Bayesian Integration of Spatial Information

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Spatial judgments and actions are often based on multiple cues. The authors review a multitude of phenomena on the integration of spatial cues in diverse species to consider how nearly optimally animals combine the cues. Under the banner of Bayesian perception, cues are sometimes combined and weighted in a near optimal fashion. In other instances when cues are combined, how optimal the integration is might be unclear. Only 1 cue may be relied on, or cues may seem to compete with one another. The authors attempt to bring some order to the diversity by taking into account the subjective discrepancy in the dictates of multiple cues. When cues are too discrepant, it may be best to rely on 1 cue source. When cues are not too discrepant, it may be advantageous to combine cues. Such a dual principle provides an extended Bayesian framework for understanding the functional reasons for the integration of spatial cues.

Keywords: Bayesian, spatial perception, locomotion, navigation, landmark

Bayesian Combination of Multiple Sources of Information for Spatial Localization

To illustrate Bayesian principles, we begin by examining some psychophysics with humans combining spatial information from different sources (for a review, see Deneve & Pouget, 2004). Bayes’ (1763) theorem can be used to specify how to combine multiple sources of information optimally. To take the simplest case, suppose that a person has two unbiased sources of information, X and Y, for estimating a particular metric value, each with its own variance, \( \sigma^2_X \) and \( \sigma^2_Y \). The person uses a weighted average of X and Y in estimation, \( W_X X + W_Y Y \), in which \( W_X + W_Y = 1 \). For the best estimate, Bayes’ (1763) theorem claims that the optimal weights are the following:

\[
W_X = \frac{\sigma^2_Y}{\sigma^2_X + \sigma^2_Y} \\
W_Y = \frac{\sigma^2_X}{\sigma^2_X + \sigma^2_Y}.
\]

Loosely speaking, sources should be weighted in inverse proportion to their variances.

We can divide cases of Bayesian combination of information conveniently into three different varieties, although further and different subdivisions are possible. (a) Two current sources of information are combined in estimating a spatial value. (b) A current source of information is combined with prior information, typically an average derived from past experience. This case is closest to Bayes’ original (1763) formulation. (c) A current source...
of information is combined with categorical information that may or may not be derived from past experience.

**Combining Two Separate Present Sources of Information**

In experiments on this Bayesian variant, three different conditions are presented to subjects. On some trials, the subject is allowed to use only source $X$; on other trials, only source $Y$ is allowed. These trials provide estimates of $\sigma^2_X$ and $\sigma^2_Y$, respectively. From these estimates, optimal values for $W_X$ and $W_Y$ can be calculated. The observed values of $W_X$ and $W_Y$ are obtained from tests in which both cue sources are provided. The dictates of these circumstances, it is optimal to integrate the two sources, weighting the source with the distribution on the left more than the source on the right. B: The two sources indicate directions far from one another. Under these circumstances, it is highly improbable that both sources stem from the same signal. This makes it unreasonable to integrate the two sources.

![Figure 1](image-url)

**Figure 1.** To integrate or not to integrate two sources of spatial information. Shown are sources of information that indicate the direction of a signal, for example, egocentric direction from the observer. Each distribution represents one source of information, for example, visual and auditory information. Each specifies a probability distribution of the direction of the signal. A: The two sources indicate directions near one another. Under these circumstances, it is optimal to integrate the two sources, weighting them in inverse proportion to their variances. In the illustration, this means weighting the source with the distribution on the left more than the source with the distribution on the right. B: The two sources indicate directions far from one another. Under these circumstances, it is highly improbable that both sources stem from the same signal. This makes it unreasonable to integrate the two sources.

with each source individually. Bimodal trials were presented to estimate the weights given to vision and audition. Results showed two important points. (a) For all 6 subjects, the observed bimodal performance did not differ significantly from the level predicted by a Bayesian analysis. Averaged across subjects, bimodal performance matched Bayesian predictions almost exactly. (b) The notion that vision always “captures” or dominates audition was contradicted. When the quality of visual information was worse than that of auditory information, all subjects weighted audition more than vision.

