



PEARL

Thinking outside of the box II: Disrupting the cognitive map.

Buckley, Matthew G.; Smith, Alastair D.; Haselgrove, Mark

Published in:
Cognitive Psychology

DOI:
[10.1016/j.cogpsych.2018.11.001](https://doi.org/10.1016/j.cogpsych.2018.11.001)

Publication date:
2019

Link:
[Link to publication in PEARL](#)

Citation for published version (APA):
Buckley, M. G., Smith, A. D., & Haselgrove, M. (2019). Thinking outside of the box II: Disrupting the cognitive map. *Cognitive Psychology*, 108(0), 22-41.
<https://doi.org/10.1016/j.cogpsych.2018.11.001>

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Wherever possible please cite the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

Thinking Outside of the Box II: Disrupting the Cognitive Map

Matthew G. Buckley ^a

Alastair D. Smith ^b

Mark Haselgrove ^c

^aDe Montfort University, UK and Durham University, UK

^bUniversity of Plymouth, UK

^cUniversity of Nottingham, UK

Revision submitted to Cognitive Psychology September, 2018

Please address correspondence to:

Matthew Buckley

Department of Psychology

De Montfort University

The Gateway

Leicester

LE1 9BH

matthew.buckley@dmu.ac.uk

Running Head: Disrupting the Cognitive Map

Abstract

A number of influential spatial learning theories posit that organisms encode a viewpoint independent (i.e. allocentric) representation of the global boundary shape of their environment in order to support spatial reorientation and place learning. In contrast to the trial and error learning mechanisms that support domain-general processes, a representation of the global-shape of the environment is thought to be encoded automatically as part of a cognitive map, and without interference from other spatial cues. To date, however, this core theoretical assumption has not been appropriately examined. This is because previous attempts to address this question have failed to employ tasks that fully dissociate reorientation based on an allocentric representation of global-shape from egocentric reorientation strategies. Here, we address this issue in two experiments. Participants were trained to navigate to a hidden goal on one side of a virtual arena (e.g. the inside) before being required to find the same point on the alternative side (e.g. the outside). At test, performing the correct search behaviour requires an allocentric representation of the global boundary-shape. Using established associative learning procedures of overshadowing and blocking, we find that search behaviour at test is disrupted when participants were able to form landmark-goal associations during training. These results demonstrate that encoding of an allocentric representation of boundary information *is* susceptible to interference from landmark cues, and is not acquired through special means. Instead, the results suggest that allocentric representations of environmental boundaries are acquired through the same kind of error-correction mechanisms that support domain-general non-spatial learning.

Keywords: Spatial learning, navigation, boundary, overshadowing, blocking

Navigation is a core component of everyday life: Knowing where we are, where we have been, and where we plan to go is fundamental to negotiating the world around us. Successfully navigating to important places in our environment requires that we maintain a sense of direction within that environment and, if we become lost for any reason, a process of reorientation must occur in order to re-establish the direction of travel. For instance, negotiating the commute between home and work may involve emerging from an underground train station via a novel exit, at which point it is necessary to reorient in order to know in which direction the workplace is in order to continue the journey. Accordingly, the processes underlying this behaviour have been studied in both translational studies conducted with animals, and also studies conducted with human children and adults. Within this fecund field, the last 30 years have witnessed an ongoing debate surrounding the relative importance of different environmental cues in the support of efficient reorientation behaviour. These have focused on the role of environmental shape (for reviews see: Burgess, 2008; Jeffery, 2010; Pearce, 2009) and two particular issues have become particularly prominent: (a) whether boundary shape information is encoded in a global or local fashion, and (b) whether learning about boundary shape is subject to interference from non-shape cues.

The notion that organisms may encode a global representation of the shape of the environment in which they navigate can be traced back to the proposals of Cheng (1986; see also: Margules & Gallistel, 1988), who conducted a series of experiments to determine whether the presence of landmarks during spatial learning influenced the performance of rats during subsequent reorientation based on the shape of the environment. In a typical reorientation experiment conducted with animals, a reward is located in one corner of a rectangle-shaped arena that contains a unique landmark in each corner. In order to find the goal, animals can rely on the ambiguous shape information provided by the corners of the arena, or on the unambiguous information provided by the unique landmark cues. Following

training, the landmarks are removed from the arena, and a number of studies conducted with a variety of animals, including rats (e.g. Cheng, 1986), mice (e.g. Fellini, Schachner, & Morellini, 2006), and chicks (e.g. Vallortigara, Zanforlin, & Pasti, 1990), have demonstrated that animals preferentially search in the correct corner, or commit a rotational error by searching in the geometrically equivalent corner that is diagonally opposite the correct corner. On the basis of these rotational errors, Cheng (1986) suggested that animals encode a metric frame of the environment formed solely from the geometric properties of surrounding boundary surfaces and, importantly, this representation was proposed to be encoded in a manner that is impervious to the influence of non-shape cues, such as landmarks. The importance of this shape-based representation for reorientation was championed by Gallistel (1990), who noted that whilst landmark cues can be used to guide some navigational behaviours, when disorientated, animals rely on the global geometric properties of an environmental boundary to re-establish orientation.

Although this seminal proposal was based upon studies conducted with non-human animals some 30 years ago, it is important to note that theorising about encoding boundary-shape information in a manner that is impervious to the influence of landmark cues is not limited to studies conducted with non-human animals, nor is it consigned to the vaults of history. Indeed, studies conducted with human adults (Redhead & Hamilton, 2007) and children (Hermer & Spelke, 1994, 1996; Hermer-Vazquez, Moffet, & Munkholm, 2001; Wang, Hermer, & Spelke 1999) have replicated the findings observed in animals, whereby the presence of a landmark cue did not prevent participants from encoding a goal location with respect to the boundary walls of an environment. In keeping with the proposals made by Cheng (1986), these findings have been interpreted as evidence that humans encode a global allocentric representation of the boundary-shape of an arena, regardless of the presence of landmark cues (e.g. Wang & Spelke, 2002, 2003).

The notion that boundaries may hold a privileged status during navigation has also been bolstered by elegant demonstrations of the importance of boundaries (Boccaro et al., 2010; Lever, Burton, Jeewajee, O'Keefe, & Burgess, 2009; Solstad, Boccaro, Kropff, Moser, & Moser, 2008; see also Barry et al., 2006; O'Keefe & Burgess, 1996) in the formation of cognitive maps in the rodent hippocampus (e.g. Lever et al., 2002; O'Keefe & Dostrovsky, 1971), along with recent accounts that implicate similar mechanisms in the human hippocampal formation (for discussion see: Hartley et al., 2014). In a series of highly influential experiments assessing the neural correlates of boundary and landmark encoding in human participants, it has been observed that encoding locations with respect to the boundaries of the environment is subserved by a hippocampal memory system, whereas learning with respect to landmarks is subserved by a striatal memory system (Doeller, King, & Burgess, 2008). In a complementary behavioural experiment, Doeller and Burgess (2008) demonstrated that encoding locations with respect to the boundaries of an environment was not hindered by the presence of a landmark cue, relative to learning that occurred with the boundary in isolation. In contrast, learning locations with respect to a landmark cue was hindered by the presence of the boundary walls, relative to learning that occurred with the landmark in isolation. On the basis of these findings, it was proposed that learning about the boundaries of an environment occurs automatically in a hippocampal mapping system, whereas landmark learning is associative in nature and occurs in a striatal system (Doeller & Burgess, 2008; Doeller et al., 2008). This position, again, espouses a privileged role for boundary shape information in spatial behaviour, and current theories of cognitive mapping highlight the importance of boundaries in forming an allocentric representation of the space in which we navigate (Bicanski & Burgess, 2018; Poulter, Hartley, & Lever, 2018).

Theories of spatial behaviour that suggest a privileged role for boundary information, and particularly the notion that we encode an allocentric representation of the global

boundary shape separately from landmarks, have received much empirical attention. Two cue competition procedures, translated from studies of animal conditioning, have dominated the approach to answering this question. These procedures are *overshadowing*, first reported by Pavlov (1928), and *blocking*, first reported by Kamin (1968). In a typical overshadowing paradigm, participants in an experimental group are trained to find a hidden goal that can be located using both the shape of the environment and landmarks within it. In contrast, for participants in a control group, only the shape of the environment can be used to locate the goal during training, which is usually achieved by establishing landmarks as uninformative (e.g. moving their location from trial to trial). Both groups then receive a test trial in which they are placed back into the same-shaped environment in the absence of any landmarks and the hidden goal, and the time spent searching in the correct corner of the environment is used to assess the extent to which participants have learned where, in the shape, the hidden goal was located. In a typical blocking paradigm, Stage 1 training for an experimental group establishes only a landmark cue as predictive of a hidden goal location, which is usually achieved by presenting the landmark within a symmetric boundary shape (e.g. a circle or square) such that shape information cannot be used to find the goal. In Stage 2 training, the same landmark continues to predict the goal location, but now training occurs in an environment where shape information can also be used to locate the goal (e.g. an isosceles triangle). As with overshadowing experiments, participants then receive a test trial conducted in the absence of any landmarks and the hidden goal, in which they are placed into the same-shaped arena that was used in Stage 2, and performance is compared to a control group that, for example, receives only Stage 2 training.

The pattern of results that has emerged from cue competition experiments in the spatial literature is mixed. Earlier overshadowing experiments indicated that landmarks did not overshadow learning about the shape of the environment (e.g. Hayward, McGregor,

Good, & Pearce, 2003), but more recent experiments have demonstrated overshadowing of shape learning by landmarks (e.g. Pearce, Graham, Good, Jones, & McGregor, 2006). Similarly, initial blocking experiments indicated that landmarks did not block learning about the shape of the environment (e.g. Hayward, Good, & Pearce, 2004), but more recent experiments have demonstrated blocking of shape learning by landmarks (e.g. Horne & Pearce, 2009). It is, however, difficult to interpret the results of these cue competition studies, because all previous experiments have trained and tested participants in the same-shaped environments. Despite the prominence of the idea that we encode a global allocentric representation of the boundaries of our environment as part of a cognitive map, it has been suggested that it is possible to account for spatial behaviours by assuming that we egocentrically encode the segments of an environmental shape that signal a goal location. For example, consider a typical reorientation experiment, in which a participant is trained to find a hidden goal in the corner of a rectangle-shaped arena, as is frequently done in experiments conducted with non-human animals (e.g. Cheng, 1986), as well as human adults (Buckley, Smith, & Haselgrove, 2016a) and children (Hermer & Spelke, 1994, 1996). According to local theories of boundary shape encoding, participants could find the hidden goal by associating it with the sight of a short wall to the left of long wall (Pearce, Good, Jones, & McGregor, 2004). Importantly, in the absence of any landmarks, this association would also lead participants to commit rotational errors, and search in the geometrically equivalent corner diagonally opposite the correct corner. Given this, navigational behaviour within a rectangle-shaped environment can be explained equally well by assuming participants reorient on the basis of global- or local-shape information, and this is true of any environmental shape. Consequently, previous overshadowing and blocking experiments demonstrate only that landmarks can interfere with learning about shape information, not whether this interference impacts upon allocentric encoding of global shape information, or

egocentric encoding of local shape cues. To date, therefore, a key proposal of cognitive mapping theories remains untested.

To assess whether global or local representations of shape are subject to interference from non-shape cues, it is necessary to first design a task where behaviour based on the representation of the global shape of an environment can be dissociated from behaviour based on local shape representation. One way in which this dissociation has been obtained is to employ a shape transformation, in which participants are trained to find a hidden goal in, say, a right-angled corner of a kite-shaped arena, before being placed in a rectangle-shaped arena that contains no hidden goal. Studies conducted with adult humans (e.g. Lew, Usherwood, Fragkioudaki, Koukoui, Austen, & McGregor, 2014) and rats (e.g. Pearce et al., 2004) have demonstrated that participants search in the corners of the rectangle that share the same local shape cues that signalled the goal location in the kite (see also: Tommasi & Polli, 2004 for a demonstration of local shape learning in chicks). As the global shape of these two environments are not congruent, it has been argued that this behaviour is based upon on local shape representations (cf. Cheng & Gallistel, 2005; but see also McGregor, Jones, Good, & Pearce, 2006), and recent studies from our laboratory have adopted this technique to demonstrate that learning about local shape information is subject to blocking from non-shape landmark cues (Buckley et al., 2016a).

