

Learning efficiency: The influence of cue salience during spatial navigation



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ABSTRACT

In three experiments, male Wistar rats were trained to find a hidden platform in the Morris water maze using two cues for five or ten days. Experiments 1 and 2 investigated two factors of cue salience; proximity to the goal and brightness. Results from Experiment 1 showed that rats tested with a bright distal cue were significantly better at locating the platform than rats tested with the proximal cue after five- and ten-day training with both cues. In Experiment 2, the position of the cues was reversed. Rats tested with a brighter proximal cue outperformed those tested with a distal cue. Findings from Experiments 1 and 2 suggest that brightness acquired more control over rats' behaviour than proximity to the goal. Animals in Experiment 3 were trained with equally bright proximal and distal cues. Unexpectedly, probe tests revealed that rats tested with the farther cue were more accurate than those tested with the proximal cue, but only after extended training. Possible explanations for this result are discussed with reference to errors in directional information estimation and cue assignment, cue elevation and the use of the pool wall as a navigational aid. Taken together, findings point towards the use of an elemental learning strategy involving the more salient of the two cues which emerged earlier when the relative saliences of the cues differed considerably.

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1. Introduction

The importance of environmental cues for successful navigation is well-documented in many species (for reviews see [Rodrigo, 2002](#); [Tommasi et al., 2012](#)). According to associative theories of spatial learning, navigating animals form representations of cues from a collection of viewpoints, which then become associated with a goal destination ([Hamilton et al., 2002](#); [Honey et al., 2014](#); [Leonard and McNaughton, 1990](#)). These associations are thought to be created in one of two ways; elementally or configurally ([Siegel and White, 1975](#); [Sutherland and Rudy, 1989](#)). Elemental learning strategies (e.g. [Miller and Shettleworth, 2007](#); [Rescorla and Wagner, 1972](#)) occur where the animal forms direct associations between each cue and the destination separately ([Pearce, 2002](#)). When navigating to the goal, the animal must therefore identify the cues and remember their discrete spatial relationships to that location. Configural learning strategies (e.g. [Rescorla et al., 1985](#); [Rudy and Sutherland, 1995](#)) involve the association of a cue configuration with the destination, where a novel configural representation (independent

of the individual cue components) is generated ([Honey et al., 2014](#); [Pearce, 2002](#)). Here, the animal is required to remember the position of the goal relative to the complete configuration.

Research in various species has attempted to discriminate between configural and elemental strategies by altering the arrangement of cues between navigational training and testing phases. Using this approach, evidence for elemental strategy use has been found in children and non-human primates ([MacDonald et al., 2004](#)), gerbils ([Collett et al., 1986](#)) and pigeons ([Spetch et al., 1996](#)). Specifically, results illustrated that, when trained to locate a goal in the centre of a fixed array of cues and tested with the distance between these cues increased, animals tended to search for the goal at the absolute distance and direction from individual cues rather than at the relative midpoint of the configuration. Moreover, [Collett et al. \(1986\)](#) showed that when one of the two trained cues was removed, gerbils searched in two distinct locations which corresponded to the distances and directions from each cue to the goal during training. On the other hand, adult humans ([Spetch et al., 1996](#); [Spetch et al., 1997](#)) and honeybees ([Cartwright and Collett, 1982](#)) have been known to search in the same relative location during testing as in training; for example, if trained to navigate to the centre of a cue arrangement, they continue to search in the centre of the expanded array, suggesting a configural strategy. More

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interestingly, the use of both strategies has been documented in Clark's *Nutcracker* birds (Kamil and Jones, 1997, 2000), indicating that configural and elemental learning may not be mutually exclusive. Rather, the use of a particular strategy may be influenced by the nature of the cues available to the animal in a given scenario.

Cue salience arguably plays a vital role in determining the type of learning strategy an animal will use, although it has not yet been studied to any great extent in the spatial domain (Rodrigo et al., 2014). The term salience can be defined as the "significance or noticeability" of a cue (Chamizo et al., 2006c, p. 340). There are a number of factors which can influence cue salience (Domjan et al., 2010). One such well-established factor is the distance of a cue from the goal location, whereby proximal cues acquire more control over navigation (i.e. become more salient) than distal cues (Artigas et al., 2005; Chamizo, 2002; Chamizo and Rodrigo, 2004; Cheng et al., 1987; Redhead and Hamilton, 2007; Spetch and Wilkie, 1994). This effect is thought to occur because proximal cues offer the most precise spatial information about the location of the goal (Spetch, 1995). That is, estimates of the distance and direction in which to travel are more variable for distant cues and, thus, more prone to error (Kamil and Cheng, 2001; Spetch, 1995). Specific features of a cue (e.g. size or luminance) have also been shown to effect salience (Chamizo et al., 2006c, 2012; Young et al., 2006). Chamizo et al. (2006c), for example, demonstrated that rats navigating in the Morris water maze with a bright distal cue performed as well as those navigating with a less luminous proximal cue.