Similarly, humans combine visual and haptic information in near optimal fashion. Ernst and Banks (2002) had subjects judge the height of a stimulus visually (information supplied through stereopsis), haptically, or bimodally. Quality of visual information varied across blocks. Again, variances obtained in unimodal judgments were used to predict optimal weightings of visual and haptic information. Ernst and Banks’ title summarizes the results well: Humans integrate visual and haptic information in a statistically optimal fashion. Gepshtein and Banks (2003) had humans judge sizes visually, haptically, or bimodally. Visual quality was manipulated by viewing orientation; presumably, an extent from left to right is much easier to judge than an extent from near to far. Again, visual and haptic information were weighted in near optimal fashion. Other studies have indicated that humans integrate visual and proprioceptive information to improve performance on pointing to a spot on a table (van Beers, Wolpert, & Haggard, 2002), and different visual sources may be combined to improve accuracy (stereo and texture cues: Knill & Saunders, 2003; stereo and skew symmetry cues: Saunders & Knill, 2001).

In the typical example of cue conflict depicted in Figure 1A, the two distributions of estimated location overlap. Intuitively, some kind of averaging makes sense here. However, if the distributions are highly separated, as in Figure 1B, averaging would mean a serious mismatch with both sources of information. Jack and Thurlow (1975) found that with 50° separation, visual and auditory stimuli are perceived as two different sources, not one. The role of the size of subjective discrepancy in Bayesian averaging processes has not been much explored in psychophysical experiments. By subjective discrepancy, we mean the discrepancy measured relative to the subjective uncertainty about the central tendency of the measure, basically in units of standard deviations. Subjective discrepancy contrasts with physical measures of discrepancy. Subjective discrepancy turns out to be a crucial variable, which we will discuss in more detail.

**Bayesian Combination of Current Source With Prior Information**

Sometimes, humans combine one source of current information with a Bayesian prior derived from past experience. The intuitive logic is that if one is somewhat unsure of what the current source indicates, one relies partly on how things have been in the past. The more uncertain the current information, the more one should rely on past experience. In the limit, when current information is absent, one’s optimal guess is the average from accumulated past experience. Formally, the logic is still embodied in Equations 1 and 2, with $X$ being the current information source and $Y$ being the prior. Experimentally, however, the optimal weights cannot be estimated directly because the prior information, typically obtained...
from a history of training, cannot be experimentally removed. Curve fitting is usually used to estimate best weights.

Catching a dropped ball provides an illustration. If a ball is propelled downward and our job is to reach out and catch it, we might think that this is a purely bottom-up process of responding to dynamic visual information. However, recent research on astronauts catching balls in space in the absence of Earth-based gravity shows that this description is incomplete (McIntyre, Zago, Berthoz, & Lacquaniti, 2001). In space, a ball propelled “downward” (from “above” the head) moves at constant velocity instead of accelerating as it does on Earth. The astronauts were systematically too early in reaching. McIntyre et al. (2001) concluded from the pattern of data that we possess and use a Newtonian model of how gravity operates on Earth. In addition to online visual information, we use a prior to improve our catching of balls. One of the multiple “cues,” then, might be statistical information derived from past experience.

Visuomotor tasks are typically used to establish an experimental prior because the motor system is malleable enough to be trained. In a paradigm case, Körding and Wolpert (2004) trained subjects to point to a target, without view of their hand, for 1,000 trials. Midway through a trial, a cursor representing the finger provided feedback. The cursor position mismatched finger position systematically, for example, according to a distribution with mean 1 cm right and standard deviation of 0.5 cm. Feedback quality was varied across trials by different amounts of blur applied to the cursor. Subjects used both the cursor position on the trial (current information) and its mean amount of mismatch (prior) in pointing. Furthermore, they weighted the current source less, and the prior more, when the current source was less reliable. This study clearly supported the hypothesis of Bayesian integration of prior and current experience in visuomotor learning, as did others (Baddeley, Ingram, & Miall, 2003; Singh & Scott, 2003).