Crucially, however, it remains to be determined whether encoding of a global-shape representation as part of a cognitive map is similarly restricted by the presence of landmarks. Part of the problem, here, lies in designing a technique in which navigational behaviour is based only on a global representation of the shape of the environment. Although it is possible to change the global shape of an environment whilst preserving some local shape cues (e.g. Lew et al., 2014; Pearce et al, 2004), it is difficult to envisage how to change some local shape cues without also altering the overall global shape of the environment. We have,

however, recently dissociated behaviour based on a global shape representation from behaviour based on local shape representations via a perspective transformation (Buckley, Smith, & Haselgrove, 2016b). Based on developmental studies conducted by Lourenco, Huttenlocher, and Vasilyeva (2005; see also Lourenco & Huttenlocher, 2007), we trained participants to find a hidden Wi-Fi signal that was located at a right-angled corner on the *inside* of a distinctively shaped virtual arena (e.g. a kite shape). Following this training, participants were tested on the *outside* the same-shaped arena without a hidden goal present, and their search time on the outside of the arena corners was measured. The results showed that participants had a clear preference for searching on the outside of the corner that had previously contained the Wi-Fi signal on its inside. This behaviour cannot be readily explained by reference to local-shape encoding, because local-shape information is thought to be encoded in a viewpoint dependent manner (i.e. it is encoded egocentrically). For example, consider training in which the hidden goal is located at the inside corner of a kite-shaped arena where a short wall is to the left of a long wall. On the outside of a kite-shaped arena, the view of the same corner is a short wall to the right of a long wall. As the relative lengths of the left- and right-sided walls are reversed from training, responding based on local shape information would not lead participants to the outside of the corner rewarded during training. In contrast, a representation of the global shape of the environment is viewpoint independent (i.e. it is encoded allocentrically), because the overall shape of an environment does not change depending on whether the walls are viewed from the inside or the outside. Consequently, navigation based upon a representation of the global shape of the environment readily explains the behaviour that was observed at test.

For the first time in this field of research, the inside-outside paradigm outlined above provides a unique opportunity to assess whether encoding of an allocentric representation of the global shape of an environment is subject to interference from landmarks. This was the

focus of the present study and, given the continued high-profile discussion of automatic allocentric encoding of boundary information in the spatial literature (Brunec, Moscovitch & Barense, 2018; Burgess, 2008; Gallistel & Matzel, 2013; Lew, 2011; Spelke & Lee, 2012; Tommasi, Chiandetti, Pecchia, Sovrano, & Vallortigara, 2012; Xu, Regier, & Newcombe, 2017), the question carries important ramifications for the manner in which cognitive maps are formed. In keeping with previous studies of cue competition effects in the spatial learning literature, we employed both overshadowing and blocking procedures to determine whether landmark cues interfere with encoding of a global shape-representation.

Experiment 1

Studies of overshadowing that have examined whether landmarks interfere with learning about environmental shape have produced mixed results. Some experiments seem to demonstrate that landmark cues do not overshadow learning about the shape of an environment. For instance, Redhead and Hamilton (2007) trained adult humans to navigate to a goal in an isosceles triangle-shaped virtual environment that contained two landmarks, located in the corners at either end of the shortest wall. For participants in an overshadowing group, the two landmarks were unique and, thus, the goal could be found on the basis of both the boundary shape of the environment and the landmarks within it. For a control group, the two landmarks within the pool were identical, thus, only the boundary shape of the pool signalled the goal location. Following training, a test trial in which both the goal and the landmarks were removed from the arena was administered, and participants were allowed to search for 45 seconds. During this test trial, participants in both groups preferentially searched in the corner that had contained the goal, compared to the corner at the other end of the shortest wall of the triangular arena, which did not previously contain the goal. In this experiment, then, the presence of a predictive landmark did not restrict learning about the

boundary shape of an environment in human participants, a finding that has been observed in experiments conducted with non-human animals also (see Table 1).

----- Insert Table 1 about here -----

Despite the abundance of observations that landmarks do not overshadow encoding the boundary shape of an environment, a number of recent experiments have found contradictory results. That is, landmarks *have* been observed to overshadow learning about the boundary shape of an environment. Redhead, Hamilton, Parker, Chan, and Allison (2013), for example, trained participants in an overshadowing group to navigate to a goal located in a trapezium-shaped environment that contained two distinctive landmarks, one in each of the corners at the end of the longest wall. The goal was also located in one of the corners at the end of the longest wall and, thus, its location was signalled by both the unique shape of the corner and the distinctive landmark within that corner. Participants in a control group received similar training; however, the landmarks presented to this group were identical. Consequently, the location of the goal was signalled only by the unique shape of the corner in which it was placed. Following training, both groups received test trials in which the landmarks and goal were removed from the environment, and it was observed that the overshadowing group spent significantly less time searching in the corner of the trapezium that had contained the goal, relative to the control group. The presence of a predictive landmark, then, overshadowed participants learning about the location of a hidden goal with reference to the boundary shape of the environment, and similar findings have also been observed in experiments conducted with non-human animals also (see Table 2).

----- Insert Table 2 about here -----

As we outlined in the introduction to this paper, however, it is difficult to interpret the results of these previous overshadowing experiments because they fail to determine what type of shape representation(s) were necessary for navigational behaviour. Consequently, the purpose of Experiment 1 in the present study was to perform an inside-outside manipulation between training and test that would allow us to determine if encoding of a global representation of shape was subject to overshadowing from landmark cues. Participants were trained to find a hidden Wi-Fi signal that was positioned at one of the right-angled corners on the inside of a kite-shaped virtual environment. A uniquely coloured spherical landmark was present in each corner of the kite-shaped arena and, for the overshadowing group, these landmarks remained in a constant position throughout training. Consequently, both the landmark and the shape of the environment signalled the goal location during training for the overshadowing group. For the control group, however, the landmarks changed position with each other between trials, meaning that only the shape of the environment predicted the goal location. Following training, both groups received a single test trial in which participants were placed on the outside of the kite-shaped arena, with no landmarks present. Unbeknownst to the participants, the hidden goal was removed during the test trial, and participants were allowed to search for 120 seconds. Given that only the shape of the environment predicted the goal location for the control group during acquisition, it was expected that control participants would search near the right-angled corner that previously contained the hidden goal when on the outside of the arena, a behaviour that we, and others, have previously argued to be based upon a global representation of the shape of the environment (Buckley et al, 2016b; Lourenco et al., 2005; Lourenco & Huttenlocher, 2007). The crucial comparison in Experiment 1 was the extent to which the overshadowing group

would display a similar behaviour to the control group. According to theories that posit a privileged role for boundary information, (e.g. Cheng, 1986; Doeller & Burgess, 2008; Gallistel, 1990; Wang & Spelke, 2002, 2003) the presence of co-predictive landmarks during training should not restrict learning about the global-shape of the kite-shaped arena. When tested on the outside of the arena, therefore, overshadowing participants should spend an equivalent amount of time searching near the right-angled corner that previously contained the hidden goal as control participants.

Method

Participants

64 students were recruited from the University of Nottingham (57 female), aged between 18 and 22 years (mean = 18.97, SD = .96), and were given course credit in return for participation. Participants were randomly allocated to the overshadowing or control group, with the stipulation that there were 32 participants in both groups. All participants provided fully-informed consent before commencing the experimental procedure, and the study was ratified by the School of Psychology Research Ethics Committee (University of Nottingham, UK).

Materials

All virtual environments were constructed and displayed using Mazesuite (v2.1) software (Ayaz, Allen, Platek, & Onaral, 2008; www.mazesuite.com). The virtual environments, which participants viewed from a first-person perspective with a field of view of 45 degrees, were run and displayed on an Apple Mackintosh model A1224 (EMC2133) with a screen of 27.40 x 43.40 cm. Assuming a walking speed similar to that in the real world (2 m/s), the perimeter of the kite-shaped arena was 72m, with the small walls being 9m in length and the long walls 27m. The height of the walls was approximately 2.5 m. The kite

was configured such that it contained two right-angled corners with the remaining two angles being 143.14° and 36.86° . The goals within the arenas were square-shaped regions (1.08m x 1.08m, invisible to participants) that were always placed 1.48 away from the walls of the arena, along on a notional line that bisected the corner.

Using the 0-255 RGB scale employed by MazeSuite, the cream-coloured walls forming the kite-shaped arena were defined as 204, 178, 127, and were located in the centre of a 780m x 780m floor, which had a grass texture applied to it. The sky was rendered as a uniform black expanse when participants were navigating both inside and outside of the arena (see figure 1). The four 90cm-diameter landmarks used in the experiment were the default red, blue, yellow, and green spheres that are supplied when downloading MazeSuite software, and were placed 1.48 away from the walls of the arena, along on a notional line that bisected the corner.

----- Insert Figure 1 about here -----

Procedure

After signing a standard consent form, participants were given the following set of instructions:

This study is assessing human navigation using a computer generated virtual environment. During this experiment, you will complete 16 trials. In each trial, you will be placed into a room that contains a Wi-Fi hot spot. Your aim is to end the trials as quickly as possible by walking into the hot spot.

You will view the environment from a first person perspective, and be able to walk into the hot spot from any direction using the cursor keys on the keyboard. Once you've found the hot spot a congratulatory message will be displayed and you should hit enter when you're ready to begin the next trial. You will always be in the centre of the arena when a trial begins, but the direction in which you face at the start of each trial will change.

To start with, you may find the hot spot is difficult to find. The hot spot does not move though, so it is possible to learn its specific location as the experiment goes along. It's a good idea to fully explore the environment on the first few trials to become aware of your surroundings. This should help you in learning where the hidden hot spot is. If you have difficulty finding the hotspot, a white flag will appear indicating the location of the hotspot zone.

This session should take around 15-20 minutes. If at any point you wish to stop this session, please notify the experimenter and you'll be free to leave without having to give a reason why. Your results will be saved under an anonymous code, and kept confidential throughout.

Participants sat not more than 50 cm from the screen and, for each of the 16 acquisition trials that were administered, they were required to navigate to the hidden goal by using the cursor keys. Presses on the “up” and “down” cursor keys permitted the participant to move forwards and backwards within the arena, respectively, while presses on the “left” and “right” cursor keys permitted them to rotate counter-clockwise and clockwise within the environment, respectively. Participants travelled at 2m/s during both acquisition and test trials (MazeSuite move parameter set to .005). There was no time limit for any acquisition trials, thus, each trial ended only when the hidden goal was found. If, however, participants had not found the hidden goal within 60s on any given trial, a white flag appeared at the

location of the hidden goal. Once the hidden goal had been found, participants could no longer move within the arena and a congratulatory message (*Wi-Fi Connected!*) was displayed on screen using the default font and character size in MazeSuite. Participants pressed enter to begin the next trial.

Participants began each trial at a point located halfway between the apex and obtuse corners, and the direction in which participants began facing was randomised for every trial. During acquisition trials, the location of the hidden goal was counterbalanced for both the overshadowing and control groups, such that half the participants within each group were required to navigate to a right-angled corner where a long wall was to the left of a short wall, whilst the other half of participants were required to navigate to a right-angled corner where a long wall was to the right of a short wall. As noted previously, a landmark cue was present in each corner of the kite-shaped environment. In a clockwise manner, the blue, red, green, and yellow landmarks were placed into an individual corner of the kite-shaped arena, and rotating this configuration of landmarks one, two, or three corners clockwise produced a total of four different landmark placements that were used during acquisition trials. For the overshadowing group, the landmarks remained in a constant position during all 16 acquisition trials so that a given landmark signalled the goal location, along with the shape of the environment. The identity of the predictive landmark was counterbalanced across participants in the overshadowing group such that each of the four landmarks signalled the goal location equally often when the goal was placed a right-angled corner where a long wall was to the left of a short wall. This was also the case when the goal was placed in the right-angled corner where a long wall was to the right of a short wall. For the control group, the landmarks moved between acquisition trials in order to render them irrelevant to finding the goal location. This was achieved by randomly presenting one of the four previously described

landmark configurations over the course of training, with the stipulation that each of the landmark configurations was used for four of the acquisition trials.

Having completed 16 acquisition trials, participants received the following instructions prior to the test trial:

In the next trial, you will again have to locate a Wi-Fi signal. The location of the Wi-Fi signal hasn't changed, so it will be in the same location as before.

However, you will be navigating around the outside of the building. As the Wi-Fi signal will be travelling through the walls of the building, it will be a bit weaker, and so it may be harder to locate.

Press enter to start.

For participants in both groups, pressing enter began a 120 second test trial in which they were placed on the outside of an arena that contained no hidden goals. Participants began the test trial facing one of the four walls of the shape, and were located 3.15m from the centre of the wall, along a notional line running perpendicular to the wall. The start location at test was counterbalanced across participants, such that each of the four possible start locations was used equally often for each of the two different goal locations for both the overshadowing and control groups. To measure behaviour during test trials, the time spent within 6.48 x 6.48m square search zones, which were centred on all points where a long and short wall met to create a right angled corner, was recorded. These search zones were orientated such that two of its edges were parallel to a long wall of an arena, and the remaining two edges ran parallel to a short wall of an arena (see Figure 2). Signal zones were located at the right-angled corners that had previously contained the hidden goal, and no-signal zones were located at the right angled corners of an environment that did not previously contain the hidden goal. Assessing spatial behaviour during extinction tests in such a manner is common

in both animal (e.g. McGregor, Horne, Esber, & Pearce, 2009), and human (e.g. Redhead & Hamilton, 2009) experiments.

----- Insert Figure 2 about here -----

Statistical analysis

For training and test data, we statistically ratified raw time data with an analysis of variance (ANOVA), and report partial eta squared (η_p^2) to estimate effect sizes. In order to generate confidence intervals that are congruent with the outcomes of an ANOVA that adopts .05 as the criterion for significance, we calculated 90% confidence intervals around η_p^2 (see Buckley et al., 2016a; 2016b). Consequently, if the confidence interval surrounding η_p^2 excludes zero, the corresponding p value will indicate significance. Calculating 95% confidence intervals around η_p^2 can lead to cases where an F -test returns a significant p value, but the confidence intervals for η_p^2 includes zero (Steiger, 2004).

