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Geometric vs. non-geometric information. Explaining male rats' selective preferences in a navigation task[☆]

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ABSTRACT

In three experiments, male rats were trained to find a hidden platform in a Morris pool which was completely surrounded by circular curtains (black in Experiments 1 and 2, and beige in Experiment 3). Experiment 1, a preliminary experiment, addressed single landmark learning and established that a plain shiny white cylinder and a striped cylinder were of different salience. Then in Experiments 2 and 3 rats were trained in a triangular-shaped pool with the platform defined in terms of two sources of information, a landmark outside the pool (either the white or the striped cylinder) and a particular corner of the pool (as in Rodríguez, Torres, Mackintosh, & Chamizo, 2010, Experiment 2). Following acquisition, a test trial without the platform pitted these two sources of information against one another. In Experiment 2, rats spent more time in the area of the pool that corresponded to the cylinder when it was white, whereas they spent more time in the distinctive corner of the pool when the cylinder was striped. However, in Experiment 3 (with beige curtains in order to reduce the salience of the white cylinder) all rats spent more time in the distinctive corner of the pool. Subsequent tests with the two cues (landmark and pool-geometry) presented individually showed that all rats in the two experiments had learned to find the platform using the two sources of information. In addition, a clear geometry advantage was found in both groups of rats tested in Experiment 3. This study shows for the first time that changing the salience of a landmark can strongly affect the preference for a geometric cue over a landmark cue in male rats.

1. Introduction

Animals have a varied range of strategies that help them to navigate. For example, Cheng (1986) was the first author to present evidence that rats can use geometric information to locate a food hidden reward. He trained male rats in a rectangular arena, where the two short walls of the arena and one of the long walls were black, while the other long wall was white. In addition, distinctive visual panels were placed in each of the arena's corners (as well as other non-geometric cues, like distinctive textures and smells). The food was hidden in one corner of the arena, and the rats had to search for it. Although rats learned to search in the correct location for the food, they made frequent rotational errors by searching in the corner diagonally across from the one where the food was hidden (the corner geometrically equivalent to the target one). This result shows that non-geometric cues were not considered very important by the rats when looking for the food. Subsequent transformation tests (with different manipulations of both the geometric cue and the non-geometric cue) confirmed the previous claim. Cheng concluded that the rats used the geometric framework of the

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arena itself to find the reward (see also Cheng & Gallistel, 1984; Gallistel, 1990). Similar results have been found not only with rats but also with other species (for reviews see Cheng & Newcombe, 2005; Spetch and Kelly, 2006; Tommasi, Chiandetti, Pecchia, Sovrano & Vallortigara, 2012).

According to Cheng (1986) and Gallistel (1990), learning about geometric information (*i.e.*, like the metric relations of distances and angles between a target place and the shape of an apparatus) occurs in a specialized module, which is impenetrable to non-geometric information. In this specialized module, features (like different wall colours or textures) and landmarks (like three-dimensional objects) are simple labels (Cheng, 1986, p. 172). The main implication of such a claim, still a controversial topic (Cheng, 2008), is that these two different sources of information (*i.e.*, geometrical and non-geometrical) should not interact. Specifically, if geometry and landmark learning represent quite independent modes of solution (Cheng, 1986; Gallistel, 1990), one might not expect to see any interaction or competition between them. Consequently, no evidence of cue competition effects (like blocking and overshadowing) should be found between geometric and non-geometric information. However, Miller and Shettleworth (2007, 2008) have claimed that changes in the associative properties of the geometric cues are governed by the same principles that apply to more traditional stimuli. Consequently, one might expect to see interactions or competition between geometric and non-geometric information. The associative model of geometry learning proposed by Miller and Shettleworth (2007, 2008), which is based on the Rescorla and Wagner model (1972), makes clear that cue competition always occurs between geometry and featural information, although choice in instrumental spatial learning does not always directly reveal it. According to these authors, geometric and featural cues are separate elements, so that for example, each corner in a specific apparatus has its own combination of the two kinds of cues, which can interact. Well-designed experiments and different authors have confirmed the two previous outcomes with male rats. For examples of interaction, see Graham, Good, McGregor, and Pearce, (2006), Kosaki, Austen, and McGregor, (2013), Horne and Pearce (2009a, 2011), Pearce, Graham, Good, Jones, and McGregor (2006), Rhodes, Creighton, Killcross, Good, and Honey (2009), for examples of no interaction, see Hayward, Good, and Pearce (2004), Hayward, McGregor, Good, and Pearce (2003), McGregor, Horne, Esber, and Pearce (2009), Pearce, Ward-Robinson, Good, Fussell, and Aydin (2001), Wall, Botly, Black, and Shettleworth (2004) (for a review see Pearce, 2009). Why is this? A possible explanation is that the failure of a landmark to overshadow or block learning about geometry in male rats occurs because the landmark is much less salient than the geometrical cue (as suggested by Hayward et al., 2003, 2004 –and subsequently confirmed by Rodríguez, Chamizo, & Mackintosh, 2011). Could the way to assess salience also be a problem (*i.e.*, the specific measure used)?

