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

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Communicated by Jan Bureš, Czech Academy of Sciences, Prague, Czech Republic, December 22, 2007 (received for review November 13, 2007)

Abstract

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 $u$ via the vector of associative strengths or “weights” $w$ according to:

$$v = w^t u$$

and the learning rule adjusts these weights according to:

$$w ightarrow w + \epsilon \delta t$$

where $\epsilon$ is a constant and $\delta t$, the prediction-error term, is the difference between expected and actual reinforcement $r$:

$$\delta t = (r - v).$$

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 $v = w^t u_1 = r$, then $\delta t = 0$ and $w_2$ will not be modified). Put simply, if one cue already accurately predicts feedback, the error term $\delta t$ 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 $\delta t$. 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: $\delta t = r(t) + \gamma(t + 1) - v(t)$; 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

Author contributions: C.F.D. and N.B. designed research; C.F.D. performed research; C.F.D. analyzed data; and C.F.D. and N.B. wrote the paper.

The authors declare no conflict of interest.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0711433105DC1.

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www.pnas.org/cgi/doi/10.1073/pnas.0711433105

PNAS | April 15, 2008 | vol. 105 | no. 15 | 5909–5914

associative learning | blocking | hippocampus | overshadowing | striatum

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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 immediately after the response and is collected) but not testing trials. (A) Virtual arena from the participant’s perspective (immediately after the response and is collected) but not testing trials. (B) Virtual arena from the participant’s perspective (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.

**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 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
to be learned to the previously unpaired cue. (iii) Finally, performance was tested with one or other cue alone (four objects tested with each cue, two paired with either cue during initial learning) to compare the strength of association to object-locations previously paired with it or with the other cue (see Fig. 3 for details). Associative reinforcement predicts that, during the compound learning phase, learning to the initially unpaired cue will be blocked by prior learning to the initially paired cue.

This design maximizes the power of the effects predicted by associative reinforcement, because the strengths of associations to either cue can be compared within-subject and will also include any effects of “learned irrelevance” (28) of the unpaired cue during initial learning. This latter effect is consistent with the associative reinforcement framework and explained by a reduction in the learning rate (or “associability”; e in Eq. 2) specifically for the unpaired cue (28); or by association of the unpaired cue to the absence of reinforcer (i.e., a negative or “inhibitory” association from that cue in Eq. 1). We refer to these as blocking experiments for convenience and because the primary effect of sufficient initial learning to the paired cue (i.e., reducing the error term to zero) would be to prevent any subsequent learning to the unpaired cue, notwithstanding the retardation of any potential learning to it due to learned irrelevance.

In all three experiments, performance improved at similar rates during initial learning for both types of cue, reaching near-asymptotic levels from which compound learning produced negligible improvement (see SI Fig. 6 and SI Text). Blocking during the compound learning phase was assessed by testing with one cue alone (e.g., L1) and comparing performance on objects initially paired with that cue with performance on objects initially paired with the other cue (e.g., L2). If learning to cue L1 during the compound phase is blocked by prior learning to L2, performance will be worse for objects initially associated with L2 compared with those initially associated with L1.

As predicted, learning to a local landmark during the compound phase was blocked by prior learning to either another landmark (experiment LL; test L1: t15 = 5.04; P < 0.001; test L2: t15 = 4.79; P < 0.001) or to the boundary (experiment LB; test L: t15 = 8.71; P < 0.001). Thus, landmark-learning appears to operate via associative reinforcement. By contrast, learning to the boundary during the compound phase was unaffected by prior learning to either a landmark (experiment LB; test B: t15 < 1; P > 0.75) or to the opposite section of boundary (experiment BB; test B1: t15 = 1.12; P > 0.25; test B2: t15 < 1; P > 0.7) (see Fig. 3). See SI Text for results of the basic ANOVAs.

Thus, unlike learning to the landmark, learning to the boundary
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 coincidently 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. Hupbach, 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,
because we found the same differential pattern of blocking between boundaries and landmarks equidistant to the object (see SI Fig. 7 and ref. 23 for further discussion).

