Place learning by mechanical contact

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SUMMARY

For some animals (e.g. the night-active wandering spider) the encounters with the habitat that result in place learning are predominantly mechanical. We asked whether place learning limited to mechanical contact, like place learning in general, entails vectors tied to individual landmarks and relations between landmarks. We constructed minimal environments for blindfolded human participants. Landmarks were raised steps. 'Home' was a mechanically indistinct location. Travel was linear. The mechanical contacts were those of walking, stepping, and probing with a soft-tipped cane. Home-orienting activities preceded tests of finding home from a given location with landmarks unchanged or (unbeknown to participants) shifted. In a one-landmark environment, perceived home shifted in the same direction, with the same magnitude, as the shifted landmark. In an environment of two landmarks located in the same direction from home, shifting the further landmark toward home resulted in a change in home's perceived location that preserved the original ratio of distances separating home, nearer landmark, and further landmark. Both findings were invariant over the travel route to the test location and repetitions of testing. It seems, therefore, that for humans (and, perhaps, for wandering spiders), mechanical contact can reveal the vectors and relations specifying places.

INTRODUCTION

Within a habitat, a place such as home can be distinguished by specific features ('beacons'), by directions and distances from individual landmarks ('vectors'), and by inclusion relations in the array of landmarks ('relative location'). Of the three, the latter is arguably the more general (Gibson, 1979; Poucet, 1993). For all animals, learning about places and learning to find one's way between them are very important kinds of learning. They result in the state of the animal being oriented to its habitat.

The two kinds of learning proceed through encounters with the habitat registered (in different degrees) by the five modes of active, overt attending [looking, hearing, smelling, tasting, and touching (Gibson, 1966; Piéron, 1952)]. For some animals, the encounters are predominantly mechanical. That is, they consist mainly of contacts that induce deformation of tissue at the segmental level, or whole body level, or both. For those animals – for example, most spiders (Barth, 2002; Foelix, 1996) – the predominant mode of attending is touching.

The well-studied (see Barth, 2002) night-active wandering spider *Cupiennius salei* provides a case in point. Its touching is primarily by the legs. The function of its legs, therefore, is twofold: to propel the body relative to the surfaces of support and to embody the mechanical information (carried in the patterns of exoskeleton deformation) arising from, and specific to (1) positions and motions of the limb segments relative to each other and to the body as a unit, (2) properties of the surface layout, and (3) positions, orientation or movement of the body as a whole, or of body segments, relative to the environment. Information of types 1 and 2 are in a propriospecific and exterospecific sense, respectively (Gibson, 1966). Information of type 3 is information in an expropriospecific sense (Lee, 1978).

In illumination, *Cupiennius salei* walks with all eight legs. In darkness, however, it is inclined to use only six for walking; deploying the first pair of legs much as a blind person deploys a cane to probe the adjacent surface layout (Barth, 2002; Schmid, 1997). When the probing forelegs contact a small object (e.g. 10 mm in height), forward locomotion is arrested, the object is explored, and the body is elevated so as to cross the object without collision and resume forward locomotion (Eckweiler and Seyfarth, 1988). The walking legs, whether eight or six, are subject to patterns of ground reaction forces, and thereby patterns of strain in the exoskeleton, that are specific to the slope (Brussel, 1987), mechanical resistance (surface viscosity) (Barnes and Barth, 1991) and, presumably, various other substrate properties of relevance to nocturnal place learning and navigation. The ability of *Cupiennius salei* to return, without benefit of vision, to the location of a previously caught but not devoured prey, underscores the significance of the legs' mechanoreceptors (Seyfarth and Barth, 1972; Seyfarth et al., 1982) and the importance of distinguishing information kinds 3 and 1 above. The exproprioceptive ability to orient to the direction and distance of the prey site (absent the prey, and absent landmarks) is severely impaired by inactivation of the legs' lyriform organs of mechanoreception. By contrast, inactivation of lyriform organs does not impair the proprioceptive ability to coordinate the legs in the normal manner of walking.

