

Distinct error-correcting and incidental learning of location relative to landmarks and boundaries

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Associative reinforcement provides a powerful explanation of learned behavior. However, an unproven but long-held conjecture holds that spatial learning can occur incidentally rather than by reinforcement. Using a carefully controlled virtual-reality object-location memory task, we formally demonstrate that locations are concurrently learned relative to both local landmarks and local boundaries but that landmark-learning obeys associative reinforcement (showing “overshadowing” and “blocking” or “learned irrelevance”), whereas boundary-learning is incidental, showing neither overshadowing nor blocking nor learned irrelevance. Crucially, both types of learning occur at similar rates and do not reflect differences in levels of performance, cue salience, or instructions. These distinct types of learning likely reflect the distinct neural systems implicated in processing of landmarks and boundaries: the striatum and hippocampus, respectively [Doeller CF, King JA, Burgess N (2008) *Proc Natl Acad Sci USA* 105:5915–5920]. In turn, our results suggest the use of fundamentally different learning rules by these two systems, potentially explaining their differential roles in procedural and declarative memory more generally. Our results suggest a privileged role for surface geometry in determining spatial context and support the idea of a “geometric module,” albeit for location rather than orientation. Finally, the demonstration that reinforcement learning applies selectively to formally equivalent aspects of task-performance supports broader consideration of two-system models in analyses of learning and decision making.

associative learning | blocking | hippocampus | overshadowing | striatum

The dominant model of learning from repeated feedback (or “reinforcement”) associates environmental cues with expected reinforcement and with actions, using a single prediction-error signal (the difference between actual and expected reinforcement) to modify these associations (1–5). However, spatial learning, a crucial aspect of daily life, has long been proposed to exemplify a qualitatively different type of learning (6, 7), whereby “incidental” and “latent” learning occur independent of reinforcement. Perhaps surprisingly, formal demonstration that spatial learning deviates from the predictions of associative reinforcement, given the additional assumption that exploration can be rewarding in itself, has not been forthcoming (8–11).

Here, we carefully dissociate two contributions to spatial learning in virtual environments: learning locations relative to a local boundary and learning locations relative to a local landmark. Learning relative to a local landmark has been shown to follow the predictions of associative reinforcement learning (10). By contrast, we predicted that boundary-related learning would be incidental, for two reasons. First, the hippocampus has been specifically implicated in incidental learning in spatial (12) and other (13–19) domains. Second, the hippocampus seems to specifically process location relative to local environmental boundaries. The firing of hippocampal place cells reflects distances and directions to local boundaries (20, 21) but not to intramaze landmarks (22), and human hippocampal activation corresponds to learning of locations relative to local boundaries but not to local landmarks (23).

Associative reinforcement operating on multiple cues, using a single error term, predicts “blocking” (24) and “overshadowing” (24, 25) between cues. We give a standard analysis, based on ref. 1,

but note that these predictions also apply to other formulations of associative learning based on an error-correcting principle (2, 4, 26). Expected reinforcement v is related to the vector of stimuli \underline{u} via the vector of associative strengths or “weights” \underline{w} according to:

$$v = \underline{w} \cdot \underline{u} \quad [1]$$

and the learning rule adjusts these weights according to:

$$\underline{w} \rightarrow \underline{w} + \varepsilon \delta \underline{u} \quad [2]$$

where ε is a constant and δ , the prediction-error term, is the difference between expected and actual reinforcement r :