How do our results relate to findings that disoriented rats (48) and toddlers (50) reorient themselves using only boundary geometry—ignoring salient local features? These are interpreted as evidence of a “geometric module” for reorientation (refs. 7, 48, and 50 but see also ref. 51). Our results are not explainable by this type of nonspecific dominance of the boundary over the landmark: Performance and learning rates to both types of cue are matched. In addition, orientation is controlled by the distal cues rather than the circular boundary. By contrast, we show that there may be specialized learning of locations relative to surface geometry, even when it does not dominate behavior, in that it proceeds via a different rule than learning relative to intramaze landmarks.

How do our results relate to the involvement of the hippocampal and striatal systems in respectively supporting “place” versus “response” learning (12, 52), or flexible—relational/declarative/episodic versus procedural memory (13–15, 17, 18, 53)? Consistent with many of these suggestions, we formally demonstrate that the two systems’ distinct roles may result from differences in the learning rule implemented in either system—and not necessarily from other differences, such as in learning rate, that were not controlled in previous less formal approaches. In this view, striatal synaptic plasticity is controlled by a single error signal reflecting deviations from expected reinforcement (1, 3, 5) possibly mediated by dopamine (54–56). This produces “trial-and-error learning” or “learning by doing” appropriate for procedural memory (15). Unsupervised hippocampal Hebbian synaptic plasticity occurs independent of error or reinforcement, although it may be boosted by novelty [i.e., inconsistency between perception and relationships stored in hippocampus (12, 17)]. This produces incidental learning or “learning by observation” appropriate with maintenance of a flexible mental model (17), “mediating representation” (19), or “cognitive map” (6, 12), and with efficient encoding of experience into episodic memory (15, 16). In addition, our results suggest that the local boundaries may dominate over local landmarks in defining the spatial context of hippocampally mediated episodic memories. More generally, our demonstration of concurrent incidental and reinforcement learning requires a broadening of the models of learning and decision-making applied to social and economic neuroscience (see also ref. 33).

Methods

Participants. One hundred thirty-two male participants (aged 18–37, mean age 21.9 years) took part in this study, which was approved by the local Research Ethics Committee. Data from three additional participants had to be excluded because of technical problems or misunderstanding of the task. Participants gave full informed written consent and were paid for participating.

Virtual Reality Environment. We used Unreal Engine 2 Runtime software (Epic Games) to display a first-person perspective view of a grassy plane surrounded by a landscape of two mountains, clouds, and the sun (created by using Terragen; Planetside Software) and projected at infinity, to provide distal cues to orientation but not to location. The arena was surrounded by a circular boundary (a cliff) in some experiments (or contained a semicircular portion of it in the BB blocking experiment). In the absence of the cliff, the grassy plane extended to infinity. A traffic cone was used as an intramaze landmark (and a bowling pin as the second landmark in some experiments (or contained a semicircular portion of it in the BB blocking experiment). In the test phase, either solely the boundary was present. Feedback was not provided in the test phase of the experiments (see below), but the blocking experiments, participants waited in the arena for 6 s (mean) after their response. A fixation cross was then presented for a variable intertrial interval (ITI) (overshadowing experiments: 2–10 s, mean 6 s; blocking experiments: 2–6 s, mean ~4 s) before the start of the next trial.

Overshadowing Experiments. Procedure and design. The overshadowing experiments comprised two phases: learning and test. Each phase was one block of 16 trials (4 trials per object; four objects). Objects were presented in pseudorandom order within blocks. Feedback was provided in the learning phase but not in the test phase. To reduce the error variance in the planned between-group comparisons, each participant of a particular group had the same configuration of object order and delay and ITI times as a matching participant in the other groups. Participants were randomly assigned to different groups.

Basic experiment. Forty-eight participants were tested in four groups of 12. In the learning phase of groups LB1 and LB2, both the landmark and the boundary were present. For group L only the landmark was present and in group B only the boundary was present. In the test phase, either solely the landmark (groups LB1 and L) or solely the boundary (groups LB2 and B) was present (see Fig. 2; see SI Text for details of the control experiment with a taller landmark (three groups of 12 participants)).