To be sufficiently general, mechanically informed place learning must involve landmarks. It is of some significance, therefore, that local variations in ground properties detectable by touching have been shown to serve as landmarks for place finding by the whip spider (Santer and Hebets, 2009) and the desert ant (Seidl and Wehner, 2006). A key question in the study of place learning has been whether it results in attunement to relations between landmarks as well as attunement to landmark-based vectors (e.g. Collett et al., 1986; Collett and Zeil, 1998). Experiments have shown that for a number of species the answer is 'yes' (Greene and Cook, 1997; Kamil and Jones, 1997; Kelly and Spetch, 2001; Sturz and Katz, 2009; Uttal et al., 2006). In these affirming experiments looking was the predominant mode of active overt attending and no modes

were explicitly excluded. To address the place finding capabilities of animals such as *Cupiennius salei*, however, requires that the question of vectors *and* relations in place learning with landmarks be posed when touching is the predominant and, ideally, exclusive mode. In the present research we posed the question in this manner with blindfolded humans, taking advantage of the known capabilities of human dynamic or effortful touching with respect to perceiving the surface layout contacted mechanically through legged locomotion and handheld implements (Turvey and Carello 1995; Carello and Turvey, 2000; Carello and Turvey, 2004; Turvey et al., 2009; Harrison and Turvey, 2009). We examined their place learning in the minimal mechanical environment depicted in Fig. 1A.

Many contemporary issues in experimental investigations of place learning by looking revolve around the contributions of the environment of extended surfaces (e.g. a room, a box) that embeds the to-be-learned place or places – specifically, the contributions of its geometry (Cheng and Newcombe, 2005; Sturz et al., 2009; Sturz and Kelly, 2009), its particular distinctive features (Cheng and Newcombe, 2005), its size (Sovrano and Vallortigara, 2006) and its boundaries relative to the place or places (Doeller and Burgess, 2008; Sturz et al., 2009). Such potential contributions to place learning are minimized, if not nullified, by the non-visibility of both the experimental setting depicted in Fig. 1A and its enclosure of extended surfaces (a corridor). Uttal et al. (Uttal et al., 2006) brought the potential contributions of landmark-based vectors and relations between landmarks into sharp relief by conducting their research with children in a prairie setting, that is, without a room-like environment. In this setting the landmarks were strictly 'small discrete proximate' [see p. 321 in Greene and Cook (Greene and Cook, 1997)]. Our research within the confines of the minimal mechanical environment of Fig. 1A, and with touching as the predominant mode, follows suit. The contribution of size of the environment remains as an issue (Chiandetti et al., 2007), as does

the contribution of boundaries, here defined strictly in terms of the limits of the path depicted in Fig. 1A, that is, as the places where direction of locomotion has to be reversed (see Fig. 1C). In sum, place learning in the setting of Fig. 1A was limited to the information made available by mechanical contact with local landmarks and by boundaries defined by direction reversals in locomotion.

MATERIALS AND METHODS
Participants
There were 46 participants in total: 10 in experiment 1, and 18 in each of experiment 2 and 3, with approximately even numbers of males and females. All were naïve to the purpose of the experiment. All participants gave their consent in accordance with the University of Connecticut's institutional review board regulations for studies with human participants, and received $20 for participating.

Materials
The mechanical environment shown in Fig. 1A was situated in a long interior hallway. It was constructed from two 30m lengths of 2cm diameter PVC pipe. Each pipe was attached to the floor with Velcro. The pipes created two verges that the blindfolded participants could explore using a handheld soft-tipped cane. The pipes were parallel and were separated by 0.8m. Three wooden steps functioned as landmarks. They were constructed to fit over the two pipes. Additional lengths of pipe, aligned with the two verges, were attached to the edges of each step. Each step was 0.8m wide, 0.6m deep and 0.12m high. The steps were designated S_1, S_2 and S_3 (Fig. 1B).