$$\delta = (r - v). \quad [3]$$

It can be seen that learning to cue 2 (i.e., adjusting weight w_2 from element u_2 of the stimulus vector) is reduced by the extent to which reinforcement is already predicted by another cue 1 (e.g., if $w_2 = 0$ and $v = w_1 u_1 = r$, then $\delta = 0$ and w_2 will not be modified). Put simply, if one cue already accurately predicts feedback, the error term δ is reduced, blocking the learning of associations from other cues. Similarly, when learning to two cues occurs concurrently, learning to one of the cues can overshadow learning to the other by reducing δ . In models of learning to act through reinforcement, the above mechanism is referred to as the “critic,” whereas an “actor” learns to associate stimuli to actions, using the same prediction-error and learning rule to modify these associations [more generally, Eq. 3 is adapted to include the effects of actions on the prediction of future reward, e.g., via the temporal difference rule: $\delta(t) = r(t) + v(t+1) - v(t)$; see refs. 5 and 27]. Thus, learned behavior (“instrumental” conditioning) is predicted to show blocking and overshadowing in the same way as learned expectation of reward (Pavlovian or “classical” conditioning). We predicted that learning relative to the landmark would show blocking and overshadowing, whereas learning relative to the boundary would continue irrespective of prior or concurrent learning to other cues.

To test these predictions, we designed a virtual environment in which locations can be learned relative to a local circular boundary or to a local intramaze landmark or landmarks. Distal cues were always present to provide orientation but could not be associated with locations as rendered at infinity. The virtual environment (a modified video game; see *Methods*) was presented in first-person perspective on a screen; the participant could navigate through it by pressing buttons to turn left or right or to move forwards. Participants initially collected several objects in turn from the virtual arena by navigating to them. In each subsequent trial, they were cued to replace an object (the object appeared on a blank background, they navigated to where they thought they had collected it

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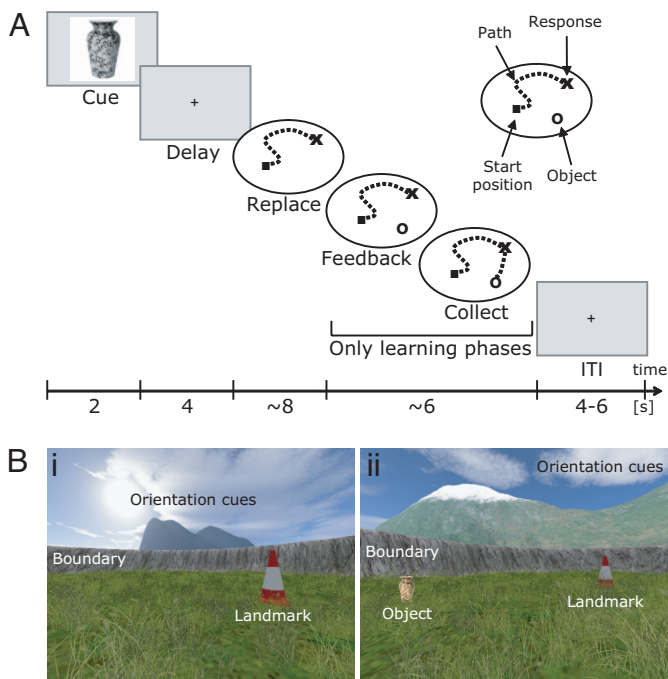


Fig. 1. Virtual reality task. (A) Trial structure (after initial collection of objects). Participants replace the cued object after a short delay phase and received feedback during learning trials (object appears in correct location immediately after the response and is collected) but not testing trials. (B) Virtual arena from the participant's perspective (i, replace phase; ii, feedback phase; different viewpoints) showing the intramaze landmark (traffic cone), the boundary (circular wall), the extramaze orientation cues (mountains, which were projected at infinity), and one object (vase). ITI, intertrial interval.

and pressed a button). Performance was measured as the distance between the participant's response and the correct location. Learning trials included feedback (the object appearing in the correct location to be collected again) from which participants learned to improve performance. "Test" trials omitted this feedback. See Fig. 1. Start positions varied between trials so that path integration could not be used.