Whilst examining the raw time that participant spent in the signal and no-signal zones at test would allow us to determine if participants preferentially searched at one location over the other, this analysis does not determine whether the time spent in the signal zone was different to that which would be expected by random search. Consequently, in addition to analysing the raw times spent in the two zones at test, we also examined whether the time spent in the signal zone was greater than would be expected by chance. In order to define a chance level of performance, there were two alternatives. First, a chance value could be defined by calculating the percentage of the entire navigable space that is defined as the signal zone (0.005%), and then assuming that participants would spend this proportion of

time in the signal zone during entire test trial. This definition of chance is flawed, however, as it requires that participants explore the entire navigable space randomly and equally. Instead, given that participants were trained to find a Wi-Fi hotspot at a corner inside of an arena, it is reasonable to expect that, at test, participants would search close to the boundary of the arena. Consequently, it is more appropriate to analyse if participants spent more time searching at the signal zone, compared to time spent in both the signal and no-signal zone. To perform this analysis, we expressed the time spent searching in the signal zone as a proportion of the time spent searching in signal and no-signal zones (see Table 1), which yielded a chance value of 50%. As this value is more conservative than 0.005%, then it stands to reason that participants who spent greater than chance amounts of time in the signal zone relative to time in both zones would also spend greater than chance amounts of time in the signal zone relative to the entire navigable space.

Results

Training

Figure 3 shows that the latency to find the hidden goal, in seconds, decreased during training in both the overshadowing and control groups, although it appeared that participants in the overshadowing group located the goal quicker than control participants in early training trials. A two-way ANOVA conducted on individual latencies to find the hidden goal, with a between-subjects factor of group (overshadowing or control), and a within-subjects factor of trial (1-16), confirmed these impressions. There were significant main effects of group $F(1, 62) = 14.29$, $MSE = 469.19$, $p < .001$, $\eta_p^2 = .19$ [.06 - .32], trial $F(15, 930) = 37.64$, $MSE = 155.01$, $p < .001$, $\eta_p^2 = .38$ [.33 - .40], and a significant interaction between group and trial $F(15, 930) = 3.75$, $MSE = 155.01$, $p < .001$, $\eta_p^2 = .06$ [.02 - .07]. Simple main effects analysis revealed that participants in the overshadowing group found the goal significantly

faster than control participants on trials 2, 3, 5, 6, 9-12 $F_s(1, 62) > 4.18, p_s < .045, \eta_p^2 > .23$ [.001 - .18]. Importantly, there was no between group difference in latency to find the goal by the end of training ($F < 1$).

----- Insert Figure 3 about here -----

Test

Figure 4 displays the amount of time overshadowing and control participants spent searching within the signal and no-signal zones during test. Participants in the control group spent more time searching in the signal than the no-signal zone. In contrast, overshadowing participants appeared to spend an equal amount of time searching in signal and no-signal zones. A two-way ANOVA conducted on individual time spent in zones, with a between-subjects factor of group (overshadowing or control), and a within-subjects factor of zone (signal or no-signal) revealed significant main effects of group $F(1, 62) = 7.19, MSE = 171.90, p = .009, \eta_p^2 = .10$ [.01 - .23], zone $F(1, 62) = 21.28, MSE = 303.82, p < .001, \eta_p^2 = .26$ [.11 - .39], and a significant interaction between group and zone $F(1, 62) = 14.18, MSE = 303.82, p < .001, \eta_p^2 = .19$ [.06 - .32]. Simple main effects analysis revealed that, within groups, overshadowing participants spent a statistically equivalent amount of time in the signal zone and no-signal zones $F < 1$; however, control participants spent significantly more time in the signal zone, compared to the no-signal zone $F(1, 62) = 35.09, p < .001, \eta_p^2 = .36$ [.20 - .49]. Between groups, participants in the control group spent significantly more time in the signal zone compared to overshadowing participants $F(1, 62) = 12.76, p = .001, \eta_p^2 = .17$ [.05 - .30], but participants in the overshadowing group spent significantly more time in the no-signal zone compared to control participants $F(1, 62) = 5.98, p = .017, \eta_p^2 = .09$ [.01 - .21].

One sample t-tests conducted on individual percentages of time spent in the signal zone revealed that whilst the control group spent more time (70 %) in the signal zone during test than would be expected by chance $t(31) = 5.53$, $p < .001$, $d = .98$, the overshadowing group (49 %) did not $t(31) = .15$, $p = .88$, $d = .16$.

----- Insert Figure 4 about here -----

Discussion

In Experiment 1, overshadowing and control participants were trained to find a hidden goal inside of a kite-shaped arena that contained four unique landmarks. For the overshadowing group, the hidden goal was signalled by the shape of the arena and the landmarks within the arena. For control participants, the landmarks moved between trials, meaning only the shape of the environment signalled the goal location. Following training, both groups received a test trial on the outside of the kite-shaped environment, in the absence of any landmarks and the hidden goal. In keeping with our previous results (Buckley et al., 2016b), control participants spent significantly more time searching at the corner that previously contained the Wi-Fi signal than the alternative right-angled corner. This behaviour is incompatible with a local-encoding analysis of reorientation following spatial navigation, but is consistent with an analysis that favours global-encoding, which, according to cognitive mapping theories, is deemed to be allocentric in nature. Intriguingly, however, overshadowing participants did not preferentially search at the right-angled corner that previously contained the Wi-Fi-signal, compared to the other right-angled corner. Along with the experiments listed in Table 2, these results demonstrate that learning about shape information is subject to interference from landmark cues. Importantly, and where our data

distinguish themselves, is that the use of a perspective transformation in the current experiment permits the conclusion that learning about *global* shape information can be overshadowed by landmark cues.

It is worthwhile noting that the overshadowing group found the goal quicker than the control group during early training trials. This difference could reflect that, for overshadowing participants, two cues signalled the goal location whereas, for control participants, only shape information predicted the goal location. Given that the data from the test trial revealed that the overshadowing group had learned little about the shape of the environment, though, it is unclear why training in which the shape predicted the goal location would yield faster latencies than the control group. An alternative explanation is that the landmark cues in the current experiment were particularly salient relative to the shape of the environment, and automatically captured attention (see Buckley, Smith, & Haselgrove, 2015). For overshadowing participants, this would mean a cue that predicted the goal location was attended to from the onset of training. In contrast, for control participants, a cue that was not predictive of the goal location would have been attended to at the onset of training, and this initial bias attention would have to be overcome before learning about the shape of the environment could occur.

In any case, theories that advocate a privileged role for boundary information in spatial learning predict that encoding a representation of the shape of an environment should be immune to the presence of more informative landmark cues (Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003), and more recent formulations of this notion have explicitly stated that the salience of a landmark cue does not impact the automatic process of encoding boundary shape as part of a cognitive map (e.g. Doeller & Burgess, 2008). Contrary to these expectations, by using an inside-outside manipulation to generate a perspective transformation between training and test, Experiment 1 provided the first evidence that

learning about the location of a hidden goal with reference to the *global* shape of the environment can be restricted by the presence of co-predictive landmarks.

Experiment 2

Scientific thinking about non-spatial learning in human and non-human animals has converged on the conclusion that cues may compete for an association with an outcome (e.g. Pearce & Bouton, 2001), and restrict learned behaviour not only in procedures that employ overshadowing designs, but also through blocking (Kamin, 1968). Indeed, both classical (e.g. Mackintosh; 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972) and more contemporary (e.g. Esber & Haselgrove, 2011; Le Pelley, 2004) analyses of association formation employ the same psychological principles to explain blocking as they do overshadowing. Thus, if overshadowing is observed using one particular behavioural procedure, then we should also expect the same procedure to support blocking. In a blocking experiment, a cue (let us call it A) is first established as a predictor of an outcome, before this cue is presented in compound with a second cue (let us call it X) and both are paired, simultaneously, with the same outcome as used in the initial stage of the experiment. Blocking is observed when little learning about the X-outcome association is expressed in a final test when X is presented in the absence of both A and the outcome.

Blocking procedures, in addition to overshadowing (see Experiment 1), have been used by a number of researchers to assess whether learning about the boundary shape of an environment is immune to interference from landmark cues. As with studies of overshadowing, a mixed pattern of results has emerged over three decades of empirical enquiry. Evidence consistent with the proposal that encoding of shape information is immune to blocking has been provided by a virtual reality experiment conducted by Redhead and Hamilton (2009). Participants in a blocking group were trained, in stage 1 of the experiment,

to locate a goal that was signalled by one of two distinctively-coloured landmarks that were contained within circular environment. Following this training, participants were placed into an isosceles triangle-shaped stage 2 arena. The same two landmarks that were presented in stage 1 were also present in this arena, one at either end of the shortest boundary wall. In this stage of the experiment, the goal that participants were required to locate was signalled by the same landmark as in stage 1, and also by the unique shape of the corner in which it was now located. A control group received trials identical to those given to the blocking group in stage 2, however, unlike the blocking group, control participants were given no stage 1 training. A test trial, conducted in an isosceles triangle-shaped arena that contained no landmarks or goals, revealed that both groups preferentially searched in the zone of the arena that previously contained the goal, relative to a zone located at the other end of the shortest wall of the environment. Importantly, both the blocking and control groups spent an equivalent amount of time in the zone of the arena where the goal was previously located. Learning the location of a goal with respect to a landmark cue, therefore, failed to restrict subsequent learning about the location of the goal with respect to boundary shape information, a finding that has also been observed in non-human animals (see Table 3).

----- Insert Table 3 about here -----

As with the overshadowing literature, however, observations of landmarks blocking learning about boundary shape have also been reported. In stage 1 of an experiment conducted by Wilson and Alexander (2008), participants in a blocking group were placed into a circular virtual environment, and required to find a hidden goal that was located at a fixed vector relative to a landmark. In stage 2 of the experiment, participants were placed into an

irregular trapezium-shaped arena that contained the same landmark that was present in stage 1. Participants were, again, required to locate a hidden goal that was located at the same fixed vector relative to the landmark as in stage 1 training. Participants in a control group received identical stage 2 training, however, in stage 1 control participants were asked to explore an unrelated maze of corridors. Following stage 2 training, test trials conducted in the same trapezium-shaped environment, but with the landmark removed, revealed that the control group took less time to locate the hidden goal compared to the blocking group. Learning the location of the hidden goal with respect to the landmark, then, prevented participants in the blocking group from learning the location of the hidden goal with respect to the boundary shape of the environment, and again this finding has been observed in non-human animals also (see Table 4).

----- Insert Table 4 about here -----

Consistent with the overshadowing experiments reviewed previously, these blocking experiments again failed to determine which type of shape representations were supporting navigational behaviour. Consequently, the purpose of Experiment 2 was to perform an inside-outside manipulation between stage 2 training and test that would allow us to determine whether encoding of a global representation of the shape of the arena was subject to blocking from landmark cues. Participants were again asked to locate a hidden Wi-Fi signal, and in Stage 1 the location of this hidden goal was signalled by one of four unique landmarks that were presented in a square-shaped arena. As the shape information provided by this arena was ambiguous, this stage of training ensured that only landmark cues could be used to locate the goal. In stage 2, participants were transferred to a kite-shaped environment that, in each

corner, contained one of the four unique landmarks that were present in Stage 1 training. For both blocking and control groups, the hidden goal was located, for example, in the right-angled corner where a long wall was to the right of a short wall. Consequently, participants in both groups could learn that the boundary of the kite-shaped environment signalled the location of the hidden goal. For the blocking group, the landmark that signalled the goal location in Stage 1 continued to signal the goal location in stage 2. For the control group, however, a different landmark signalled the goal location in stage 2, relative to stage 1. According to associative analyses of learning, this control treatment will induce a large prediction error on trial 1 of stage 2, permitting learning to take place to all stimuli present on that trial – including the shape of the environment. Following training, to examine what had been learned about shape, participants were given a 120s test trial that was conducted on the outside of the kite-shaped arena in the absence of any landmarks and the hidden goal. In keeping with Experiment 1, it was expected that the control participants would search near the right-angled corner that previously contained the hidden goal when on the outside of the arena.

As with Experiment 1, the crucial comparison was the extent to which the blocking group would display a similar behaviour to the control group. According to theories which afford the boundaries of an environment a privileged status (e.g. Cheng, 1986; Doeller & Burgess, 2008; Gallistel, 1990; Wang & Spelke, 2002, 2003), training in Stage 1 that establishes a landmark as predictive of the goal location should not prevent learning about the global-shape of the kite-shaped arena during Stage 2. When tested on the outside of the kite-shaped arena, therefore, blocking participants should spend an equivalent amount of time searching near the right-angled corner that previously contained the hidden goal relative to control participants. Given the results of Experiment 1, however, we may have reason to doubt the accuracy of this prediction.

Method

Participants

64 students were recruited from the University of Nottingham (53 female), aged between 18 and 23 years (mean = 19.09, SD = 1.17), and were given course credit in return for participation. Participants were randomly allocated to the blocking or control group, with the stipulation that there were 32 participants in both groups. All participants provided fully-informed consent before commencing the experimental procedure, and the study was ratified by the School of Psychology Research Ethics Committee (University of Nottingham, UK).

