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The effect of disrupting configural information on rats' performance in the Morris water maze

Ciro Civile^{a,*}, V.D. Chamizo^b, N.J. Mackintosh^c, I.P.L. McLaren^a^a University of Exeter, United Kingdom^b University of Barcelona, Spain^c University of Cambridge, United Kingdom

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ABSTRACT

Many experiments on spatial navigation suggest that a rat uses the configuration of extra-maze landmarks to guide its choice of arm or location to visit. In the present study, based on Chamizo Rodríguez, Espinet, and Mackintosh's (2012) navigation paradigm, we conducted a series of experiments in which we focused on how changes to the configuration of stimuli surrounding the maze, implemented by transposing the location of both near and far landmarks, significantly affected rats' performance (Experiment 1, Test Phase 1). Subsequent tests demonstrated that it was the near landmarks that played the major role in this navigation task (Experiment 1, Test Phases 2 and 3). Experiment 2 provided evidence for a novel type of inversion effect in the water maze, by showing that rotation by 180° of the location of one set of landmarks relative to a directional cue also strongly affected performance.

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The use of visual cues to find a specific target has been demonstrated in numerous organisms including insects (Chittka, Geiger, & Kunze, 1995), turtles (Lopez et al., 2000), fish (Sovrano, Bisazza, & Vallortigara, 2003), rats (Suzuki, Augerinos, & Black, 1980), birds (Cheng, 1989), non-human primates (Sutton, Olthof, and Roberts, 2000) and humans (Spetch, 1995). These studies have revealed several ways in which spatial information from visual cues near a target may be encoded and used to remember the target location. Some findings on the use of landmarks by animals other than humans, such as the preference for landmarks near a target and competition between landmarks, have been demonstrated to be general across species from insects to humans (for reviews, read Cheng & Spetch, 1998; MacDonald, Spetch, Kelly, & Cheng, 2004).

Some of the most important findings on spatial navigation concern the use of landmark configurations. One design that has been deployed with several species involves training in which the target is hidden at a fixed location relative to a set of two or more identical landmarks all contained within a larger environment. Thus, the landmarks are located within a well-defined search space which provides directional cues, but the set of landmarks and the corresponding target are moved within the search space so that the landmarks must be used to localise the precise location of the target (MacDonald et al., 2004). There could be several ways in which spatial information about the landmarks is used in these experiments. For example, the subject could encode the entire set of landmarks as a configuration and learn the location of the target with respect to this configuration. Alternatively, a second strategy would be to encode the direction and the distance of the target from each landmark individually, but this is not so useful when the landmarks presented are visually identical.

* Corresponding author at: Washington Singer Laboratories, University of Exeter, Perry Road, Exeter EX4 4QG, United Kingdom.
E-mail address: c.civile@exeter.ac.uk (C. Civile).

Another approach that could be used is to simply search for the target close to the landmark array, thus using the landmarks collectively as a beacon. This could be very useful if the landmarks are extremely close to the target. Different manipulations of the landmarks have been implemented to investigate the various strategies used by animals and human in solving this type of problem. An example of such a manipulation is to enlarge the landmark array by moving all the landmarks farther apart. Interestingly, the results of these studies on various species have shown that honeybees and humans spontaneously use a fully configural representation of a landmark array (see [Cartwright & Collett, 1982](#) for studies on training honeybees with three landmarks; [Spetch, Cheng, & MacDonald, 1996](#) for studies on humans using both computer screen and table top tasks).

In this paper we investigate the effect that disruption and inversion of landmark configurations has on rats' navigation in a water maze. The classic study in the radial maze on this issue is perhaps that by [Suzuki et al. \(1980\)](#), in which they trained rats to run the radial maze using landmarks at the end of each arm, and then showed that random transposition of these landmarks severely disrupted performance, but rotation of the landmarks as a whole simply rotated the rats choices on test. Their interpretation of this result is that performance is based on the landmarks, but that they do not act as "beacons" either in isolation or collectively, but instead it is the configuration of landmarks that provides the information used for navigating in the radial maze. In other words, the spatial arrangement of the landmarks matters, and the whole configuration is more than just the sum of its parts.