Results

Overshadowing Experiments. In everyday life, locations are learned in the presence of multiple stable cues of both types [local landmarks (L) and boundaries (B)]. How do both types of learning interact? Four groups of 12 participants each learned four object-locations over four trials per object with either a landmark or a boundary present alone ("simple learning," groups L and B) or both cues present together ("compound learning," groups LB1 and LB2). Performance on all four objects was then tested with one or other cue alone (group LB1 tested with L; group LB2 tested with B) to compare the strengths of associations formed to that cue during compound learning with the strengths of equivalent associations formed during simple learning (i.e., group L tested with L; group B tested with B) (see Fig. 2). Associative reinforcement predicts a reduced associative strength after compound learning compared with simple learning because of overshadowing.

As predicted, learning to the landmark was reduced (overshadowed) by the presence of the boundary during compound learning, consistent with associative reinforcement, while learning to the boundary occurred incidentally, unaffected by the presence or absence of the landmark. ANOVA of the test performance of the four groups as a function of learning-situation (simple vs. compound) × test-cue (L vs. B) revealed a significant interaction ($F_{1,44} = 5.57; P < 0.05$) and no main

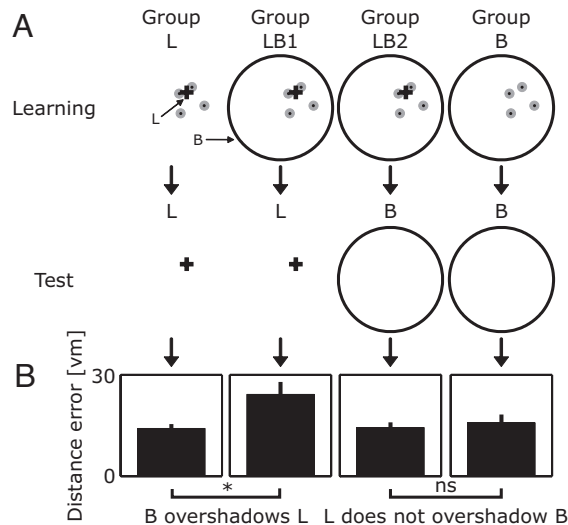


Fig. 2. Overshadowing experiment. The landmark is overshadowed by the boundary but not vice versa. (A) Four different groups (columns, 12 participants per group) learned four object-locations with either one of (simple learning) or both of the landmark (L) and boundary (B) present (compound learning; Upper) and were tested with either landmark or boundary alone (Lower). (B) Boundary overshadows landmark (i.e., the presence of the boundary during learning reduces learning to the landmark in group LB1 compared with group L) but not vice versa (i.e., the presence of the landmark during learning does not reduce learning to the boundary in group LB2 compared with group B). Bars indicate mean distance between response and correct location during test phase in virtual meters, ± SEM; *, $P < 0.05$; ns, not significant. +, landmark; circle, boundary; dots, object locations.

effects of learning-situation ($F_{1,44} = 3.16; P > 0.08$) or test-cue ($F_{1,44} = 2.79; P > 0.1$). Posthoc tests verified the greater replacement error of group LB1 than group L (both tested with landmark; $t_{22} = 2.58, P < 0.05$), whereas groups LB2 and B did not differ (both tested with boundary; $t_{22} < 1, P > 0.6$). These differential effects were not due to differences in performance during the learning phase with either cue [no difference in simple learning to L and B: $t_{22} < 1, P > 0.7$; see supporting information (SI) Fig. 5 and SI Text].

Thus, the presence of the boundary during compound learning overshadowed learning to the landmark, as predicted by associative reinforcement. By contrast, the presence of the landmark during compound learning did not affect learning to the boundary. Simple learning to either cue alone did not differ, ruling out differences in the salience of the two cues. Nonetheless, we also explicitly manipulated the visual salience of the landmark: running new groups L', LB1', and LB2' in a second experiment with a landmark three times as tall as previously (group B never saw the landmark). We found identical effects; overshadowing of the landmark was unaffected by its visual salience (see SI Fig. 4 and SI Text).