A Bayesian prior has also been used to explain other phenomena in human perception. Weiss, Simoncelli, and Adelson (2002; see also Cobo-Lewis & Smallwood, 2002; Hürlimann, Kiper, & Carandini, 2002) accounted for motion illusions by positing that subjects combine current motion information with a prior biased toward slow motions. Read (2002) used a prior preference for small disparities to help account for stereoscopic perception of depth and motion perception from seeing two successive frames. Nieuemier, Crawford, and Tweed (2003) used a prior preference for a stationary object to help account for transsaccadic perception. Geisler, Perry, Super, and Galloghy (2001) analyzed scene statistics to develop a prior for contour detection, and Kersten and Yuille (2003) reviewed the role of a prior in object perception.

**Combining Categorical and Metric Information**

Humans may divide space, time, and other dimensions into conceptually natural regions with boundaries and central tendencies. In remembering a location or a point in time, accuracy is improved by averaging the category to which an instance belongs, as represented by its prototype, with the metric estimate of the instance. Estimates made in this fashion will be less variable and more accurate on average than will be uncorrected individual memories, but they will be biased toward the prototype (Huttenlocher, Hedges, & Prohaska, 1988; Huttenlocher, Hedges, & Duncan, 1991; Huttenlocher, Hedges, & Vevea, 2000).

As a spatial example, subjects had to remember the location of a dot in a circle (Figure 2). Humans naturally divide the circle into quadrants, with the vertical and horizontal lines through the center forming mental boundaries. In this task, subjects were biased systematically toward the centroids of each quadrant of the circle, the prototype of each category (Huttenlocher, Hedges, Corrigan, & Crawford, 2004; Huttenlocher et al., 1991). Subjects thus average the prototype with memory of the instance. The amount of bias varies with the quality of the metric memory, in accord with Bayesian principles. An interference task given after a dot was presented and before it was reproduced (Huttenlocher et al., 1991) resulted in greater bias toward the prototype, presumably because it worsened the metric memory.

**Integration of Cues in Human Locomotion: Use of Multiple Dynamic Cues**

In human movement, multiple dynamic cues are used and calibrated with one another. When we move to a stationary target (a beacon) on the ground ahead, for example, the beacon itself provides one visual cue that we can aim toward. When we start moving, the visual texture on the ground and on objects moves systematically relative to us, providing a dynamic cue, optic flow (Gibson, 1950; Warren & Hannon, 1988; Warren, Kay, Zosh, Duchon, & Sahue, 2001). In addition, various body senses feed us information about the course of travel. Separate vestibular systems register rotation and translation (Berthoz, 2000; Ivanenko, Grasso, Israel, & Berthoz, 1997), and proprioceptive cues in the joints and
possibly copies of command signals to the muscles (efference copies) inform us about limb movements.

**Use of Multiple Dynamic Cues in Locomotion**

Humans use both optic flow and beacon aiming to head toward an object (beacon). Warren et al. (2001) used virtual reality to provide subjects with a head-mounted display with stereoscopic views that presented an abnormal pattern of optic flow. When we face a real beacon and walk toward it, the optical pattern appears to expand from the beacon. The focus of expansion is at the target object. Warren et al. decoupled the focus of expansion by 10° from the heading of the subject, making the trajectory based on beacon aiming and the trajectory based on optic flow different. The amount of optic flow was also manipulated from virtually none (a uniform display with no visual texture at all) to very rich (ground texture, a doorway, and vertical posts standing along the route). People combined both kinds of cues in executing their trajectories. Consistent with Bayesian principles, the richer the optic flow cues, the more subjects relied on them.