Materials

All virtual environments were created and displayed as described in Experiment 1. Details pertaining to the kite-shaped environment and landmarks were also the same as described in Experiment 1. The square-shaped arena used in Stage 1 of the current experiment was built from the same cream coloured walls defined in Experiment 1. Assuming a walking speed of 2 m/s, the perimeter of the square was 72m (each wall: 18m), and the height of the walls creating the square was, again, approximately 2.5 m. The walls were again located in the centre of a 780m x 780m floor, which had a grass texture was applied to it, and the sky was again rendered as a uniform black expanse. As with the kite-shaped arena, the goal within the square-shaped arena was a square region (1.08m x 1.08m, invisible to participants), the centre of which was always located 1.48m away from the walls of the arena, along on a notional line that bisected a right-angled corner in half. Also in keeping with the kite-shaped arena, the four 90cm-diameter red, blue, yellow, and green landmarks were placed in the corners of the arena, 1.48 away from the walls along on a notional line that bisected the corner.

Procedure

Any details not outlined in the following section are identical to Experiment 1. After signing a standard consent form, participants were given the same standard set of instructions described in Experiment 1, save for being told the Experiment would consist of 21 trials, and would last approximately 30 minutes. Participants first completed 16 trials in a square-shaped arena, beginning each trial at the centre of the arena, facing a randomly-selected direction on every trial. The square-shaped arena contained one of the four unique landmarks in each corner, and the landmarks maintained the same clockwise blue, red, green, and yellow configuration across participants. The location of the hidden goal was then counterbalanced such that each of the four unique landmarks signalled the goal location for an equal number of participants in both the blocking and control groups.

Immediately after completing Stage 1, participants completed four trials in a kite-shaped arena that, in each corner, contained one of the four landmarks that were presented in Stage 1. For half the participants in the blocking and control groups, the hidden goal was located in the right-angled corner where a short wall was to the left of a long wall. For the remaining half of participants in each group, the goal was located in the right-angled corner where a long wall was to the left of a short wall. The four configurations of landmark placements that were used in Experiment 1 were also employed during Stage 2 of the current experiment. For the blocking group, the unique landmark that previously predicted the goal location in the square shaped arena of Stage 1 continued to predict the goal location in the kite-shaped arena in Stage 2, thus, the previously rewarded landmark was located at the rewarded right-angled corner of the kite-shaped environment. For the control group, however, the landmark that previously signalled the goal location in Stage 1 no longer signalled the goal location in Stage 2. Here, the previously rewarded landmark was located at the non-rewarded right-angled corner of the kite-shaped environment. It is important to note here that

stage 2 training was identical for both groups, therefore, it was the landmark that signalled the goal location in stage 1 that differed between the blocking and control groups (see Figure 5)

Following Stage 2, participants received the same pre-test instructions as Experiment 1, before completing a 120s test trial on the outside of the kite-shaped arena, in the absence of any landmarks or the hidden goal. The location and counterbalancing of start locations at test was identical to Experiment 1, as was the manner in which performance was measured using search zones.

Statistical Analysis

Data were treated in the same manner as described for Experiment 1.

Results

Training Stage 1

The top panel of Figure 6 shows that the latency to find the hidden goal, in seconds, decreased during stage 1 training in both the blocking and control groups, with both groups displaying similar latencies to find the goal across all stage 1 trials. A two-way ANOVA conducted on individual latencies to find the hidden goal during stage 1 trials, with a between-subjects factor of group (blocking or control), and a within-subjects factor or trial (1-16) confirmed these impressions. There was a significant main effect of trial $F(15, 930) = 44.82, MSE = 124.97, p < .001, \eta_p^2 = .42 [.37 - .45]$, indicating that participants found the hidden goal quicker as training progressed, but not a significant main effect of group, or a significant interaction between group and trials (both $F_s < 1$).

----- Insert Figure 6 about here -----

Training Stage 2

The bottom panel of Figure 6 displays the latency to find the hidden goal, in seconds, during stage 2 training for participants in the blocking and control group. It appeared that blocking participants were quicker to find the goal on trial 1 compared to control participants, but on all remaining trials both groups displayed similar latencies to find the goal. A two-way ANOVA conducted on individual latencies to find the hidden goal during stage 1 trials, with a between-subjects factor of group (blocking or control), and a within-subjects factor of trial (1-16) confirmed these impressions, revealing a significant main effect of group $F(1, 62) = 37.12, MSE = 95.59, p < .001, \eta_p^2 = .37 [.22 - .50]$, trial $F(3, 186) = 33.16, MSE = 93.29, p < .001, \eta_p^2 = .35 [.25 - .42]$, and a significant interaction between group and trial $F(3, 186) = 34.77, MSE = 93.29, p < .001, \eta_p^2 = .36 [.26 - .43]$. Simple main effects analysis revealed that blocking participants located the hidden goal quicker than control participants on trial 1 only $F(1, 62) = 39.06, p < .001, \eta_p^2 = .39 [.23 - .51]$. Importantly, by the end of training there was no between group difference in latency to find the goal ($F < 1$).

Test

Figure 7 displays the amount of time blocking and control participants spent searching within the signal and no-signal zones during test. In keeping with the results of Experiment 1, participants in the control group spent more time searching in the signal than the no-signal zone. In contrast, blocking participants appeared to spend an equal amount of time searching in both signal and no-signal zones. A two-way ANOVA conducted on individual time spent

in zones, with a between-subjects factor of group (blocking or control), and a within-subjects factor of zone (signal or no-signal) revealed significant main effects of group $F(1, 62) = 6.043$, $MSE = 100.34$, $p = .017$, $\eta_p^2 = .09$ [.01 - .21], zone $F(1, 62) = 4.74$, $MSE = 121.78$, $p = .033$, $\eta_p^2 = .07$ [.003 - .19], and a significant interaction between group and zone $F(1, 62) = 4.80$, $MSE = 121.78$, $p = .032$, $\eta_p^2 = .07$ [.003 - .19]. Simple main effects analysis revealed that, within groups, blocking participants spent a statistically equivalent amount of time in the signal zone and no-signal zones $F < 1$; however, control participants spent significantly more time in signal zone compared to the no-signal zone $F(1, 62) = 9.54$, $p = .003$, $\eta_p^2 = .13$ [.03 - .26]. Between groups, participants in the control group spent significantly more time in the signal zone compared to blocking participants $F(1, 62) = 7.96$, $p = .006$, $\eta_p^2 = .11$ [.02 - .24], but blocking and control participants spent statistically equivalent amounts of time in the no-signal zone ($F < 1$).

One sample t-tests conducted on individual percentages of time spent in the signal zone revealed that whilst the control group spent more time (58%) in the signal zone during test than would be expected by chance $t(31) = 2.58$, $p = .015$, $d = .46$, the blocking group (51%) did not $t(31) = .55$, $p = .58$, $d = .10$.

----Insert Figure 7 about here----

Discussion

In stage 2 of the present experiment, participants received training in which a hidden goal was located in a right-angled corner of a kite-shaped environment, and also by a unique landmark. For blocking participants, the unique landmark that signalled the goal location in stage 2 had previously been established as a signal for the hidden goal. In contrast, for control

participants, the unique landmark that signalled the goal location in stage 2 had not previously signalled the location of the hidden goal. Following stage 2 training, both groups received a test trial on the outside of the kite-shaped environment, in the absence of any landmarks and the hidden goal. Consistent with the results of Experiment 1, blocking participants did not preferentially search at either of the right-angled corners at test, but control participants demonstrated a clear preference for searching near the previously rewarded right-angled corner. Moreover, control participants spent significantly more time searching at the corner that previously contained the Wi-Fi signal compared to blocking participants. Along with the experiments listed in Table 4, these results demonstrate that learning about shape information is subject to interference from landmark cues. Importantly, and where our data again distinguish themselves, is that the use of a perspective transformation in the current experiment permits the conclusion that learning about *global* shape information can be blocked by learning about landmarks.

In the interest of clarity, it is worthwhile to discuss the fact that the blocking group were faster to find the goal on trial 1 of stage 2 relative to the control group, even if this observation merely validates our experimental preparation. For the blocking group, the landmark that signalled the goal location in stage 1 continued to signal the goal location in stage 2, and so approaching that landmark on the first trial of stage 2 training would mean locating the goal. In contrast, for the control group, the landmark that signalled the goal location in stage 1 no longer signalled the goal location in stage 2, and so approaching the previously rewarded landmark on the first trial of stage 2 training would mean not locating the goal. Consequently, the observation that control participants had longer latencies to find the goal compared to blocking participants at the onset of stage 2 reflects the fact that landmarks exerted strong control over behaviour following stage 1 training.

As noted previously, contemporary theories of spatial learning continue to propose that encoding a representation of the boundary shape of an environment should be immune to the presence of landmark information (e.g. Doeller & Burgess, 2008), and this notion still attracts high-profile discussion in the spatial learning literature (e.g. Bicanski & Burgess, 2018; Brunec, Moscovitch & Barense, 2018; Gallistel & Matzel, 2013; Poulter et al., 2018; Xu, Regier, & Newcombe, 2017). By again using an inside-outside manipulation to generate a perspective transformation between training and test, the results from Experiment 2 provide the first empirical evidence that encoding allocentric global-shape information is subject to blocking from landmarks, a result that is contrary to the predictions of cognitive mapping theories (e.g. O'Keefe and Nadel, 1978).

General Discussion

In Experiment 1, participants in an overshadowing group were trained to find a hidden Wi-Fi signal that was located in a right-angled corner of a kite-shaped environment and by a unique landmark. For participants in a control group, the landmark cues moved between training trials, meaning only the shape of the environment could be used to locate the Wi-Fi signal. In a test trial conducted on the outside of the kite-shaped environment, in the absence of any landmarks or a hidden goal, participants in the control group preferentially searched at the right-angled corner that had previously contained the Wi-Fi-signal, relative to the other right-angled corner, whereas participants in the overshadowing group did not. In Experiment 2, participants in both blocking and control groups were initially trained to find a hidden Wi-Fi signal that could only be located based upon the landmark cues that were presented in a square-shaped environment. Participants from both groups were then placed into a kite-shaped environment that contained the same four landmarks that were presented in stage 1. For participants in the blocking group, the landmark that signalled the goal location in stage 1 continued to signal the goal location in stage 2 and, in addition, the boundary of the kite-

shaped environment now predicted the goal location as well. For participants in the control group, the boundary of the kite-shaped environment also predicted the goal location, but the landmark that predicted the goal location in stage 2 was not the same landmark that predicted the goal location in stage 1. Following stage 2 training, participants received a test trial in which they were again placed on the outside of the kite-shaped environment, in the absence of any landmarks or a hidden goal. Consistent with the results of Experiment 1, participants in the control group preferentially searched at the right-angled corner that had previously contained the Wi-Fi-signal, relative to the other right-angled corner, whereas participants in the blocking group did not.

In order to provide an explanation for the current studies, it is informative to note that previous work from our laboratory has suggested that the amount of attention that is paid to environmental boundaries may be altered by learning (e.g. Buckley, Smith, & Haselgrove, 2014, 2015). Citing a role for a cognitive function such as attention is not inconsistent with the traditions of learning theory and, indeed, the results of the current experiments can be interpreted according to attentional accounts of associative learning (e.g. Esber & Haselgrove, 2011; Mackintosh, 1975), in a manner that is consistent with animal studies of spatial navigation (e.g. Trobalon, Miguelez, McLaren, & Mackintosh, 2003). As we alluded to in the discussion of Experiment 1, the landmark cues in our environment were likely to be inherently more salient than the shape cue provided by the boundary of the arena (Buckley et al., 2015). This being the case, the landmark cues may have been more likely to capture attention at the beginning of training for Experiment 1. For the control group, this would have little impact on the formation of a shape-goal association, because the landmarks did not signal the goal location. For the overshadowing group, however, the landmark cues did predict the goal location, and directing more attention to them, compared to shape of the

arena, at the beginning of training would allow the landmark cues to be better established as predictors of the goal location.

In Experiment 2, participants in both the blocking and control groups were initially trained to find the goal with reference to landmark cues within a geometrically ambiguous square arena. As only the landmark cues signalled the goal location, these trials might ensure that the attention directed towards the landmarks was high at onset of stage 2 training for both groups. During stage 2, participants were required to locate a goal within a kite-shaped arena that contained the same landmarks that were present in stage 1 training. Importantly, for the blocking group, the same landmark that predicted the goal location in stage 1 continued to predict the goal location in stage 2. Consequently, the attention directed towards landmarks might remain high and, therefore, little attention would be directed to the shape of the environment. For the control group, however, a different landmark in stage 2 signalled the goal location relative to stage 1 training. In the parlance of associative learning theory, the large prediction error generated by this surprising event would serve to reduce attention to the landmarks, increase the attention paid to the shape of the environment and, ultimately, permit encoding of a representation of the allocentric global-shape of the environment together with the location of the goal.