Blocking Experiments. In three further experiments, we examined blocking between two local landmarks L1 and L2 (Experiment LL), between a local landmark L and a local boundary B (Experiment LB), and between opposite sections B1 and B2 of the local boundary (Experiment BB). Each experiment occurred in three phases: (i) During an initial learning phase (known as "prelearning"), the two cues (L1 and L2, L and B, or B1 and B2) moved relative to each other at the start of each block of trials (eight blocks, 14 trials per object in total) with four object-locations paired with either cue; i.e., after the two cues moved, four objects kept a fixed bearing to the first cue (but not to the second), whereas the other four objects kept a fixed bearing to the second cue (but not to the first). (ii) Next, during compound learning, both cues and object-locations remained fixed (six trials per object), allowing associations

occurs incidentally, irrespective of the level of error: Object-locations already successfully predicted by another cue were nonetheless learned relative to the boundary and to the same accuracy as object-locations paired with the boundary throughout.

As with the overshadowing results, the differential blocking of landmarks but not boundaries does not reflect differences in learning rates (see above), or greater salience of boundaries (initial performance is, if anything, slightly better for objects paired with landmarks (see *SI Fig. 6* and *SI Text*). In further analyses, of objects equidistant to both cues during compound learning, we additionally ruled out that differential blocking effects were due to differential cue proximity (see *SI Fig. 7* and *SI Text*).

Finally, we note that the absence of any performance differences, when tested with a boundary in experiments LB and BB, between objects initially paired or unpaired with the boundary also rules out any effects of learned irrelevance. Both learned irrelevance and blocking should produce a performance difference in this situation, and none was found.

Discussion

Although associative reinforcement via a single prediction-error signal provides a powerful, almost ubiquitous, model for learning over repeated experience, it captures the acquisition of some types of knowledge, but not others, even when both are learned concurrently in formally identical conditions (see ref. 29; O. Hardt, A. Hupbach, and L. Nadel, unpublished data). More specifically, learning object-locations relative to intramaze landmarks obeys associative reinforcement (showing overshadowing and blocking or learned irrelevance), whereas learning relative to environmental boundaries is incidental, occurring independently of behavioral error or the presence of other predictive cues (showing neither overshadowing nor blocking nor learned irrelevance).

The two types of learning occur in parallel within the same task, without differences in the time-courses of learning and stimulus presentation, performance levels, instructions, location-cue proximity, or cue salience. Thus, learning to the boundary seems fundamentally inconsistent with associative reinforcement based on a single prediction-error term, and would potentially require separate error signals for landmarks and for each segment of boundary in the environment (see also ref. 30).

The differential learning relative to the boundary compared with that relative to the landmark over the three blocking experiments is also inconsistent with the many elaborations of basic associative reinforcement. Thus, increased learning rates to more salient stimuli (2) cannot explain our results, because performance indicates that the landmark was always at least as salient as the boundary. There was also no effect of tripling the landmark's height. Goal-directed reinforcement learning, in which information about the nature of the reinforcer is learnt (refs. 31 and 32; see also ref. 33) cannot explain our differential results, because learning to both cues results from the same feedback. Other potential explanations are that poor predictors during initial learning will have an increased learning rate during compound learning (4), that the presence of a good predictor will aid the learning to a poor predictor by increasing reward frequency ("feature enhancement") (34), that a cue's associability varies with its associative history (35), or that performance changes after removal of a cue reflect a "generalization decrement" (36, 37) cannot easily explain the differential blocking seen in experiment LL compared with experiment BB in which the contingencies of the two landmarks and the two boundaries are identical.