Path integration (sometimes also called dead reckoning) is the ability to keep track of the distance and direction one has moved (Etienne & Jeffery, 2004; Klatsky, Loomis, & Gollende, 1997; Wehner & Srinivasan, 2003). Directional cues may be based on an external compass, such as the sky compass used by insects (Wehner, 1994) or on inertial cues generated by self-movement, such as the vestibular cues used by mammals (Etienne & Jeffery, 2004). In most work on human path integration, visual cues are excluded by blindfolding subjects (Klatsky et al., 1997). However, two studies in which subjects sometimes traveled with visual cues concluded that both visual cues and cues from body senses are used in path integration (Kearns, Warren, Duchon, & Tarr, 2002; Nico, Israël, & Berthoz, 2002).

**Calibration**

Cues from optic flow and body senses are constantly calibrated with each other. For example, normally a certain amount of optic flow is associated with a typical step. However, the calibration can be experimentally altered. Rieser, Pick, Ashmead, and Garing (1995) pulled subjects along behind a tractor while subjects walked on a treadmill. In this way, walking speed was controlled by the speed of the treadmill, whereas rate of optic flow was controlled by the speed of the tractor. The body senses were recalibrated after a few minutes of this experience. On tests, subjects looked at another person standing some meters in front of them and then had to walk to the target person blindfolded. If the tractor moved too slowly during recalibration, so that the amount of optic flow experienced per step was artificially reduced, subjects tended to overshoot after the training. On the other hand, if the tractor moved too quickly, so that the amount of optic flow experienced per step was artificially increased, subjects tended to undershoot after the training. A later study with virtual technology replicated this pattern of results (Proffitt, Stefanucci, Banton, & Epstein, 2003). Rotatory motion can also be similarly recalibrated after active (Pick, Rieser, Wagner, & Garing, 1999; Rieser et al., 1995) or passive movement (Viaud-Delmon, Ivanenko, Berthoz, & Jouvent, 1998). Indeed, aftereffects of exposure to spatially conflicting inputs are seen with a variety of pairs of modalities (review in De Gelder & Bertelson, 2003).

In effect, rather than exposing subjects to brief discrepancies between spatial cues to probe how the cues are weighted, recalibration experiments reveal the effect of prolonged exposure to discrepant information on how cues are evaluated. In normal life, such calibrational processes probably go on constantly and from an early age in a large range of multicellular animals. Most animals grow bigger in the course of their life, and thus the meaning of a step forward, of an amount of binocular disparity, of a given interaural difference in time of arrival of a sound, and so on, all change gradually. Perceptual–motor calibration is likely to be a very common process of integration in navigation.

**Bayesian Prior in Human Locomotion**

In perceiving dynamic cues, a Bayesian prior may be invoked. Ivanenko et al. (1997), for example, found that humans who were passively transported without vision were not good at registering translation but were much better at registering rotation. Subjects tended to assume that they moved in the direction they were facing, a Bayesian prior. This meant that trajectories that contained passive sideways displacements were systematically misperceived.

Glennerster, Tcheang, Gilson, Fitzgibbon, and Parker (2006) used virtual reality to present subjects one standard object on the wall of a room. The subjects then walked toward the other end of the room, where another comparison object hung. Their task was to compare the sizes of the two objects. In a crucial manipulation, the room expanded optically by fourfold as the subjects walked a few virtual meters. Two results are of interest. First, subjects did not notice the virtual room expanding, contrary to the stereoscopic and motion-parallax cues that clearly indicated so. Second, under these conditions the comparison object had to be bigger than the standard object before subjects judged that they were equal in size, sometimes much bigger.

Two Bayesian principles were invoked to explain the results. First, subjects had a prior assumption that the room did not expand as they walked because rooms never expanded in real life when they walked in them. Given this assumption, if an object’s size is judged by reference to its surrounding texture, the comparison object would have to be four times as big to match the standard object (matching ratio 4:1). If stereo and parallax cues are used for size judgments, on the other hand, the matching comparison object would equal the standard object in size (matching ratio 1:1). The actual matching sizes fell between those ratios. Subjects averaged the dictates of multiple cues. Furthermore, stereo and parallax cues deteriorate in quality with increasing distance, whereas the quality of texture cues is not very sensitive to distance. According to Bayesian principles then, as viewing distance increased, subjects should rely relatively more on the texture cues and have bigger matching ratios. The results showed just this pattern and were well-fitted by a model with one free parameter incorporating these Bayesian principles.