A tape measure was used during the experiments to record participants' reproductions of set outbound distances walked in the training phase of each experiment, and judgments of the location of home in the test phase of each experiment. The experimenters used markers laid out adjacent to the PVC pipes (Fig. 1A) to identify
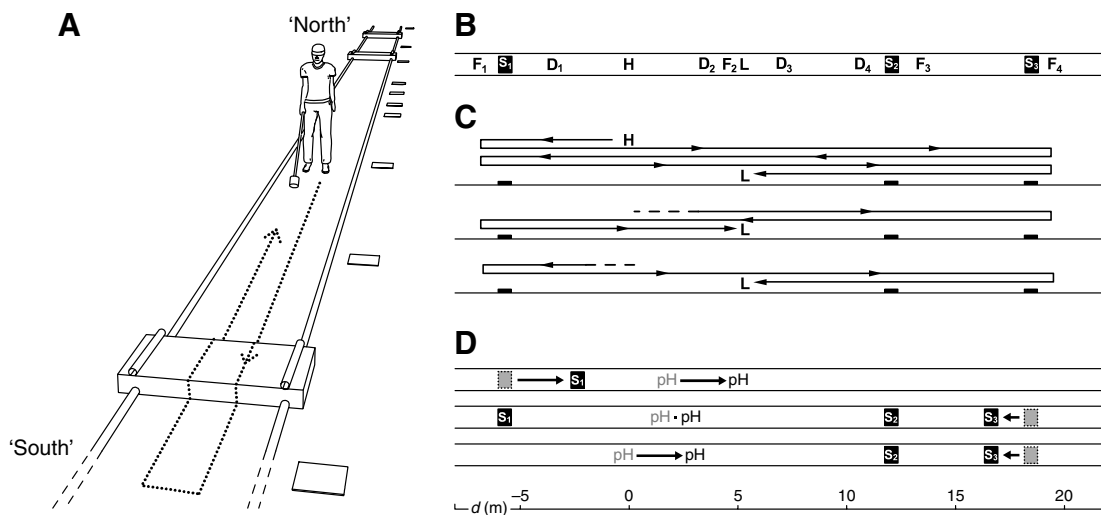

Fig. 1. (A) A minimal mechanical environment for blindfolded human participants. The participant is shown standing at 'home' – an unmarked place that was learnt over the course of the experiment. The square markers placed next to the environment allowed the experimenter to control the training and test phases by means of simple verbal instructions. (B) Schematic representation of the experimental environment showing the placement of steps as landmarks (S_1, S_2 and S_3) and the home location (H) learnt by participants during the training phase. On each training trial, participants were indirectly guided to H *via* a distal location (either F_1, F_2, F_3 or F_4) before performing a simple homing task from one of four set distances (either D_1, D_2, D_3 and D_4). On each trial in the test phase, participants were indirectly led to a test location L before attempting to return to H. (C) Travel routes prior to the tests. Route traveled on trial 1 (top), trials 2, 4 and 6 (middle), and trials 3 and 5 (bottom). Note that following an initial transient the route traveled on trial 1 is identical to the routes traveled on trials 3 and 5. (D) Perturbation of landmarks S_1 and S_3 at test (with gray squares showing landmark locations used during training) in experiment 1 (top), experiment 2 (middle) and experiment 3 (bottom), and corresponding shift in perceived location of home (pH) across the non-perturbation (gray pH) and perturbation group (black pH).

the various distances and locations constituting the experimental variables depicted in Fig. 1B.

The blindfold was a pair of blacked-out swimming goggles. The cane was constructed from a 1 cm diameter wooden dowel and was 1.2 m long. Participants gripped the cane at one end. Padding the cane's tip minimized noise as participants explored by back and forth sweeping motions.

Procedure

Each experiment was conducted on weekends when the facility was quiet. The hallway was smooth and polished. The only sounds were the footsteps and voices of the participant and the primary experimenter.

Participants arrived at the building housing the experiment without having seen the experimental environment, and with no foreknowledge of where in the building the experiment would be conducted. At the outset of each experiment, each participant was taken to an office where they were given a brief overview of the upcoming task, provided with the cane and blindfolded. The participant was then led circuitously through other hallways to the experimental test area, thus avoiding any experience of the experimental layout prior to the experiment proper. Participants stepped into the environment at the test location [L; distance (d)=6 m from 'home'; see Fig. 1B].

Each experiment comprised three distinct phases. Throughout all three phases the participant was engaged in conversation. Conducting the experiment in this manner both protected against mental fatigue, and the likelihood that participants would focus on developing mental strategies to 'solve' the simple orientation tasks posed by the experimenter, such as counting number of strides, or estimating durations between landmarks.

Exploration phase

The first 10 min within the mechanical environment were spent teaching the participant to navigate comfortably up and down the length of the environment. In this exploratory phase, participants learned to become comfortable walking blindfolded with the cane, turning to face the opposite direction, and detecting and navigating the steps in the environment *qua* landmarks. The steps detected with the cane were not stepped over. Rather, all participants found it most comfortable to step up on the steps. Once participants reported becoming more comfortable with the basic task of navigating the environment, they then practiced walking at the three different paces (slow, comfortable and fast) to be used in the subsequent training phase.