Recently, Rodrigo et al. (2014) examined the effects of varying the salience of a cue configuration on the type of strategy employed by rats in the Morris water maze. Cues ranged from having approximately the same salience to having different saliences across conditions. Probe trials revealed that rats could adopt different spatial strategies, depending on the similarity of the cues' saliences (Rodrigo et al., 2014). Namely, when the salience was comparable, rats relied on the arrangement of cues (i.e. a configural strategy), and when salience was dissimilar, they used an elemental strategy involving the more salient of the two cues to reach the platform (Rodrigo et al., 2014). Notably, Rodrigo et al. (2014) suggest that the emergence of these distinct strategies may be somewhat dependant on a prolonged training period. Although this idea has not yet been thoroughly examined in a spatial learning context, visual discrimination research in honeybees has demonstrated that extended training can in fact produce a change in the chosen strategy, from elemental to configural (Giurfa et al., 2003).

Giurfa et al. (2003) also showed that, at longer training lengths, perceptual similarity between cues promoted a configural learning approach.

The current study aimed to expand on previous work in two ways; firstly, by further exploring the effects of altering cue salience on spatial learning strategies used in the Morris water maze, and secondly, by delineating the influence of training length on the type of strategy used. Experiment 1 examined two components of cue salience; distance from the goal and brightness. Rats were trained with a proximal (near) cue and a bright distal (far) cue for five or ten days and subsequently tested with both or one of these cues. We hypothesised that if one cue acquired more salience than the other, rats would initially adopt an elemental strategy with the high salience cue; however, if both cues became equally salient, rats should readily incorporate both into a configural strategy after only five days of training. Experiments 2 and 3 examined animals' learning behaviour in the presence of two cues with more distinct saliences. In Experiment 2, rats were trained with the original positions of the cues reversed. Here, as one cue was both brighter and closer to the goal, we expected rats to employ an elemental strategy with this cue. In Experiment 3, rats were trained with equally bright near and far cues. We predicted that rats would favour an elemental strategy involving the proximal cue to begin with, but after further training, may incorporate the farther cue into a configural strategy (similar to Giurfa et al., 2003).

2. Experiment 1

Experiment 1 had three aims; firstly to establish which component of cue salience (proximity or brightness), if any, acquired more control over navigation, secondly to identify if rats were using an elemental or configural learning strategy, and thirdly to determine if increased training could lead to a change in strategy. Rats were trained in the hidden platform version of the water maze (Morris, 1981) for five or ten days with a near cue and a brighter far cue, followed by testing with two cues or one cue.

2.1. Method

2.1.1. Subjects and housing

Subjects were 39 male Wistar rats (three months old at the beginning of training, 250–300 g) obtained from Charles River, UK. All rats were given a number with a non-toxic marker pen for

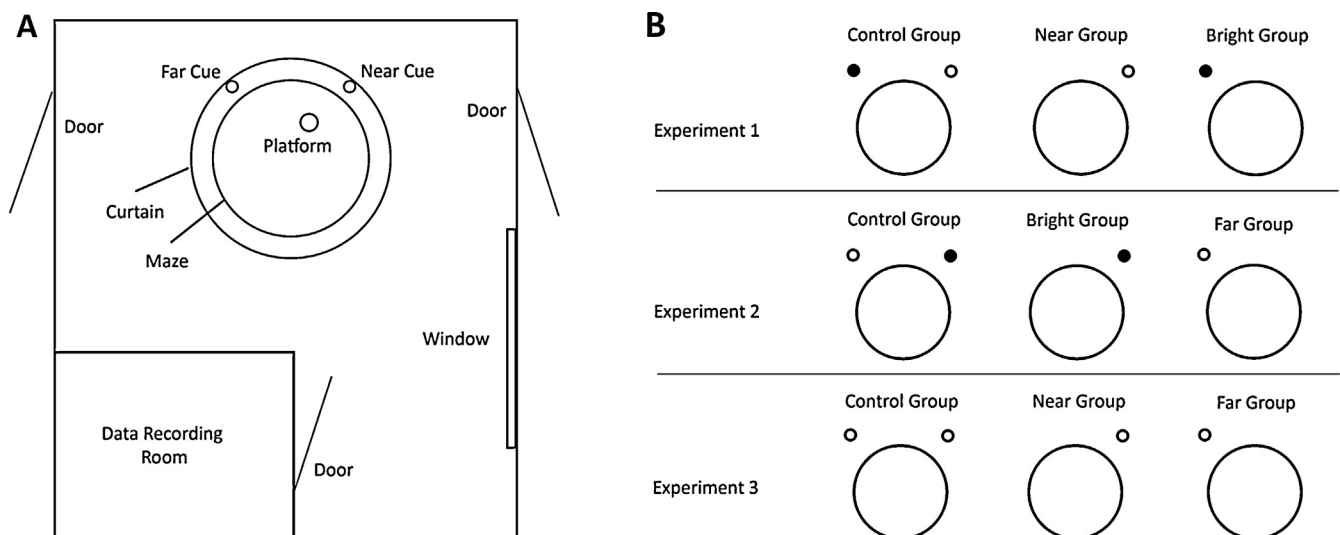


Fig. 1. (A) Schematic diagram of the training and testing environment. (B) Representation of the type and number of cues available to groups during testing for Experiments 1–3. Open circles denote the 25 W light bulb and closed circles denote the brighter 40 W light bulb.

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