**Integrating Multiple Cues in Animal Navigation**

Most of what we know about how nonhuman animals use multiple spatial cues comes from research on rodents (rats and hamsters) in the laboratory (for reviews, see Jeffery, 2003; Thinus-
Blanc, 1996) and on insects (ants and honeybees) foraging on naturalistic spatial scales (for reviews, see Cheng, 2006; Collett & Collett, 2002; Wehner, 2003). The cues that have been considered include beacons, landmarks, self-generated (idiothetic) cues, external compasses, and the geometry of objects and surfaces in space. Our review will concentrate on (a) the use of landmarks and (b) interactions of path integration with other cues. The discrepancy of cues once again plays a major role in determining how cues are integrated.

**Landmarks 1: Cue Competition**

Cue competition is a much-discussed topic in classical conditioning (Pavlov, 1927). A predictor (conditioned stimulus, CS) for a biologically significant event (unconditioned stimulus, US) might be less effective because of what is learned about other predictors. Two key phenomena characterize cue competition: blocking and overshadowing. In blocking (Kamin, 1969), initial training with one cue reduces (i.e., blocks) learning about a second, redundant cue that is added to it later. Thus, if A is learned in Phase 1, and A + B are presented in Phase 2, then B might not be learned well (it is blocked). In overshadowing (Pavlov, 1927), when two cues, A and B, presented together predict the US, less may be learned about either A or B than if it were the only predictor of the US.

In the spatial domain, cue competition has been readily demonstrated with landmarks (Chamizo, 2003; Cheng, in press). We illustrate with a case each of blocking and overshadowing. A. D. L. Roberts and Pearce (1999) demonstrated that a beacon can block the learning of surrounding landmarks. In a swimming task (Morris, 1981), rats were trained to escape from a pool of water onto a visible dry platform that was in a consistent place relative to surrounding landmarks. The rats thus had a beacon and landmark cues for navigation. A group of rats trained with the landmarks visible from the outset learned to use the landmarks: When the platform was removed and the landmarks were the only cues available, they searched most at the platform’s usual location. Such landmark learning was blocked, however, in rats that had previous experience finding the visible platform without the landmarks.

Pigeons can learn to search for an unmarked goal location on a computer monitor, with graphic objects as landmarks and responses recorded by a touch-sensitive frame (touch screen; e.g., Spetch, Cheng, & Mondloch, 1992; for a review, see Cheng, Spetch, Kelly, & Bingman, 2006). In a touch-screen study on both pigeons and humans, Spetch (1995) demonstrated overshadowing in landmark use. A landmark of interest, X, was compared under two training conditions. In the control condition, X was the closest landmark to the target. In the overshadowing condition, X was at the same absolute distance from the target as it was in the control condition, but another landmark was even closer to the target. Tests with X alone measured how well subjects had learned to use this landmark of interest. Both humans and pigeons performed better with X alone when it was the closest landmark (control condition) than when it was not (overshadowing condition). In short, a very close landmark overshadowed the learning of a medium-distance landmark. Similar overshadowing effects have been demonstrated in the food-storing Clark’s nutcracker searching on the floor of a room (Goodyear & Kamil, 2004) and in rats in a swimming task (Chamizo, Mantiega, Rodrigo, & Mackintosh, 2006).

At first glance, cue competition seems to show less than the full use of available information, contrary to a Bayesian framework. On the other hand, if different performance levels reflect different weighting given to cues, then reconciliation with a Bayesian framework may be possible. Blocking by a beacon might indicate that the animal has strong prior information about the goal location, based on experience with the beacon. The beacon might have become a particularly good cue and thus be weighted strongly. Overshadowing too might be interpreted as a matter of different weighting on different landmarks. The naturally stronger or more salient landmarks are weighted more. We suppose that different weighting in turn leads to differential learning. Those cues weighted more are learned better, but we have no evidence currently that larger weighting leads to better learning. As for quantitative measures of weights given to landmarks, the literature on the use of multiple landmarks in pigeons provides one case that we can analyze.