Training phase

On completion of exploration, each participant was taken to a constant location identified to the participant as the 'home spot' (H in Fig. 1B). No beacons identified the home spot. It was featureless. At H, the participant was turned to face either in the direction of S_3 or S_1 (see Fig. 1B). These directions were identified to the participant as 'north' and 'south', respectively. The participant was then instructed to walk in the direction faced, at either a pace faster than or slower than normal. When walking southward the participant was stopped at marker D_1. When walking northward the participant was stopped at either marker D_2, D_3 or D_4. The travel distances away from H to markers D_1, D_2, D_3 and D_4 (see Fig. 1B) were –3.5, 3.5, 7.0 and 10.5 m, respectively. On reaching an assigned D, the participant was turned to face H and instructed to walk at normal pace to its perceived location. Once the participant indicated perceived H (pH) by stopping, the experimenter then led the

participant at a comfortable pace indirectly back to the actual H by way of one of four 'filler' locations (F_1, F_2, F_3, F_4; see Fig. 1B) with each filler location used an equal number of times. The training consisted of 32 such trips, divided into four blocks of eight. In a block, participants walked to each of the four set distances D once at a slow and once at fast pace, with distance and pace randomized. The exploration and training phases took approximately 1 h.

Test phase

On completion of training, the participant was led directly to H from the final filler location. The participant was told: "Before the last part of the experiment can be completed, repairs need to be made to the experimental setup". If the participant had been randomly assigned to the non-perturbation condition the environment was checked for any damage caused by the participant's explorations with the cane. If the participant was in the perturbation condition, then S_1 was moved (experiment 1) or S_3 was moved (experiments 2 and 3) as depicted in Fig. 1B during the 'check for damage'. The participant was then informed that the current location was H and instructed that for the final part of the experiment he or she would be (a) guided along a route through the environment, (b) stopped at a random location, and (c) instructed to find H. Specifically, the participant was instructed to turn in the direction of H and then to walk to H. One condition was placed on the task, namely, if a participant overestimated the location of H to a degree that he or she arrived at a step, the participant was not allowed to turn around and walk back to H. In such cases the position the participant was standing at when the cane contacted the step was recorded.

In the test phase, the participant was guided over different specific routes that all terminated at the fixed location H shown in Fig. 1B, the location from which H had to be found. There were six test trials. They are depicted in Fig. 1C. On trial 1 the participant was led along the route depicted in top panel of Fig. 1C. On this route the participant contacted S_1 four times. On the succeeding five trials the participant was alternately led along the routes depicted in the middle and lower panels of Fig. 1C. On these trials, the participant contacted S_1 twice.

RESULTS

During training in experiments 1–3, participants that would comprise, and be tested in, the non-perturbed and perturbed groups, performed equally well in the task of reproducing outbound distances from home (all $P>0.05$ in analysis of variance with distance and group as factors).

Experiment 1

The first experiment was modeled on the one-landmark manipulation of Uttal et al. (Uttal et al., 2006). Fixing the start location, they trained children to find a toy located in a specific direction at a specific distance from a single, small landmark. Manipulation of the position of the landmark at test (see Collett et al., 1986) revealed that the children had learned the toy's landmark-based vector.

In experiment 1 we limited the mechanical environment to S_1. We tested the hypothesis that during exploration and training, the location of home would come to be specified by its direction and distance from S_1. At test, the location of S_1 was shifted, for five participants, by 3 m in the direction of home (Fig. 1D, top). For the other five participants, the location of S_1 remained the same as during exploration and training. Confirmation of the hypothesis required that the perturbation participants would locate home 3 m further from S_1 than the non-perturbation participants. It also required that the expected difference between the perturbation and non-perturbation

participants in the perceived location of home (pH) would be independent of the travel route (the specific sequence of mechanical contacts) taken to reach the test location (L) from which participants were to find home (Fig. 1C). To reiterate, on test trials 2, 4 and 6, participants arrived at L from the 'south', thereby facing away from H but having just contacted S_1. By contrast, on test trials 1, 3 and 5, participants arrived at L from the 'north', thereby facing H but having traveled more than 45 m since last contacting S_1.