The study by Rodríguez et al. (2011), where cue competition designs were used, was conducted with male and female rats. It tested whether the relative salience of two cues (a particular corner of a pool and a landmark outside the pool) would affect the direction of overshadowing in a different way for each sex. As expected, the results showed an asymmetrical overshadowing effect in both sexes. In males, geometry overshadowed landmark learning, but landmark learning did not overshadow learning about geometry; in females, landmark learning overshadowed learning about geometry, but geometry learning did not overshadow landmark learning. Therefore, it was the more discriminable, salient, or preferred source of information (geometry for males and landmark for females –as previously shown by Rodríguez, Torres, Mackintosh, & Chamizo, 2010) that overshadowed the less discriminable, salient, or preferred cue –although see Torres, Rodríguez, Chamizo, and Mackintosh (2014), Chamizo, Rodríguez, Torres, Torres, and Mackintosh (2014), for some restrictions related to females. That geometry is more salient for males and landmarks more salient for females is also consistent with work with humans (for reviews see Coluccia & Louse, 2004; Kimura, 1999; Halpern, 2012; Mackintosh, 2011). How strong is this apparent predisposition in male rats?

The set of experiments with male rats by Kosaki et al. (2013 -see also Austen, Kosaki, & McGregor, 2013; Horne & Pearce, 2011) conducted in a modified Morris pool with a rhomboid-shape is worth highlighting. This study tested whether two sets of corners of the pool (the acute and obtuse corners of a rhomboid-shaped pool) could be overshadowed by discrete beacons. In Experiment 1, a preliminary experiment, it was established that the two sets of corners were of different salience: the acute corners were more salient than the obtuse corners. Then Kosaki et al. (2013) found that the beacon cue overshadowed the corner cue but only in those rats trained and tested with the obtuse corner; this was not the case with the animals trained and tested with the acute corner (for a related study, in humans, see Redhead, Hamilton, Parker, Chan, & Allison, 2013). These results showed that a beacon could overshadow the weakly salient geometric cue (*i.e.*, the obtuse corners of the pool), but it could not overshadow the more salient geometric cue (*i.e.*, the acute corners of the pool).

A logical extension within this controversy would be to see whether, after compound learning, the salience of a single landmark could affect what the males prefer (*i.e.*, how they perform) in a conflict test in the presence of both geometric and non-geometric cues. It is well known that performance is determined by other factors in addition to learning (Miller & Shettleworth, 2007). Would compound training (*i.e.*, learning in the presence of a discrete landmark and a geometric pool cue) alter the subsequent males' preference for using the geometric information provided by the shape of a specific corner of a pool, depending on the salience of the interfering landmark? We believe this is an important question worth testing. Very few animals would survive without an ability to remember and find places (Spetch & Kelly, 2006). But how do they do it? Our intention in this paper is to explore this possibility while using a protocol (Rodríguez et al., 2010, Experiment 2–see also Chamizo, Rodríguez, Sánchez, & Marmol, 2016; Keeley, Tyndall, Scott, & Saucier, 2013; Rodríguez et al., 2011; Rodríguez, Chamizo, & Mackintosh, 2013) that has revealed a clear male preference for geometry.

2. Experiment 1

In Experiment 1, a preliminary experiment, two groups of male rats were trained in a circular pool to find a hidden platform in the presence of a single landmark. The pool was completely surrounded by black curtains and two landmarks were used: A plain shiny

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