Whilst attentional learning theories (e.g. Esber & Haselgrove, 2011; Mackintosh, 1975) are able to provide an account of our results, it is worthwhile noting that the present results are also amenable to explanations based upon Bayesian weighting of cues, in which learning about individual cues is weighted according to their usefulness to complete the current task (Xu et al., 2017; see also: Cheng & Newcombe, 2005; Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Nardini, Jones, Bedford, & Braddick, 2008; Ratliff & Newcombe, 2008; Twyman & Newcombe, 2010). Here, cues that are higher in salience, or more relevant to the task, will be ascribed more weight, and therefore favoured over cues that

are ascribed less weight. Consequently, the explanation offered by Bayesian weighting of cues is nearly identical to those provided by attentional learning mechanisms, and it is unlikely that any cue competition designs will be able determine which of these theories offers the best explanation of spatial behaviour. However, one manner in which it might be possible to dissociate these explanations is through eye-tracking procedures. Here, differences in the overt attention (see Le Pelley, Beesley, & Griffiths, 2011; Le Pelley, Pearson, Griffiths, & Beesley, 2015) paid to cues may be reflected in fixation behaviour during navigation, whereas more central changes in Bayesian weighting might not necessarily be reflected by eye movements.

Humans have now been observed to reorient on the basis of egocentrically encoded local shape information (Lew et al., 2014), and an allocentrically encoded representation of the global shape of an environment (Buckley et al., 2016b). Moreover, previously reported shape-transformation experiments (Buckley et al., 2016a), and the perspective transformations reported in the current experiments, have demonstrated that encoding of both egocentric local- and allocentric global-shape representations are subject to interference from landmarks. Human participants have also been reported to reorient using the principal axis of an environment (Bodily, Eastman, & Sturz, 2011; Sturz & Bodily, 2011), but the reference frame in which this representation is encoded, and whether it is subject to interference from non-shape cues, remains to be determined. Nevertheless, evidence that humans navigate using multiple representations of the shape of the environment is mounting and, on the basis of extant evidence, it appears that encoding of any shape-based representation is subject to interference from non-shape cues. Given this, it is important to consider the implications of our results in terms of how multiple representations of landmarks and boundaries combine to support spatial behaviour. So far, our discussion has focussed on how attentional or Bayesian mechanisms may influence whether landmark cues interfere with encoding an allocentric

representation of global boundary shape, but there is no reason these frameworks cannot be extended in order to account for how we adaptively learn about which of multiple boundary and landmark cues are most suited to completing the navigation task at hand.

For three decades there has been a continuous debate in the spatial literature concerning the proposed primacy of encoding of boundary shape information, and this notion has received renewed attention following highly-cited failures to find cue-competition between boundary and landmark cues (e.g. Doeller & Burgess, 2008), in conjunction with neuroimaging studies demonstrating that boundary and landmark cues activate separate hippocampal and striatal pathways, respectively (Doeller et al., 2008). There are, however, reasons to question the evidence in support of the primacy of global boundary shape encoding. First, as we have mentioned previously, past experiments have not adequately dissociated reorientation based on a global allocentric representations of shape from egocentrically-encoded local shape representations. Second, evidence in support of automatic encoding of boundary information comes from studies in which overshadowing or blocking groups have shown equivalent performance to appropriate control groups. It is, however, possible to account for these null results without supposing that boundaries hold a privileged role in spatial learning. For instance, differences in the relative salience and validity of cues (Kosaki, Austen, & McGregor, 2013), a failure to perceive both boundary and landmark cues at the same time (Austen, Buckley, & McGregor, In prep; see also Pearce et al., 2006), and the presence of within-compound associations that counteract cue competition effects (Austen, Kosaki, & McGregor, 2013; Horne & Pearce, 2009, 2011; Kosaki et al., 2013), may all explain why learning about boundary information appears unimpaired in the presence of landmark cues. That being said, by adapting the novel inside-to-outside paradigm reported by Buckley et al. (2016b) to examine competition between encoding landmarks and boundary information, the present experiments clearly demonstrate that encoding of allocentric

boundary information can be subject to interference from landmark cues. Our data, then, constitute a challenge to the behavioural predictions made by cognitive mapping theories that have an increasingly neuroscientific focus. Instead, we advocate that neuroanatomical specificity in the encoding of boundary and landmark cues (e.g. Jeffery, 2010) may not be sufficient to support the notion of psychologically separate memory systems, and that any claims of independent memory systems require evidence from behavioural-level studies that unequivocally demonstrate that separate memory systems are governed by different rules of operation (See Buckley, Austen, Smith, Lew, & McGregor, In prep for detailed discussion).

The foregoing discussion concerning how attentional or Bayesian mechanisms govern the encoding of multiple boundary- and landmark-based spatial representations may have important ramifications for cognitive mapping theories that advocate privileged processing of boundary shape information. These neural-inspired accounts of spatial navigation provide no apparent role for attentional mechanisms or, indeed, other features of learning or cognition. Instead, an allocentric representation of boundary shape is seen to be automatically instantiated in the hippocampus through exploration alone, whilst landmark encoding is subserved by striatal areas (Doeller et al., 2008). The results of our experiments, in which landmark cues have interfered with encoding boundary information, challenge this notion. However, it remains to be determined how the attentional or Bayesian mechanisms that we have discussed so far are reflected in the complex neural systems that support navigational behaviour. It has been suggested that there is competition between hippocampal and striatal systems during learning (Kosaki et al., 2015), and so it is possible that Bayesian or attentional mechanisms result in some spatial representations being selectively encoded over others - sometimes to the detriment of a flexible hippocampus-based allocentric representation of space. An alternative possibility is that competition between hippocampal and striatal systems is reflected by response competition for behavioural output (see Packard & Poldrack, 2003;

Poldrack, Clark, Pare-Blagoev, Shohamy, Moyano, & Gluck, 2001). Here, learning in the hippocampal and striatal systems may operate in parallel, and upstream areas such as mPFC mediate which system controls behaviour when it receives competing inputs (Doeller et al., 2008). Speculatively, our results favour the former interpretation. Take, for example, the overshadowing group of Experiment 1. If, during training, participants learned the Wi-Fi location with respect to both the boundary and landmark cues, then, at test when only the boundary information was available, participants should have preferentially searched at the signal zone, over the no signal zone. Instead, we observed that participants in the overshadowing group displayed no preference for either the signal or no-signal zone, a result that is consistent with striatal processing of landmarks interfering with a hippocampal encoding of boundary shape during learning. We note here, though, that there is a clear need to combine behavioural and neural methods in order to better understand the relationship between behavioural-level observations, and their neural underpinnings (Krakauer, Ghazanfar, Gomez-Marin, MacIver, & Poeppel, 2017).

Finally, it is worthwhile discussing the results obtained from our inside-outside paradigm in terms of how we form a workable understanding of *phenomenological* space. Specifically, it is possible to argue that successful reorientation in our paradigm might be based on mentally transforming egocentrically encoded local shape information (see Meilinger & Vosgerau, 2010; Riecke & McNamara, 2017). For instance, consider a participant trained to find a hidden goal on the inside of a kite-shaped arena, before receiving a test trial on the outside of the kite. Successful reorientation behaviour on the outside of the kite could, theoretically, be based upon an egocentrically encoded local-shape cue, providing that participants are able to mentally transform the representation they learned on the inside of the shape in order to guide spatial behaviour on the outside of the environment. However, we have previously reported evidence against this interpretation. In Experiment 2 reported by

Buckley et al. (2016b), participants were trained to find a goal on the inside of a rectangle-shaped environment before, at test, being placed on the outside of a kite-shaped arena. As the global shapes of the training and test environments were different, behaviour based on any mental-transformation of the local-shape that was encoded on the inside of the rectangle-shaped environment should have resulted in participants searching at the exterior corner of the kite-shaped environment that shared the same local-shape cues. However, this result was not obtained, and participants displayed no preference for any exterior corner of the kite – a result that cannot be accounted for without assuming that participants encoded, and based their navigation, on an allocentric global-shape representation. In addition, we have recently trained participants on the inside of a cross-shaped maze, before administering a test trial on the outside of the same shape (Buckley, Holden, Spicer, Smith, & Haselgrove, submitted). This environmental shape is notable, in that the local cue that was rewarded during training is also present on the outside of the environment at test. Despite this, participants displayed no indication of searching on the basis of the local-shape cues. Together with Experiment 2 reported by Buckley et al. (2016b), these results suggest that, at least in our inside-outside paradigm, reorientation following a transfer across a boundary is based upon an allocentric representation of the global boundary shape. What is not clear, however, is how the allocentric representation is formed from egocentric experience. That is, whilst there are detailed accounts of the properties of cells that form the navigation network (for a review see Chersi & Burgess, 2015), it is not clear from these hippocampus-inspired narratives how the information that is coded by these cells forms a conscious representation of our environment that we use to guide everyday spatial behaviour (Smith, Buckley, & Haselgrove, In prep). A future challenge, therefore, will be to examine how neural coding of allocentric relations in space ultimately forms a workable understanding of *phenomenological* space.

Over the last three decades, a number of influential navigational theories have afforded the boundary walls of an environment a spatial status during learning, and the notion that learning about global-shape information is immune to interference from non-shape cues persists in contemporary theories of spatial behaviour. The results presented here offer the first empirical evidence that encoding a representation of the allocentric *global-shape* of an environment is subject to interference from non-shape cues – a result that is incompatible with current cognitive mapping theories. Together with our recently-reported shape transformation experiments (Buckley et al., 2016b), we have now demonstrated that encoding of global- and local-shape representations appears to proceed according to the same mechanisms that govern learning in many domain-general procedures. Moreover, our evidence that landmark and boundary cues interact at a behavioural-level is divergent from the neural-level literature, in which it has been consistently demonstrated that boundary and landmark cues are processed in separate neuroanatomical systems. The challenge for future work will be to determine how cognitive attentional mechanisms influence encoding of spatial representations that were once thought to be automatically instantiated, and identify the neural correlates of this process.

Acknowledgements

We are grateful to Eleanor Smith and Francesca Richards for their assistance with data collection.

References

- Austen, J. M., Buckley, M. G., & McGregor, A. (In prep). Landmarks overshadow boundaries.
- Austen, J. M., Kosaki, Y., & McGregor, A. (2013). Within-compound associations explain potentiation and failure to overshadow learning based on geometry by discrete landmarks. *Journal of Experimental Psychology: Animal Behavior Processes*, 39(3), 259 - 272.
- Ayaz, H., Allen, S. L., Platek, S. M., & Onaral, B. (2008). Maze Suite 1.0: A complete set of tools to prepare, present, and analyze navigational and spatial cognitive neuroscience experiments. *Behavior Research Methods*, 40(1), 353-359.
- Barry, C., Lever, C., Hayman, R., Hartley, T., Burton, S., O'Keefe, J., ... & Burgess, N. (2006). The boundary vector cell model of place cell firing and spatial memory. *Reviews in the Neurosciences*, 17(1-2), 71-98.
- Bicanski, A., & Burgess, N. (2018). A neural-level model of spatial memory and imagery. *eLife*, 7, e33752.
- Boccaro, C. N., Sargolini, F., Thoresen, V. H., Solstad, T., Witter, M. P., Moser, E. I., & Moser, M. B. (2010). Grid cells in pre-and parasubiculum. *Nature Neuroscience*, 13(8), 987.
- Bodily, K. D., Eastman, C. K., & Sturz, B. R. (2011). Neither by global nor local cues alone: evidence for a unified orientation process. *Animal Cognition*, 14(5), 665-674.
- Brunec, I. K., Moscovitch, M., & Barense, M. D. (2018). Boundaries Shape Cognitive Representations of Spaces and Events. *Trends in Cognitive Sciences*, 22(7), 637-650.

- Buckley, M. G., Holden, L. J., Spicer, S., Smith, A. D., & Haselgrove, M. (Submitted). Crossing boundaries: Allocentric reorientation following transfer across an environmental boundary. *Journal of Experimental Psychology: Animal Learning and Cognition*.
- Buckley, M. G., Austen, J. M., Smith, S. P., Lew, A. R., & McGregor, A. (In prep). The effects of spatial stability and cue type on blocking in spatial learning.
- Buckley, M. G., Smith, A. D., & Haselgrove, M. (2014). Shape shifting: Local landmarks interfere with navigation by, and recognition of, global shape. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 40(2), 492-510.
- Buckley, M. G., Smith, A. D., & Haselgrove, M. (2015). Learned predictiveness training modulates biases towards using boundary or landmark cues during navigation. *The Quarterly Journal of Experimental Psychology*, 68(6), 1183-1202.
- Buckley, M. G., Smith, A. D., & Haselgrove, M. (2016a). Blocking spatial navigation across environments that have a different shape. *Journal of Experimental Psychology: Animal Learning and Cognition*, 42(1), 51.
- Buckley, M. G., Smith, A. D., & Haselgrove, M. (2016b). Thinking outside of the box: Transfer of shape-based reorientation across the boundary of an arena. *Cognitive Psychology*, 87, 53-87.
- Burgess, N. (2006). Spatial memory: how egocentric and allocentric combine. *Trends in Cognitive Sciences*, 10(12), 551-557.
- Burgess, N. (2008). Spatial cognition and the brain. In A. Kingstone & M. B. Miller (Eds.), *Year in cognitive neuroscience 2008* (Vol. 1124, pp. 77-97).
- Cheng, K. (1986). A purely geometric module in the rats spatial representation. *Cognition*, 23(2), 149-178.