Blocking Experiments. Procedure and design. The three blocking experiments (16 participants in each experiment) comprised three phases: Initial learning (or prelearning), separated into eight blocks of one to three trials per object (14 trials per object in total; eight experimental objects); compound learning (one block of six trials per object; test phase, comprising two blocks in which memory for four experimental object-locations was tested in the presence of one cue alone, followed by testing of memory for the other four object locations in the presence of the other cue alone (six trials per object). Feedback about the correct object position was provided in the initial learning and compound learning phases but not in the test phase. Objects were presented in pseudorandom order within blocks (trials with two control objects were interspersed among regular trials; these trials do not require spatial memory: the objects are collected from an infinite grassy plane with blue background and are always visible, as used in our fMRI experiment, see ref. 23 for details). Initial learning phase. The experimental objects were separated into two sets: four objects associated with cue 1 (L1 in Experiment LL; L in Experiment LB; or B1 in Experiment BB) and four objects associated with cue 2 (L2 in Experiment LL; B in Experiment LB; or B2 in Experiment BB). In Experiment LL, the two landmarks were moved relative to each other between blocks (using three different spatial configurations of the two landmarks). After each change, four objects maintained a fixed bearing to landmark L1 (but not to landmark L2); the other four objects maintained a fixed bearing to landmark L2 (but not to landmark L1). In Experiment LB, the landmark and boundary moved relative to each other between blocks (using four different landmark positions approximately in the middle of the NE, SE, SW, and NW sectors of the arena, as defined by the distal orientation cues). After each change, four objects maintained a fixed bearing to the boundary B (but not to the landmark L), the other four objects maintained a fixed bearing to the landmark L (but not to the boundary B).

In Experiment BB, the radius of the circular boundary changed between blocks (three sizes: the one used in all other experiments including a boundary, a 20% smaller radius, and a 20% larger radius). After each change, four objects maintained a fixed bearing to the Western part of the cliff, boundary B1 (but not to boundary B2); the other four objects maintained a fixed bearing to the Eastern part of the cliff, boundary B2 (but not to boundary B1).

Thus, over the course of the initial learning phase, the positions of four objects were predicted by cue 1 but not by cue 2, whereas the positions of the other four objects were predicted by cue 2 but not by cue 1 (see Fig. 3).
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 LB, 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.

ACKNOWLEDGMENTS. This work was funded by the Biotechnology and Biological Sciences Research Council and the U.K. Medical Research Coun-

50. Hermer L, Spekle E (1996) Modularity and development: The case of spatial reorien-
**SI Fig. 4. Overshadowing and landmark salience.**
Three new groups (magenta, see yellow area in (C)), groups LB1', L', and LB2' (columns, 12 participants per group) learned 4 object-locations with a more salient landmark (3x taller) and were tested with either landmark or boundary alone (bottom row). The asymmetric overshadowing effect of the main experiment was also observed with this more salient landmark: the boundary overshadows the landmark (cf. replacement error for groups LB1'-L') but not vice versa (cf. groups LB2'-B). For comparison we also depict the findings of the original 3 groups with the normal landmark (blue; note that group B learned and was tested with the boundary only: black). See Fig. 2. These data show that the differential overshadowing effects are not due to differential landmark-salience.
**SI Fig. 5. Overshadowing experiments: Performance during learning.**
The figure shows mean replace errors for the 7 groups of the 2 overshadowing experiments (original and salient landmark) during the learning phase. There was no difference between learning with the landmark and with the boundary alone, nor was there a difference between learning with the original and with the more salient landmark alone. Performance was better when both cues, landmark and boundary, were present than when only one cue was present. See Fig. 2 and text for details.
SI Fig. 6. Blocking experiments: performance in the initial learning and compound learning phases.
Plots show mean distance errors in (A) the initial learning phase (or ‘prelearning’; separate plots for all trials and for the last trial) and (B) the compound learning phase of all 3 blocking experiments (Exp. LL, Exp. LB, and Exp. BB). Initial learning to landmark and boundary occurs at similar rates, and reached near-asymptotic levels from which compound learning produced negligible improvement.
Bars: mean replacement error: distance between response and correct object location/virtual metres, +/- SEM.
See Fig. 3 and text for details.
**SI Fig. 7. Differential blocking in objects equidistant to both cues during compound and testing phases.**
The plots show the mean distance errors in the test phase of the LL and BB blocking experiments for two objects which had the same distance to both cues during the compound and learning phases. Analyses revealed the same statistical pattern as in the analyses including all objects: landmark L1 blocked landmark L2 and vice versa (Exp. LL); and boundaries B1 and B2 did not block each other (Exp. BB). These data show that the differential blocking effects are not due to differential cue proximity.