What causes the distinct characteristics of learning to landmarks and boundaries in our experiments? One potential explanation would be that the two cues interact differently with visual behavior (see also ref. 34) such that the previously paired landmark is not seen during some compound learning trials, allowing learning to the boundary, whereas the (larger) boundary is nearly always seen and therefore provides more potent blocking. However, participants

started each trial from a position toward the edge of the arena looking inwards, with all cues visible, and often made an entire rotation during the feedback phase. In addition, this explanation would predict at most a graded difference (i.e., with some learning for the unpaired landmark in experiment LL and some blocking of the unpaired boundary in experiment BB), rather than the stark contrast observed. Thus, this explanation applies more readily to failures of transiently presented stimuli in blocking continuous "contextual" cues (38) (i.e., temporal or environmental cues, although incidental learning to environmental boundaries might also contribute to the latter).

Our interpretation, and the hypothesis behind our design, is that the contributions of landmarks and boundaries to spatial memory are supported by distinct striatal and hippocampal systems operating different learning rules. To test for this, participants in an fMRI experiment (23), performed four blocks of trials, each block identical to the learning phase of compound groups LB1 and LB2 in our overshadowing experiment. However, at the start of each block, the landmark and boundary were moved relative to each other, with two of the four objects paired with either cue (similarly to the initial learning phase of our blocking experiments). The association of each object location to landmark or boundary was learned at similar rates for either cue. Significantly, learning relative to the boundary corresponded to activation in the right posterior hippocampus, whereas right dorsal striatum activation reflected learning of landmark-related locations. In this view, the incidental learning to boundaries comprises unsupervised Hebbian association between hippocampal place cells [whose firing represents conjunctions of bearings to boundaries (20, 21)] and object locations, whenever both representations are coincidentally active.

Previous studies of associative reinforcement in spatial learning have produced mixed results. Our present data in combination with our identification of distinct systems for processing local boundaries versus local landmarks (23) helps to clarify these previous findings. Thus, rats in the water maze task use the boundary to locate the platform (39), a task that is hippocampal-dependent (40), and boundary-learning did not show blocking in our study. Conversely, learning the platform location relative to an intramaze landmark in the water maze is not hippocampal-dependent (41), and blocking has been observed in the processing of intramaze landmarks both in rats (10) and our study. Note that we avoided using intramaze landmarks placed exactly at the target location, because these can impede learning of more distant cues simply by focusing attention on the target location alone (11, 42). We also ensured that orientation depended solely on distal cues. Otherwise, orientation might depend on many types of cue, combining outside of the hippocampus in the head-direction circuit (43) and possibly by associative reinforcement. Thus, asymmetrical boundary geometry and distal cues combine to orient participants (44) [and place cell firing (45)] and can overshadow and block each other in doing so (8, 9, 46, 47). Whether or not distal cues do block each other in determining orientation depends on many factors, including task instructions (O. Hardt, A. Humpbach, and L. Nadel, unpublished data). Even though boundary geometry can dominate intramaze cues to orientation in some circumstances (7, 48) and this can result in an absence of blocking or overshadowing of the boundary in determining orientation (49), it is hard to rule out associative explanations invoking the differential salience of the cues (2) or feature enhancement because of interactions between cues mediated by behavioral choice (34).

What distinguishes a local boundary from a local landmark? The finding that firing of hippocampal place cells is well described as a match to the distances to obstacles in all directions around the animal (20, 21) indicates that an important attribute for hippocampal processing is simply the horizontal angle subtended by the obstacle at the animal. Thus, "boundaryness" may simply reflect extent as seen from the participant's viewpoint. Note that the distinction is not due to differential proximity to the object-location,

Compound Learning Phase. During compound learning, both cues predicted the position of all eight experimental objects, remaining in the same locations throughout.

Test Phase. Memory for four of the object locations defined in the compound learning phase was tested with only one cue present (L1 in Experiment LL, L in Experiment LB, B1 in Experiment BB), and the other four were tested with only the other cue present (L2 in Experiment LL, B in Experiment LB, B2 in Experiment

BB). Two cue 1-related objects and two cue 2-related objects entered each test. The order of test runs was counterbalanced across subjects.

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