- 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*(2), 254-259.
- Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin and Review*, *12*(1), 1-23.
- Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin*, *133*(4), 625.
- Chersi, F., & Burgess, N. (2015). The cognitive architecture of spatial navigation: hippocampal and striatal contributions. *Neuron*, *88*(1), 64-77.
- Cole, M. R., Gibson, L., Pollack, A., & Yates, L. (2011). Potentiation and overshadowing of shape by wall color in a kite-shaped maze using rats in a foraging task. *Learning and motivation*, *42*(2), 99-112.
- Doeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(15), 5909-5914.
- Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(15), 5915-5920.
- Esber, G. R., & Haselgrove, M. (2011). Reconciling the influence of predictiveness and uncertainty on stimulus salience: a model of attention in associative learning. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1718), 2553-2561.
- Fellini, L., Schachner, M., & Morellini, F. (2006). Adult but not aged C57BL/6 male mice are capable of using geometry for orientation. *Learning and Memory*, *13*(4), 473-481.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.

- Gallistel, C. R., & Matzel, L. D. (2013). The Neuroscience of Learning: Beyond the Hebbian Synapse. *Annual Review of Psychology*, *64*, 169 - 200.
- 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*(1), 44-59.
- Gray, E. R., Bloomfield, L. L., Ferrey, A., Spetch, M. L., & Sturdy, C. B. (2005). Spatial encoding in mountain chickadees: features overshadow geometry. *Biology Letters*, *1*(3), 314-317.
- Hartley, T., Lever, C., Burgess, N., & O'Keefe, J. (2014). Space in the brain: how the hippocampal formation supports spatial cognition. *Philosophical Transactions of the Royal Society B*, *369*(1635), 20120510.
- Hayward, A., Good, M. A., & Pearce, J. M. (2004). Failure of a landmark to restrict spatial learning based on the shape of the environment. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology*, *57*(4), 289-314.
- 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 Section B: Comparative and Physiological Psychology*, *56*(1), 114-126.
- Hermer-Vazquez, L., Moffet, A., & Munkholm, P. (2001). Language, space, and the development of cognitive flexibility in humans: the case of two spatial memory tasks. *Cognition*, *79*(3), 263-299.
- Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition*, *61*(3), 195-232.

- Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young-children. *Nature*, 370(6484), 57-59.
- Horne, M. R., Iordanova, M. D., & Pearce, J. M. (2010). Spatial Learning Based on Boundaries in Rats Is Hippocampus-Dependent and Prone to Overshadowing. *Behavioral Neuroscience*, 124(5), 623-632.
- Horne, M. R., & Pearce, J. M. (2009). A landmark blocks searching for a hidden platform in an environment with a distinctive shape after extended pretraining. *Learning and Behavior*, 37(2), 167-178.
- Horne, M. R., & Pearce, J. M. (2011). Potentiation and overshadowing between landmarks and environmental geometric cues. *Learning and Behavior*, 39(4), 371-382.
- Jeffery, K. J. (2010). Theoretical accounts of spatial learning: A neurobiological view (commentary on Pearce, 2009). *Quarterly Journal of Experimental Psychology*, 63(9), 1683-1699.
- Kamin, L. J. (1969). Selective association and conditioning. In N. J. Mackintosh & W. K. Honig (Eds.), *Fundamental issues in associative learning* (pp. 42 - 64). Halifax, Nova Scotia, Canada: Dalhousie University Press.
- Kelly, D. M., Spetch, M. L., & Heth, C. D. (1998). Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. *Journal of Comparative Psychology*, 112(3), 259-269.
- Kosaki, Y., Austen, J. M., & McGregor, A. (2013). Overshadowing of Geometry Learning by Discrete Landmarks in the Water Maze: Effects of Relative Salience and Relative Validity of Competing Cues. *Journal of Experimental Psychology: Animal Behavior Processes*, 39(2), 126-139.

- Kosaki, Y., Poulter, S. L., Austen, J. M., & McGregor, A. (2015). Dorsolateral striatal lesions impair navigation based on landmark-goal vectors but facilitate spatial learning based on a “cognitive map”. *Learning & Memory*, 22(3), 179-191.
- Krakauer, J. W., Ghazanfar, A. A., Gomez-Marin, A., MacIver, M. A., & Poeppel, D. (2017). Neuroscience needs behavior: correcting a reductionist bias. *Neuron*, 93(3), 480-490.
- Le Pelley, M. E. (2004). The role of associative history in models of associative learning: A selective review and a hybrid model. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology*, 57(3), 193-243.
- Le Pelley, M. E., Beesley, T., & Griffiths, O. (2011). Overt attention and predictiveness in human contingency learning. *Journal of Experimental Psychology: Animal Behavior Processes*, 37(2), 220 – 229.
- Le Pelley, M. E., Pearson, D., Griffiths, O., & Beesley, T. (2015). When goals conflict with values: Counterproductive attentional and oculomotor capture by reward-related stimuli. *Journal of Experimental Psychology: General*, 144(1), 158-171.
- Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). Boundary vector cells in the subiculum of the hippocampal formation. *Journal of Neuroscience*, 29(31), 9771-9777.
- Lever, C., Wills, T., Cacucci, F., Burgess, N., & O'keefe, J. (2002). Long-term plasticity in hippocampal place-cell representation of environmental geometry. *Nature*, 416(6876), 90.
- Lew, A. R. (2011). Looking Beyond the Boundaries: Time to Put Landmarks Back on the Cognitive Map? *Psychological Bulletin*, 137(3), 484-507.

- Lew, A. R., Usherwood, B., Fragkioudaki, F., Koukoumi, V., Smith, S. P., Austen, J. M., & McGregor, A. (2014). Transfer of spatial search between environments in human adults and young children (*Homo sapiens*): Implications for representation of local geometry by spatial systems. *Developmental Psychobiology*, *56*(3), 421-434.
- Lourenco, S. F., & Huttenlocher, J. (2007). Using geometry to specify location: Implications for spatial coding in children and nonhuman animals. *Psychological Research*, *71*(3), 252-264.
- Lourenco, S. F., Huttenlocher, J., & Vasilyeva, M. (2005). Toddlers' Representations of space: The Role of Viewer Perspective. *Psychological Science*, *16*(4), 255-259.
- Mackintosh, N. J. (1975). A theory of attention: Variations in associability of stimuli with reinforcement. *Psychological Review*, *82*(4), 276-298.
- Margules, J., & Gallistel, C. R. (1988). Heading in the rat: Determination by environmental shape. *Animal Learning and Behavior*, *16*(4), 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*(3), 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*(3), 314-321.
- Meilinger T., Vosgerau G. (2010) Putting Egocentric and Allocentric into Perspective. In: Hölscher C., Shipley T.F., Olivetti Belardinelli M., Bateman J.A., Newcombe N.S. (eds) *Spatial Cognition VII. Spatial Cognition 2010*. Lecture Notes in Computer Science, vol 6222.

- Miller, N. Y., & Shettleworth, S. J. (2007). Learning about environmental geometry: An associative model. *Journal of Experimental Psychology: Animal Behavior Processes*, 33(3), 191-212.
- Miller, N. Y., & Shettleworth, S. J. (2008). An associative model of geometry learning: A modified choice rule. *Journal of Experimental Psychology: Animal Behavior Processes*, 34(3), 419-422.
- Miller, N. Y., & Shettleworth, S. J. (2013). Associative models of instrumental learning: A response to Dupuis and Dawson. *Journal of Experimental Psychology: Animal Behavior Processes*, 39(3), 287-293.
- Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology*, 18(9), 689-693.
- O'Keefe, J., & Burgess, N. (1996). Geometric determinants of the place fields of hippocampal neurons. *Nature*, 381(6581), 425.
- O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map: Preliminary evidence from unit activity in the freely-moving rat. *Brain research*, 34, 171 -175.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, UK: Oxford University Press.
- Pavlov, I. P. (1927). *Conditioned reflexes* (G. V. Anrep, Trans.). London: Oxford University Press.
- Pearce, J. M. (2009). The 36th Sir Frederick Bartlett Lecture: An associative analysis of spatial learning. *Quarterly Journal of Experimental Psychology*, 62(9), 1665-1684.
- Pearce, J. M., & Bouton, M. E. (2001). Theories of associative learning in animals. *Annual review of psychology*, 52(1), 111-139.

- 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*(2), 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*(3), 201-214.
- Pearce, J. M., & Hall, G. (1980). A model for pavlovian learning: Variations in the effectiveness of conditioned but not of unconditioned stimuli. *Psychological Review*, *87*(6), 532-552.
- Pearce, J. M., Ward-Robinson, J., Good, M., Fussell, C., & Aydin, A. (2001). Influence of a beacon on spatial learning based on the shape of the test environment. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*(4), 329-344.
- Poldrack, R. A., Clark, J., Pare-Blagoev, E. J., Shohamy, D., Moyano, J. C., Myers, C., & Gluck, M. A. (2001). Interactive memory systems in the human brain. *Nature*, *414*(6863), 546 - 550.
- Poldrack, R. A., & Packard, M. G. (2003). Competition among multiple memory systems: converging evidence from animal and human brain studies. *Neuropsychologia*, *41*(3), 245-251.
- Poulter, S., Hartley, T., & Lever, C. (2018). The Neurobiology of Mammalian Navigation. *Current Biology*, *28*(17), R1023-R1042.
- Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting When Cues Conflict: Evidence for an Adaptive-Combination View. *Psychological Science*, *19*(12), 1301-1307.

- Redhead, E. S., & Hamilton, D. A. (2007). Interaction between locale and taxon strategies in human spatial learning. *Learning and Motivation*, 38(3), 262-283.
- Redhead, E. S., & Hamilton, D. A. (2009). Evidence of blocking with geometric cues in a virtual watermaze. *Learning and Motivation*, 40(1), 15-34.
- Redhead, E. S., Hamilton, D. A., Parker, M. O., Chan, W., & Allison, C. (2013). Overshadowing of geometric cues by a beacon in a spatial navigation task. *Learning and Behavior*, 41(2), 179-191.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and non-reinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory*. (pp. 64 - 99). New York Appleton-Century-Crofts.
- Riecke, B. E., & McNamara, T. P. (2017). Where you are affects what you can easily imagine: Environmental geometry elicits sensorimotor interference in remote perspective taking. *Cognition*, 169, 1-14.
- Smith, A. D., Buckley, M. G., Haselgrove, M. (in prep). From neurons to navigation: Uniting theories of human spatial learning.
- Solstad, T., Boccara, C. N., Kropff, E., Moser, M. B., & Moser, E. I. (2008). Representation of geometric borders in the entorhinal cortex. *Science*, 322(5909), 1865-1868.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2003). Modularity as a fish (*Xenotoca eiseni*) views it: Conjoining geometric and nongeometric information for spatial reorientation. *Journal of Experimental Psychology: Animal Behavior Processes*, 29(3), 199-210.
- Spelke, E. S., & Lee, S. A. (2012). Core systems of geometry in animal minds. *Royal Society Philosophical Transactions Biological Sciences*, 367(1603), 2784-2793.

- Steiger, J. H. (2004). Beyond the F test: effect size confidence intervals and tests of close fit in the analysis of variance and contrast analysis. *Psychological methods*, 9(2), 164.
- Sturz, B. R., & Bodily, K. D. (2011). Is surface-based orientation influenced by a proportional relationship of shape parameters? *Psychonomic Bulletin and Review*, 18(5), 848-854.
- Trobalon, J. B., Miguelez, D., McLaren, I. P. L., & Mackintosh, N. J. (2003). Intradimensional and extradimensional shifts in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes*, 29(2), 143 – 152.
- Tommasi, L., Chiandetti, C., Pecchia, T., Sovrano, V. A., & Vallortigara, G. (2012). From natural geometry to spatial cognition. *Neuroscience and Biobehavioral Reviews*, 36(2), 799-824.
- Tommasi, L., & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick (*Gallus gallus*). *Animal Cognition*, 7(1), 53-59.
- Twyman, A. D., & Newcombe, N. S. (2010). Five Reasons to Doubt the Existence of a Geometric Module. *Cognitive Science*, 34(7), 1315-1356.
- 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(3), 248-254.
- Vargas, J. P., López, J. C., Salas, C., & Thinus-Blanc, C. (2004). Encoding of Geometric and Featural Spatial Information by Goldfish (*Carassius auratus*). *Journal of Comparative Psychology*, 118(2), 206-216.
- Wall, P. L., Botly, L. C. P., Black, C. K., & Shettleworth, S. J. (2004). The geometric module in the rat: Independence of shape and feature learning in a food finding task. *Learning and Behavior*, 32(3), 289-298.

- Wang, R. F., Hermer, L., & Spelke, E. S. (1999). Mechanisms of reorientation and object localization by children: A comparison with rats. *Behavioral Neuroscience, 113*(3), 475-485.
- Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences, 6*(9), 376-382.
- Wang, R. F., & Spelke, E. S. (2003). Comparative approaches to human navigation. In K. Jeffery (Ed.), *The Neurobiology of Spatial Behavior* (pp. 119 - 143). Oxford, UK: Oxford University Press.
- Wilson, P. N., & Alexander, T. (2008). Blocking of Spatial Learning Between Enclosure Geometry and a Local Landmark. *Journal of Experimental Psychology: Learning Memory and Cognition, 34*(6), 1369-1376.
- Wilson, P. N., & Alexander, T. (2010). Enclosure shape influences cue competition effects and goal location learning. *Quarterly Journal of Experimental Psychology, 63*(8), 1552-1567.
- Xu, Y., Regier, T., & Newcombe, N. S. (2017). An adaptive cue combination model of human spatial reorientation. *Cognition, 163*, 56-66.