Displacing S_1 in the one-step environment affected the direction taken in finding H. Perturbation participants walked from L in the direction of H on only 53% of the trials compared with 80% of the trials for the non-perturbation participants. A measure that incorporates both the direction component and the distance component of pH is the constant error – the signed difference between pH and H with the latter assigned the value of 0. Average pH was 2.07±2.13 m for non-perturbation and 5.07±2.17 m for perturbation. That is, following a +3 m shift in S_1, pH shifted, on average, +3 m. If trials in which participants walked in the wrong direction from L (when participants were disoriented) are ignored, then pH was 0.47 m for non-perturbation and 2.70 m for perturbation. The contrasting distributions of non-perturbation pH and perturbation pH are shown in Fig. 2A, $\chi^2(12, N=60)=23.46, P<0.05$.

Constant error averaged over participants of each group at each of the six test trials depicted in Fig. 1C is shown in Fig. 3A. A 2 (perturbation) × 6 (trial) ANOVA confirmed the effect of perturbation, $F(1, 8)=7.76, P<0.001, \eta_p^2=0.49$, and identified an interaction of perturbation and trial, $F(5, 40)=2.76, P<0.05, \eta_p^2=0.26$, with no trial effect, $F<1$. A constant error greater than 5 m indicates that walking from L occurred in the direction opposite

to H (see Fig. 1B). The marginal interaction was primarily due to the fact that of the six instances (out of 30) of disorientation in the non-perturbation group, three occurred on trial three (a trial in which participants arrived at L facing home, Fig. 1C bottom) with a mean value of 8.7 m. Of the 14 instances of disorientation in the perturbation group, only one (7.7 m) occurred on trial 3. When debriefed, none of the participants, in either the non-perturbation or perturbation conditions, reported any noticeable changes in the environment between training and test.

In sum, place learning involving a single landmark, and achieved through dynamic touching, was consistent with the vector coding principle commonly observed in place learning by animals and humans under conditions that impose no explicit restriction on the modes of attending (e.g. Cartwright and Collett, 1983; Collett et al., 1986; Uttal et al., 2006).

Experiment 2

Experiment 2 was conducted in the three-step environment. We examined whether performance in the test phase would be affected by shifting a landmark that was remote from home in the sense that at least one other landmark in the same direction was closer to home than it. Specifically, we asked whether a displacement in the test phase of S_3 by 1.5 m in the direction of S_2, with the locations of S_1 and S_2 unchanged (see Fig. 1D), would affect pH. If participants in the perturbation condition orient to H through vector coding relative to either S_1 or S_2, or orient to H so as to preserve the relationship of H to S_1 and S_2, then pH in the perturbation condition should not differ from pH in the non-perturbation condition. A different expectation follows, however, if participants in the perturbation condition orient to H so as to preserve the ratio between distance of H from S_2 and distance of S_2 from S_3. On the presumption that the perceived location of H (that is, pH) in the non-perturbation condition is equal to H (with coordinate 0; see Fig. 1D), then, given:

$$\frac{S_2 - H}{S_3 - S_2} = \frac{12.25 - 0}{18.25 - 12.25} = 2.04 \tag{1}$$

for the non-perturbation condition, it should be the case that in the perturbation condition, with S_3 displaced toward H by 1.5 m:

$$\frac{S_2 - pH}{S_3 - S_2} = \frac{12.25 - pH}{16.75 - 12.25} = 2.04 . \tag{2}$$

Satisfying the latter equation requires that in the perturbation condition, pH equals 3.07 m.

Average constant error for the non-perturbation participants and for the perturbation participants, at each of the six test trials, is shown in Fig. 3B. Displacing S_3 in the three-step environment did not affect the direction taken in finding home. Non-perturbation and perturbation participants walked from the start location L in the direction of H on 92.6% and 85.2% of the trials, respectively, and walked past H on 16% and 13% of the trials, respectively. Fig. 2B suggests a common distribution for non-perturbation pH and perturbation pH, $\chi^2(11, N=108)=10.47, P=0.48$.

