navigation, it should be expected that in a single exposure to geometric and non-geometric cues, the geometric cues should be processed independently of the non-geometric features, particularly in our case, in which rats have to reorient using the geometry of the arena to detect the familiarity of the object locations. While other studies discussed above suggest that non-geometric cues can interact with geometric cues over time, our experiments are the first to show that non-geometric cues are rapidly encoded along with geometric cues with only a single exposure to the cues in compound. Whether this is through a form of view-based memory (see Cheng, 2008), an associative process (e.g., Whitt, Haselgrove, & Robinson, 2012), or because non-geometric cues integrate with geometry in some other way not expected by current versions of the geometric module hypothesis, is open to question.

References

- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, *23*, 149-178.
- Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences*, *12*, 355-361.
- Cheng, K., & Gallistel, C.R. (2005) Shape parameters explain data from spatial transformations: Comment on Pearce et al. (2004) and Tommasi & Polli (2004). *Journal of Experimental Psychology: Animal Behavior Processes*, *31*, 254-259.

- Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review*, *12*, 1-23.
- Cheng, K., & Spetch, M. L. (1998). *Mechanisms of landmark use in mammals and birds*. In S. Healy (Ed.), *Spatial representation in animals* (pp. 1–17). Oxford, England: Oxford University Press.
- Cowan, P. E. (1976). The new object reaction of *Rattus rattus* L.: the relative importance of various cues. *Behavioral Biology*, *16*, 31-44.
- Dellu, F., Fauchey, V., LeMoal, M., & Simon, H. (1997). Extension of a new two-trial memory task in the rat: Influence of environmental context on recognition processes. *Neurobiology of Learning and Memory*, *67*, 112-120.
- Dix, S. L., & Aggleton, J. P. (1999). Extending the spontaneous preference test of recognition: evidence of object-location and object-context recognition. *Behavioural Brain Research*, *99*, 191-200.
- Dudchenko, P. A., Goodridge, J. P., Seiterle, D. A., & Taube, J. S. (1997). Effects of repeated disorientation on the acquisition of spatial tasks in rats: Dissociation between the appetitive radial arm maze and aversive water maze. *Journal of Experimental Psychology: Animal Behavior Processes*, *23*, 194-210.
- Eacott, M. J., & Norman, G. (2004). Integrated memory for object, place, and context in rats: A possible model of episodic-like memory? *Journal of Neuroscience*, *24*, 1948-1953.
- Ennaceur, A., & Delacour, J. (1988). A new one-trial test for neurobiological studies of memory in rats. 1: Behavioral data. *Behavioural Brain Research*, *31*, 47-59.
- Ennaceur, A., Neave, N., & Aggleton, J. P. (1997). Spontaneous object recognition and object location memory in rats: The effects of lesions in the cingulate cortices, the medial prefrontal cortex, the cingulum bundle and the fornix. *Experimental Brain Research*, *113*, 509-519.
- Esber, G. R., McGregor, A., Good, M. A., Hayward, A., & Pearce, J. M. (2005). Transfer of spatial behaviour controlled by a landmark array with a distinctive shape. *Quarterly Journal of Experimental Psychology*, *58B*, 69-91.
- Gallistel, C. R. (1990). *The Organization of Learning*. Cambridge, MA: MIT Press.
- Gallistel, C. R., & Matzel, L. D. (2012). The neuroscience of learning: beyond the Hebbian synapse. *Annual Review of Psychology*, Epub July 2012.
- Golob, E. J., & Taube, J. S. (2002). Differences between appetitive and aversive reinforcement on reorientation in a spatial working memory task. *Behavioural Brain Research*, *136*, 309-316.
- Good, M. A., Barnes, P., Staal, V., McGregor, A., & Honey, R. C. (2007). Context- but not familiarity-dependent forms of object recognition are impaired following excitotoxic hippocampal lesions in rats. *Behavioral Neuroscience*, *121*, 218-223.
- Gouteux, S., Thinus-Blanc, C., & Vauclair, J. (2001). Rhesus monkeys use geometric and nongeometric information during a reorientation task. *Journal of Experimental Psychology: General*, *130*, 505-519.
- Graham, M., Good, M. A., McGregor, A., & Pearce, J. M. (2006). Spatial learning based on the shape of the environment is influenced by properties of the objects forming the shape. *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 44-59.