Figures and Tables

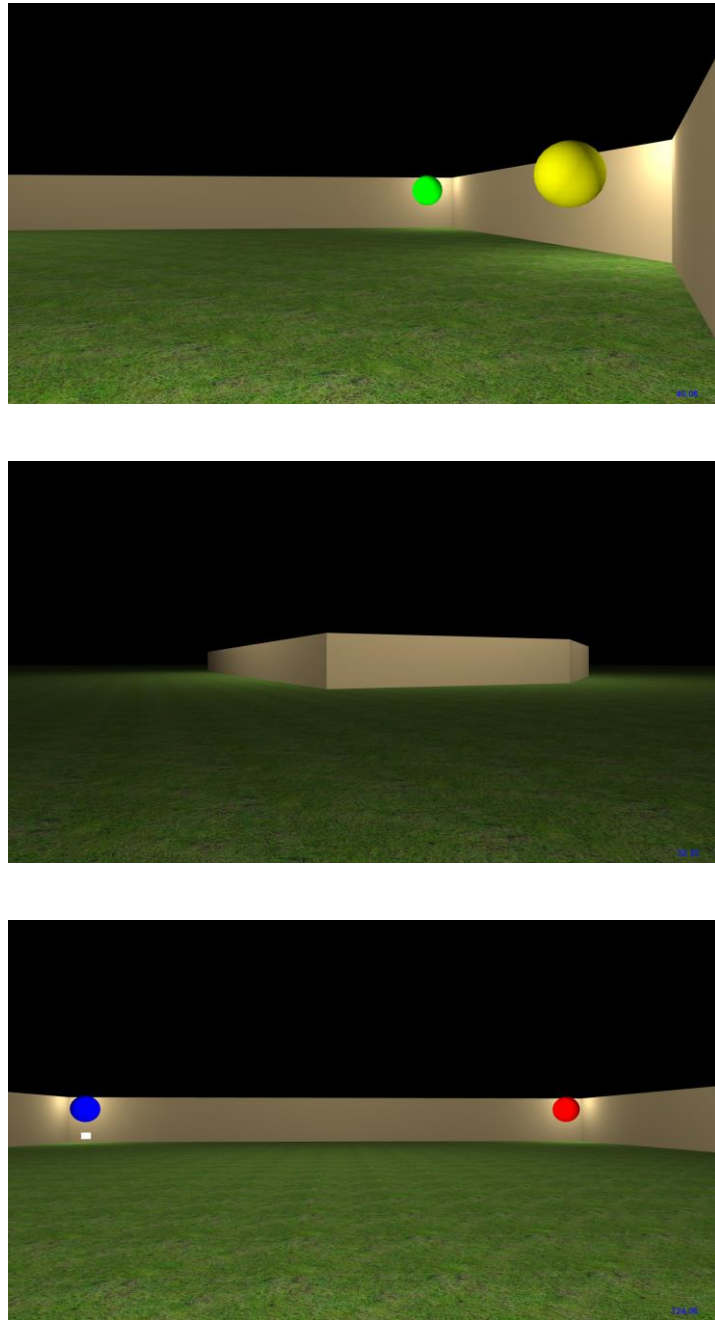


Figure 1: Views of the kite-shaped training (top) and testing (middle) environments used in Experiment 1 and 2, and the square-shaped arena used in stage 1 training in Experiment 2 (bottom). The bottom picture also displays the white flag that appeared at the goal location after 60s of any training trial.

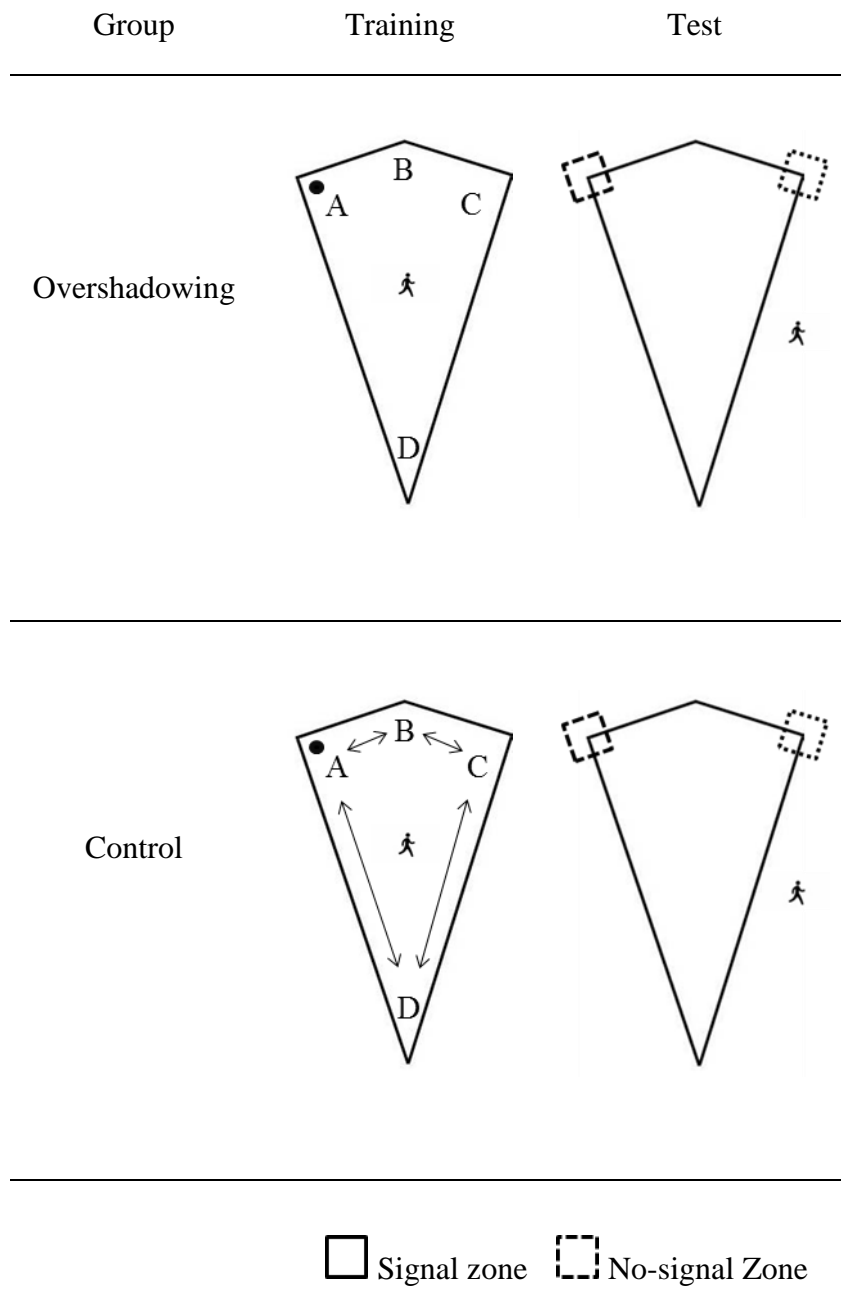


Figure 2: Schematic views of the arenas used to assess if a global-shape representation can be overshadowed by landmarks. Black circles represent the hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena. Letters A, B,

C, and D represent different landmarks. The arrows between the landmarks for the control condition represent the fact that they change position on every trial.

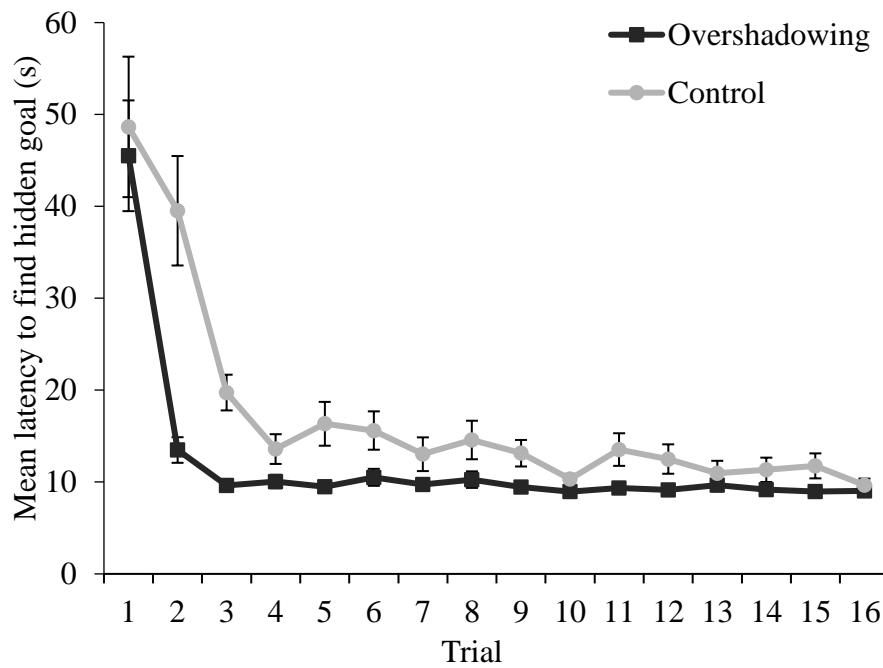


Figure 3: Mean latencies for overshadowing and control participants to find the hidden goal during the acquisition trials of Experiment 1. Error bars show 1 +/- standard error of the mean.

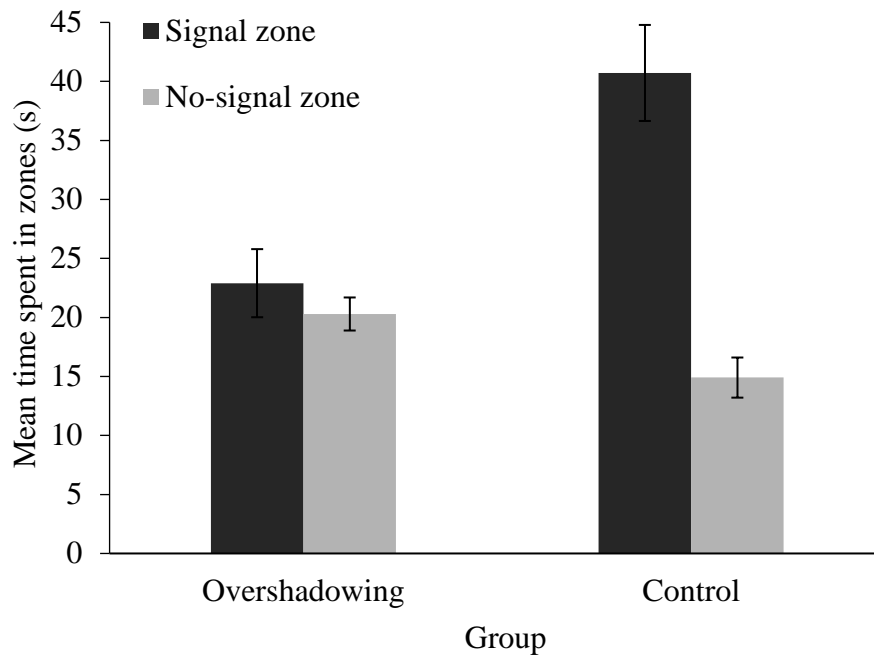


Figure 4: Mean time spent by overshadowing and control participants in the signal and no-signal zones during the test trial of Experiment 1. Error bars show 1 +/- standard error of the mean.