In respect of mean pH, the non-perturbed value was 1.54±2.52 m and the perturbed value was 2.51±2.67 m. That is, following a perturbation to S_3 of −1.5 m, pH was shifted by +0.97 m on average – a shift that was shown by a 2 (perturbation) × 6 (trial) ANOVA performed on the constant errors of the 18 participants to be non-significant, $F(1, 16)=1.67, P>0.05$. Similarly the main effect of trial and the perturbation by trial interaction (both $F<1$) were non-significant. In common with experiment 1, no participants in either the non-perturbation or perturbation conditions reported any noticeable changes in the environment between training and test.
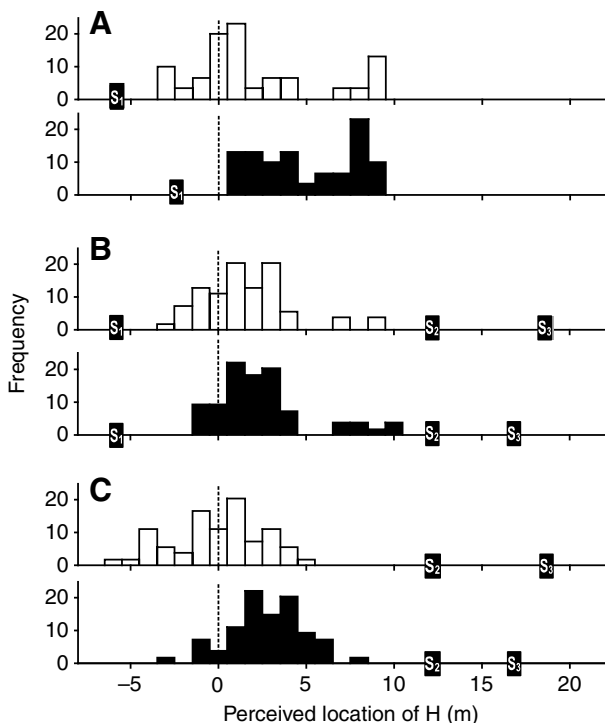

Fig. 2. Distribution (each trial of each participant) of perceived location of home (H) in (A) experiment 1, (B) experiment 2 and (C) experiment 3 for the non-perturbation group (white bars) and the perturbation group (black bars). Placement of landmarks (S_1, S_2, and S_3) during the test is shown on the abscissa. The vertical dotted line marks the location of H.

Given the redundancy of the specification of H within the mechanical contacts afforded by the three-step environment, the nonsignificant influence of the S_3 shift is, perhaps, not so surprising. Participants could have perceived H in terms of its direction and distance from S_1 (as in experiment 1), or its direction and distance from S_2, or both. In addition to these sources of vector attunement, participants could have perceived H in terms of the unchanged relationship between the distances separating H from S_1 and S_2 (e.g. Sutton, 2002). This argument from redundancy presumes, however, that the mechanically informed place learning involved the three landmarks in multiple vector and relational 'codes'. In our third experiment we reduced the redundancy by removing S_1 on the expectation that, in the two-step environment, the relation between H, S_2 and S_3 would be more salient. Countering this expectation is the likelihood that place learning will be constrained solely by the nearest landmark, S_2. A preference for nearer than further landmarks in place learning has been reported for a number of species (Cheng and Spetch, 1998; Cook and Tauro, 1999; Spetch and Kelly, 2006) including humans (Foo et al., 2007).

Experiment 3

Displacing S_3 in the two-step environment had no effect on the direction taken in finding home. Non-perturbation participants and perturbation participants walked from L in the direction of home (and away from S_2 and S_3) on 98% and 94% of the test trials,

respectively. Displacing S_3, however, did affect the frequency with which participants walked past home: 48% of the trials for the non-perturbation participants, 11% of the trials for the perturbation participants. The contrasting distributions of non-perturbation pH and perturbation pH are shown in Fig. 2C [$\chi^2(14, N=108)=33.92$, $P<0.01$].

Constant error averaged over participants of each group at each of the six test trials is shown in Fig. 3C. A 2 (perturbation) $\times$ 2 (trial) ANOVA performed on the constant errors of the 18 participants revealed an effect of perturbation, $F(1,16)=9.49$, $P<0.01$, $\eta_p^2=0.82$, an effect of trial, $F(5,80)=2.46$, $P<0.05$, $\eta_p^2=0.13$, and no interaction of perturbation and trial, $F(5,80)=1.96$, $P>0.05$. For non-perturbation participants, pH was a mean distance of $-0.20\pm2.28\,\mathrm{m}$ away from H. For perturbation participants, pH was a mean distance of $2.74\pm1.84\,\mathrm{m}$ away from H. In short, following a perturbation to S3 of $-1.5\,\mathrm{m}$, pH shifted, on average, $+2.94\,\mathrm{m}$, close to the expected value of $+3.07\,\mathrm{m}$ (Fig. 1D). When debriefed, none of the participants, in either the non-perturbation or perturbation conditions, reported any noticeable changes in the environment between training and test.