- Hayward, A., McGregor, A., Good, M. A., & Pearce, J. M. (2003). Absence of overshadowing and blocking between landmarks and the geometric cues provided by the shape of a test arena. *Quarterly Journal of Experimental Psychology*, *56B*, 114-126.
- Hodges, H. (1996). Maze procedures: The radial-arm and water maze compared. *Cognitive Brain Research*, *3*, 167-181.
- Horne, M. R., & Pearce, J. M. (2009). Between-cue associations influence searching for a hidden goal in an environment with a distinctive shape. *Journal of Experimental Psychology: Animal Behavior Processes*, *35*, 99-107.
- Jones, P. M., Pearce, J. M., Davies, V. J., Good, M. A., & McGregor, A. (2007). Impaired processing of local geometric features during navigation in a water maze following hippocampal lesions in rats. *Behavioral Neuroscience*, *121*, 1258-1271.
- Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2011). Re-orienting in space: do animals use global or local geometry strategies? *Biology Letters*, *7*, 372 – 375.
- Margules, J. & Gallistel, C. R. (1988). Heading in the rat: Determination by environmental shape. *Animal Learning & Behavior*, *16*, 404-410.
- McGregor, A., Horne, M. R., Esber, G. R., & Pearce, J. M. (2009). Absence of overshadowing between a landmark and geometric cues in a distinctively shaped environment: A test of Miller and Shettleworth (2007). *Journal of Experimental Psychology: Animal Behavior Processes*, *35*, 357-370.
- McGregor, A., Jones, P. M., Good, M. A., & Pearce, J. M. (2006). Further evidence that rats rely on local rather than global spatial information to locate a hidden goal: Reply to Cheng and Gallistel (2005). *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 314-321.
- Pearce, J. M., Good, M. A., Jones, P. M., & McGregor, A. (2004). Transfer of spatial behavior between different environments: Implications for theories of spatial learning and for the role of the hippocampus in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes*, *30*, 135-147.
- Pearce, J. M., Graham, M., Good, M. A., Jones, P. M., & McGregor, A. (2006). Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 201-214.
- Poucet, B., Chapuis, N., Durup, M., & Thinus-Blanc, C. (1986). A study of exploratory behavior as an index of spatial knowledge in hamsters. *Animal Learning & Behavior*, *14*, 93-100.
- Rhodes, S. E. V., Creighton, G., Killcross, A. S., Good, M., & Honey, R. C. (2009). Integration of geometric with luminance information in the rat: Evidence from within-compound associations. *Journal of Experimental Psychology: Animal Behavior Processes*, *35*, 92-98.
- Skov-Rackette, S. I., & Shettleworth, S. J. (2005). What do rats learn about the geometry of object arrays? Tests with exploratory behavior. *Journal of Experimental Psychology: Animal Behavior Processes*, *31*, 142-154.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2002). Modularity and spatial reorientation in a simple mind: Encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition*, *85*, 51-59.
- Sutton, J. E. (2009). What is geometric information and how do animals use it? *Behavioural Processes*, *80*, 339-343.

- Tommasi, L., & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick (*Gallus gallus*). *Animal Cognition*, *7*, 53-59.
- Vallortigara, G., Zanforlin, M., & Pasti, G. (1990). Geometric modules in animals' spatial representations: A test with chicks (*Gallus gallus domesticus*). *Journal of Comparative Psychology*, *104*, 248-254.
- Vargas, J. P., Petruso, E. J., Bingman, V. P. (2004). Hippocampal formation is required for geometric navigation in pigeons. *European Journal of Neuroscience* *20*, 1937-1944.
- Whitt, E., Haselgrove, M., & Robinson, J. (2012). Indirect object recognition: Evidence for associative processes in recognition memory. *Journal of Experimental Psychology: Animal Behavior Processes*, *38*, 74-83.
- Whyte, J. T., Martin, G. M., & Skinner, D. M. (2009). An assessment of response, direction and place learning by rats in a water T-maze. *Learning and Motivation*, *40*, 376-385.
- Wright, A. A. (1997). Concept learning and learning strategies. *Psychological Science*, *8*, 119-123