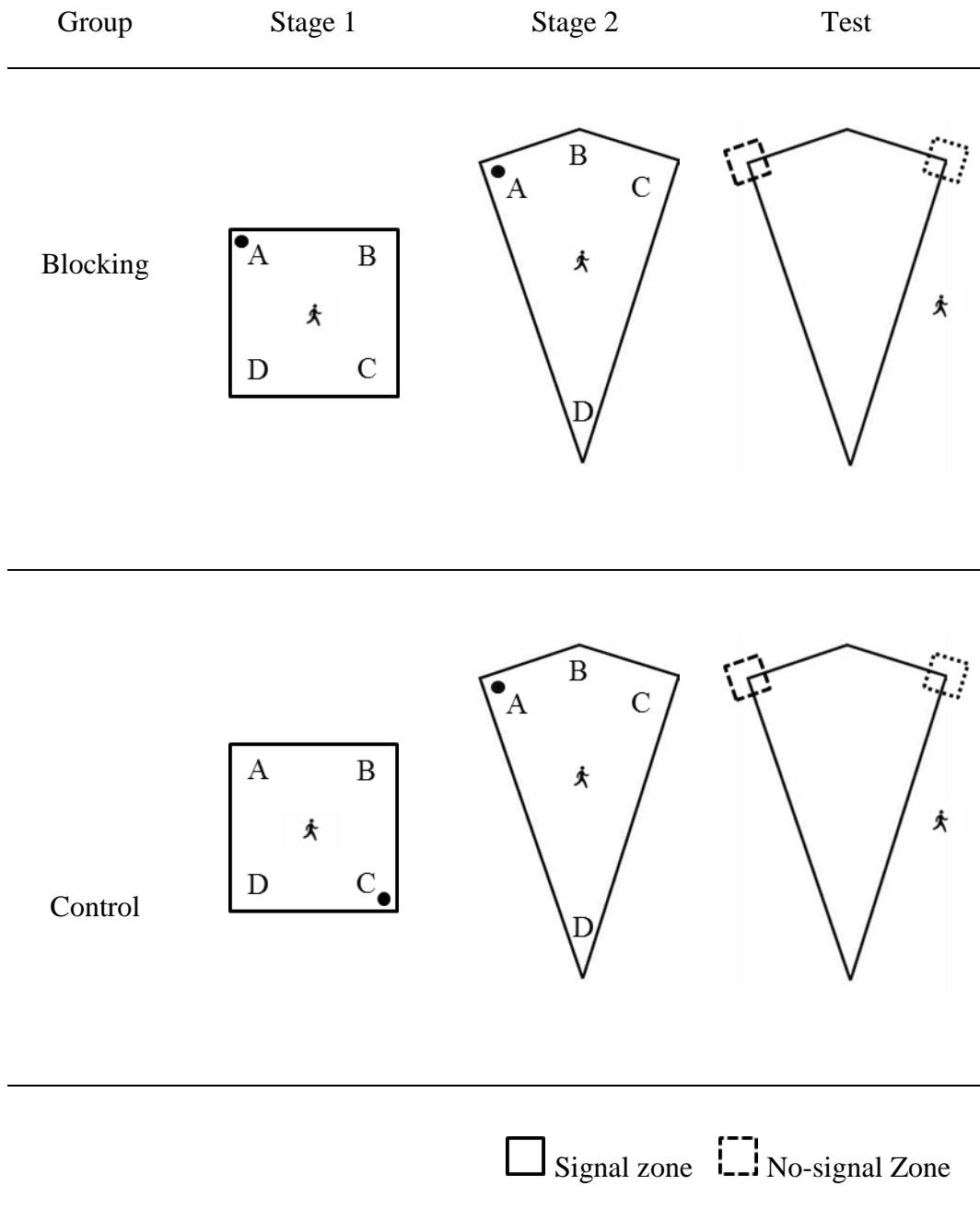


Figure 5: Schematic views of the arenas used to assess if a global-shape representation can be blocked by landmarks. Black circles represent the hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena. Letters A, B, C, and D represent different landmarks.

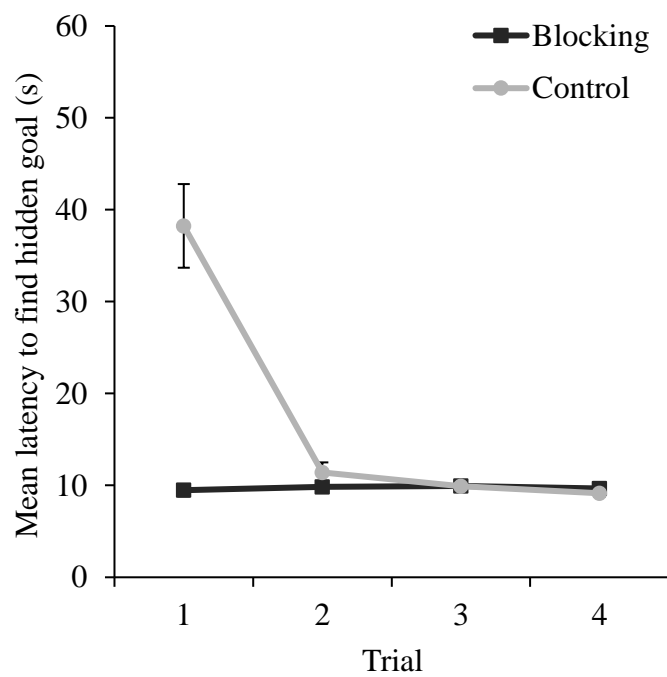
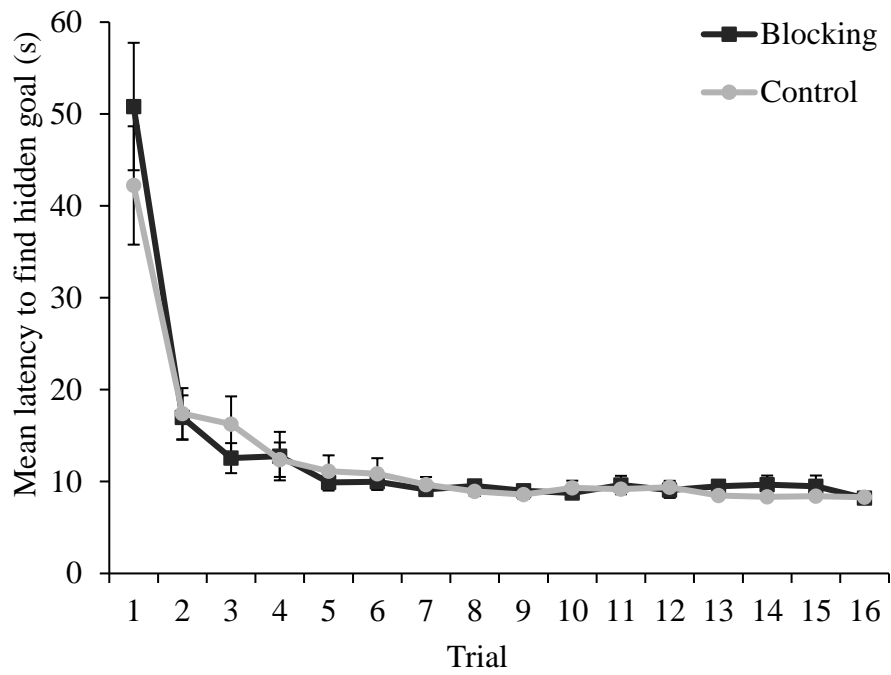


Figure 6: Mean latencies for blocking and control participants to find the hidden goal during the stage 1 (top panel) and stage 2 (bottom panel) acquisition trials of Experiment 2. Error bars show 1 +/- standard error of the mean.

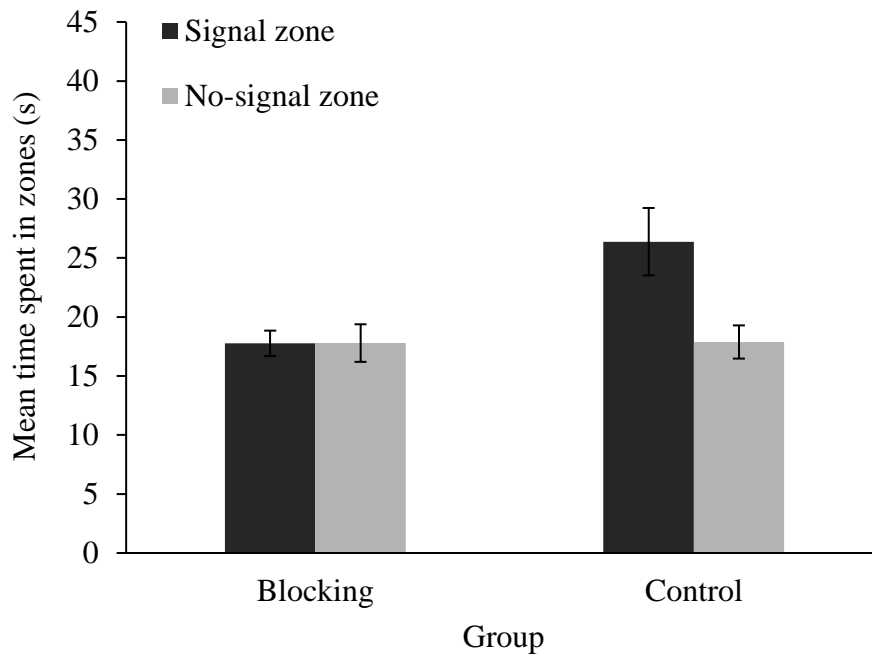


Figure 7: Mean time spent by blocking and control participants in the signal and no-signal zones during the test trial of Experiment 2. Error bars show 1 +/- standard error of the mean.

Table 1: Published experiments in which landmarks have failed to overshadow learning about information provided by the boundaries of an environment. Only experiments in which learning to a compound of boundary and landmark information was compared to learning in a control group that learned only about boundary information are included. From left-to-right, details about the species tested, authors, environments, landmarks, and boundary information are presented in separate columns.

Species	Authors	Environment	Landmarks	Boundary information
Adult humans	Doeller & Burgess (2008)	Virtual	Intra-maze traffic cone	Circle, distal landmarks
Adult humans	Doeller et al. (2008)	Virtual	Intra-maze traffic cone	Circle, distal landmarks
Rats	Graham et al. (2006)	Water-Maze	Black, and white, walls	Kite-shape walls
Rats	Hayward et al. (2003)	Water-Maze	Sphere	Rectangle-shaped walls
Rats	Hayward et al. (2003)	Water-Maze	Distal room cues	Triangle-shaped walls
Rats	Hayward et al. (2004)	Water-Maze	White and black sphere	Rectangle-shaped walls
Pigeons	Kelly et al. (1998)	Dry-Maze	Distinct 3D objects in each corner	Rectangle-shaped walls
Pigeons	Kelly et al. (1998)	Dry-Maze	Distinct 2D panels in each corner	Rectangle-shaped walls
Rats	McGregor et al. (2009)	Water-Maze	Black foam ball	Triangle-shaped walls
Rats	Pearce et al. (2001)	Water-Maze	White disc attached to a black rod	Triangle-shaped walls
Adult humans	Redhead & Hamilton (2007)	Virtual	Visible black, and white, platforms	Triangle-shaped walls

Table 2: Published experiments in which landmarks have overshadowed learning about information provided by the boundaries of an environment. Only experiments in which learning to a compound of boundary and landmark information was compared to learning in a control group that learned only about boundary information are included. From left-to-right, details about the species tested, authors, environments, landmarks, and boundary information are presented in separate columns.

Species	Authors	Environment	Landmarks	Boundary information
Rats	Cole et al. (2011)	Dry-Maze	Black, white, and stripped walls	Kite-shaped walls
Chickadees	Gray et al. (2005)	Dry-Maze	Single blue wall, long or short	Rectangle-shaped walls
Rats	Horne et al. (2010)	Water-Maze	Camping lantern	Circle, distal room cues
Rats	Horne & Pearce (2011)	Water-Maze	Black or white A4 cards	Rectangle-shaped walls
Rats	Kosaki et al. (2013)	Water-Maze	Black tennis ball	Rhombus-shaped walls
Rats	Pearce et al. (2006)	Water-Maze	Black, and white, walls	Rectangle-shaped walls
Adult humans	Redhead et al. (2013)	Virtual	Black cube	Trapezium-shaped walls

Table 3: Published experiments in which landmarks have failed to block learning about information provided by the boundaries of an environment. From left-to-right, details about the species tested, authors, and environments are presented in separate columns. The 2 right-most columns present details about the landmark that signalled the goal location in stage 1 of the experiment, and details about the to-be-blocked boundary information in stage 2 of the experiment. Subscript letters in the landmark column indicate the shape created by the walls of the arena that contained the landmark in stage 1: c = circle, n = no walls r = rectangle, s = square, t = triangle.

Species	Authors	Environment	Landmarks	Boundary information
Adult humans	Doeller & Burgess (2008)	Virtual	Traffic cone, distal landmarks ⁿ	Circle, distal landmarks
Adult humans	Doeller et al. (2008)	Virtual	Traffic cone, distal landmarks ⁿ	Circle, distal landmarks
Rats	Hayward et al. (2003)	Water-Maze	Sphere ^r	Triangle-shaped walls
Rats	Hayward et al. (2004)	Water-Maze	White and black sphere ^r	Triangle-shaped walls
Rats	Hayward et al. (2004)	Water-Maze	White and black sphere ^t	Rectangle-shaped walls
Rats	Pearce et al. (2001)	Water-Maze	White disc attached to a black rod ^c	Triangle-shaped walls
Adult humans	Redhead & Hamilton (2009)	Virtual	Visible black, and white, platforms ^c	Triangle-shaped walls
Rats	Wall et al. (2004)	Dry-Maze	Black plastic corner panel ^s	Rectangle-shaped walls

Table 4: Published experiments in which landmarks have blocked learning about information provided by the boundaries of an environment. From left-to-right, details about the species tested, authors, and environments are presented in separate columns. The 2 right-most columns present details about the landmark that signalled the goal location in stage 1 of the experiment, and details about the to-be-blocked boundary information in stage 2 of the experiment. Subscript letters in the landmark column indicate the shape created by the walls of the arena that contained the landmark in stage 1: c = circle, s = square, t = triangle.

Species	Authors	Environment	Landmarks	Boundary information
Rats	Horne & Pearce (2009a)	Water-Maze	Black sphere ^t	Triangle-shaped walls
Rats	Horne & Pearce (2009a)	Water-Maze	Black sphere ^c	Triangle-shaped walls
Rats	Pearce et al. (2006)	Water-Maze	Black and white walls ^s	Rectangle-shaped walls
Adult humans	Wilson & Alexander (2008)	Virtual	3D grey cross ^c	Trapezium-shaped walls
Adult humans	Wilson & Alexander (2010)	Virtual	3D cube, cross, and pyramid ^c	Circle, four colour walls