Experiment 3 was designed to assess whether place learning entailed relationships between landmarks over and above vectors tied to individual landmarks. In respect to the vector interpretation, if participants encoded home as distance from S_2, and the $-1.5\,\mathrm{m}$ displacement of S_3 (in the capacity of an anchor or boundary) (Doeller and Burgess, 2008) was registered as a $+1.5\,\mathrm{m}$ displacement of S_2, then subtracting 1.5 m from pH in the perturbation condition should yield zero, on average. A simple one-tailed t-test on the six trials of each of the nine perturbation participants revealed that the difference (pH -1.5) exceeded zero: mean difference=1.24 m, $t(53)=4.27$, $P<0.0001$. With respect to the relational interpretation, if participants encoded home in terms of the ratio of distances H to S_2 and S_2 to S_3, as detailed in experiment 2, then subtracting 3.07 m from pH in the perturbation condition should yield zero, on average. For the relational interpretation, the t-test revealed that the difference (pH -3.07) did not differ from zero: mean difference=-0.33 m, $t(53)=-1.15$, $P=0.26$.

In summary, experiment 3 suggests that participants defined home in terms of a ratio of distances. Their homing behavior, under perturbation of the environment, kept the ratio of distances invariant, not the actual distances.

DISCUSSION

We have found that place learning achieved primarily by touching has key aspects in common with place learning in which looking is the predominant mode of active overt attending, and no modes are explicitly excluded. In the minimal environments of our research, both vectors tied to individual landmarks and relationships between landmarks were found to constrain the perception of home (Uttal et al., 2006). The persistence of the learned vectors and relations across the six trials testing the ability to find home is shown in Fig. 2. For all three experiments it is reasonable to claim that the perturbation effect was the same from trial to trial. It seems that whatever had been learned – specific vectors or specific relations, or both – was employed in the test phase as the basis for finding home in exactly the same way by both groups of participants. The participants in the perturbation group were not doing anything extraordinary. One can also conclude for both groups that finding H from L was unaffected by (1) the specific sequence of changes in contact stimulation prior to L, and (2) the 'postural viewpoint' at L (whether facing H or not) (cf. Collett and Zeil, 1998).
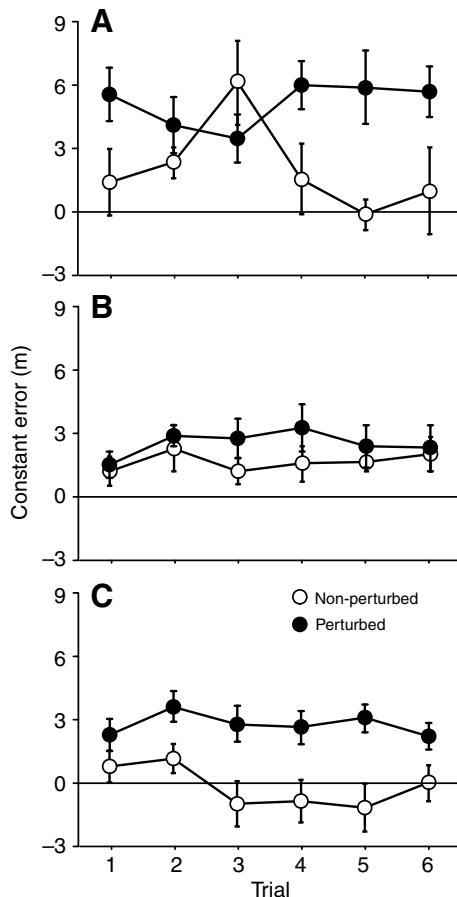

Fig. 3. Constant error of perceived home at test in (A) experiment 1, (B) experiment 2 and (C) experiment 3, as a function of perturbation and test trial.