We also know that rotation of landmarks in the Morris water maze will cause the animals to track the orientation of the configuration of landmarks and use this as their reference for navigation, not least because this is now standard procedure in training in such a maze for the type of experiment reported here. Studies in the Morris water maze have shown that animals trained with four (i.e., A, B, C and D) landmarks performed less accurately when tested with sets of two landmarks alone than animals initially trained with these two landmarks in isolation. This could be because B and C, or D and A landmarks alone are perceived as different from A, B, C and D all together, and the response established to one stimulus configuration cannot be transferred perfectly to a different configuration, resulting in generalisation decrement ([Chamizo, Rodríguez, Espinet, & Mackintosh, 2012](#); [Pearce, 1987, 1994](#)). Another way of expressing this result would be to say that the four landmark case suffers from greater overshadowing of one landmark by the others than the two landmark case, but we note that [Chamizo et al. \(2012\)](#) demonstrated that the addition of two new landmarks, and the removal of two old ones, both disrupted performance. They argued that these results were consistent with the proposition that a change in the stimulus conditions from the training phase to the test phase led to generalisation decrement. There is no doubt that [Pearce's \(1987\)](#) theory is one of those capable of providing both effects via one similarity-based mechanism (for other theories capable of generating this result, see [Honey, 2000](#); [McLaren, Forrest, & McLaren, 2012](#)). We also agree that a simple elemental theory employing something like the Rescorla–Wagner algorithm ([Rescorla & Wagner, 1972](#)) would have to appeal to a process such as external inhibition in combination with overshadowing to explain this result, making it a less plausible account of these results. More sophisticated theories of this type, such as the replaced elements model ([Wagner & Brandon, 2001](#)) and [McLaren and Mackintosh's \(2000, 2002\)](#) extension of [McLaren, Kaye, and Mackintosh \(1989\)](#), do possess mechanisms that would produce external inhibition (elements active when A and D were presented together would decrease in activity or disappear altogether when C and D were added), however, and could explain this finding equally well. Putting any difficulty in pinpointing the precise mechanism generating this effect to one side, our point here is that the simple addition or deletion of landmarks seems to significantly influence performance in the water maze, once again suggesting that the configuration of landmarks is key.

In the same study, [Chamizo et al. \(2012\)](#) investigated whether rats learn about the identity of the landmarks in these experiments. Their results showed that rats knew about the identity of the landmarks learnt during the training phase, because a rat's performance was significantly disrupted by swapping the landmarks original positions. Given that there were only two landmarks, and that the platform was always between them, the fact that performance was impaired when the landmarks were swapped indicates that rats were distinguishing between them and not just treating them as a configuration of two identical features, but as specific landmarks at specific locations. And we are able to conclude that performance is not only affected by adding and removing landmarks, but is also affected by something akin to the type of transposition used by [Suzuki et al. \(1980\)](#). The weakness of this study, of course, is that only two landmarks were used, and we address this point in the experiments that follow.

Taken together, these results strongly imply that rats use the spatial configuration of the landmarks present in order to find the platform location. In this study we used [Chamizo et al.'s \(2012\)](#) rat navigation paradigm by always employing a configuration of four landmarks during the acquisition phase and test phase. Our intention was to examine the extent to which the landmark configuration is important by means of various subtle (and not so subtle) changes to that configuration between training and test. As a secondary issue, we also examined the extent to which our manipulations differentially affected performance of male and female rats, i.e. whether any sex-based differences could be observed as a consequence of our manipulations. Recent research ([Chamizo et al., in press](#); [Torres, Rodríguez, Chamizo, & Mackintosh, 2014](#)) has shown that the appearance of landmarks can produce a substantial and reliable sex difference. For example, in the study by [Torres et al. \(2014, Experiment 2\)](#), male and female rats were trained in a triangular-shaped pool to find a hidden platform, whose location was defined in terms of two sources of information, a landmark outside the pool and a particular corner of the pool. Two identical cylinders were used as landmarks, one plain white and the other divided into four vertical segments, each "patterned" differently. On the test trial where the two sources of information (landmark and pool geometry cues) were pitted against one another, female rats preferred the plain white cylinder to the geometrical cue, but this preference was reversed

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