Our results with blindfolded humans dovetail with experimental observations of place learning without vision by other species. Limited to ambulatory mechanical contact through their second antennae, blindfolded freshwater crayfish (*Cherax destructor*) learn about the relative distances of surrounding surfaces (Basil and Sandeman, 2000). Blind Mexican fish limited to mechanical contact with the field-like structure of water flow arising from locomotion relative to surrounding objects, both stationary and mobile (Hassan, 1992; Montgomery et al., 2001), learn the spatial relationships between landmarks configured as square arrays (Burt de Perrera, 2004). And as highlighted in the Introduction, blindfolded wandering spiders, *via* the mechanical contacts of locomotion, learn the place of a previously caught but uneaten prey (Seyfarth and Barth, 1972; Seyfarth et al., 1982).

Our results also dovetail with recent experimental findings on geometric and metric details of place learning by looking. A frequent observation is that place learning within a given area is constrained primarily by perpendicular distances from the extended surfaces that bound the area (Doeller and Burgess, 2008; Doeller et al., 2008; Hartley et al., 2004) (for reviews see Burgess, 2006; Burgess, 2008). In experiments with rats in a Morris maze (Morris, 1981), Benhamou and Poucet (Benhamou and Poucet, 1998) found that place learning was constrained by an intramaze configuration of landmarks indifferent to both the individual identities of the landmarks and the extramaze environment. In experiments with domestic dogs, Fiset (Fiset, 2009) showed that in a room of approximately $12\,\text{m}^2$ shifting an individual landmark for a learned food place either laterally, perpendicularly or diagonally by 25 cm relative to an extended surface (a wall), resulted in the dogs shifting their search between 0 and 25 cm in the direction of the landmark shift. The implication is that the dogs' place learning was primarily in terms of local landmark-based vectors. Experiments by Sturz et al. (Sturz et al., 2009) with humans in real and simulated environments were directed at the consequences of no correlation between locations of places within a circumscribed area and the extended surfaces that bounded that area. The experiments revealed that, despite the absence of the aforementioned correlation, learning of relationships between local places within the area (real or simulated) was achieved successfully. At a minimum, the results of Benhamou and Poucet (Benhamou and Poucet, 1998), Fiset (Fiset, 2009), and Sturz et al. (Sturz et al., 2009) demonstrate that place learning, with looking as the predominant mode of attention, need not be conditional on a surround of extended surfaces that embeds the to-be-learned place or places. The implication of the latter conclusion, in the perspective of the present data, is that place learning by looking and place learning by touching are more similar than they are different.

Our landmarks were of the kind referred to as "small discrete proximate" by Greene and Cook [p. 321 in Greene and Cook (Greene and Cook, 1997)] in contrast to the large, global, distal landmarks characterizing most place-learning studies. In agreement with Greene and Cook (Greene and Cook, 1997) and other studies with looking as the predominant attention mode (e.g. Benhamou and Poucet 1998; Jones et al., 2002; Kamil and Jones, 1997; Uttal et al., 2006), we found (in experiment 3) the small discrete proximate landmarks to be sufficient for the expression of relational influences on place learning. Also in agreement with Greene and Cook and other studies with looking as the predominant attention mode (e.g. Kamil and Cheng, 2001; Spetch and Kelly, 2006) is the suggestion in our data that the number of landmarks matter. With one landmark (experiment 1), disorientation was relatively frequent: 20% of the non-

perturbation trials and 47% of the perturbation trials. The corresponding frequencies for disorientation were considerably smaller given two landmarks (2% and 6%) and three landmarks (6% and 15%).

For animals that orient to their habitats mechanically, we are inclined to think of landmarks as *necessarily* small discrete proximate. This is because of a traditional conception of touching as proximal and narrow in span relative to looking, and capable of revealing only properties of immediately adjacent surfaces and objects. Particular differences, however, between touching and looking from a stationary point of observation need not hold for an ambulatory point of observation, the condition of perceiving that characterizes the present experiments and the foraging of the wandering spider. The heart of the problem of orientation is how one becomes aware, *via* locomotion, of the places and mutual separations of places that compose one's habitat. On this latter perspective, the limits on place learning by ambulatory touching and by ambulatory looking are set similarly, by the limits on the habitat contactable (mechanically, optically) by legged locomotion. This hypothesis with respect to mechanical contact could be elaborated through experiments that are immediate extensions of the present experiments: ambulatory touching in mechanical environments that define home in two coordinates.

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