**Landmarks 2: Bayesian Pigeons?**

Theoretically, the more landmarks an animal relies on, the more accurately it can pinpoint a goal (Kamil & Cheng, 2001). Research on pigeons, and on some other birds, has suggested that they do use multiple landmarks in pinpointing a target location (for a review, see Cheng et al., 2006). Pigeons learned to search in an arena for food buried at a constant location cued by multiple landmarks. After suitable training, cues were shifted to test the weights given to landmarks. For example, when a stripe on a wall near the buried grain was the only cue moved, the pigeons’ peak place of searching shifted in the same direction as the landmark shift although usually by a smaller distance (Cheng, 1988). The birds thus compromised between the dictates of the stripe and those of some unmoved features of the enclosure (e.g., a corner). The amount of shift indicated the weighting given to the stripe versus the unmoved features. In this and other cases (e.g., Cheng, 1989), optimality based on Bayesian principles could not be determined because data from requisite single-cue tests (search given only the stripe, on the one hand, and given all cues except the stripe, on the other hand) were lacking. With the appropriate choice of landmarks and set ups, however, such data are not difficult to obtain.

In one study using the touch screen, results of single-cue tests and landmark-displacement tests were both published (Spetch & Mondloch, 1993). Pigeons had to search in the middle of four distinct graphic landmarks, placed in an enclosure (e.g., a corner). The amount of shift indicated the weighting given to the stripe versus the unmoved features. In this and other cases (e.g., Cheng, 1989), optimality based on Bayesian principles could not be determined because data from requisite single-cue tests (search given only the stripe, on the one hand, and given all cues except the stripe, on the other hand) were lacking. With the appropriate choice of landmarks and set ups, however, such data are not difficult to obtain.

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Averaging across birds, a predicted weight of 0.66 for the preferred landmark was obtained.

The actual weight assigned to the preferred landmark can be estimated from landmark-shift tests, in which the preferred landmark was shifted with respect to the other three (Figure 8 of Spetch & Mondloch, 1993). Measurements of a digital copy of the graph show that over four tests, the peak location shifted on average 68% of the distance of the landmark shift, indicative of an average

Figure 3. Data from 1 pigeon in a study by Spetch and Mondloch (1993, Figure 4). The bird was presented with an array of graphic landmarks, indicated by the variously shaped symbols (top panel). It had to peck at an unmarked target location, indicated by the black dot, to obtain a reward. During training, the entire array of landmarks and goal was shifted from trial to trial on the monitor screen, but they maintained their spatial relations to one another. The panels show performance on unrewarded tests with different arrays, with the target position at 0, 0 in all panels. The top panel shows tests with the training set up. The bottom four panels show performance when the bird was presented with each landmark on its own. On tests, as during training, the target location was not marked. The single-landmark tests of this bird showed that it performed well with the pacman landmark (bottom left panel) but poorly with any of the other landmarks. Adapted from Control of Pigeons’ Spatial Search by Graphic Landmarks in a Touch-Screen Task, by M. L. Spetch and M. V. Mondloch, Journal of Experimental Psychology: Animal Behavior Processes, Vol. 19, p. 360. Copyright 1993 by the American Psychological Association.
weight of 0.68 for the preferred landmark. Needless to say, this post hoc analysis is far from ideal but indicates that a Bayesian analysis is certainly possible and worth obtaining.

Pigeons sometimes encode the configuration of landmarks (Sutton, 2002), and evidence suggests that rats do too (Rodrigo, Chamizo, McLaren, & Mackintosh, 1997). In Sutton’s (2002) work, pigeons were trained with two different configurations composed of the same landmark elements. Each configuration had a different goal location and each remained in the same place in the room. A crucial finding was that when any single landmark was displaced, it was ignored; the birds searched at the location dictated by the remaining three. On an interpretation of weightings given separately to each individual landmark, this would mean that each landmark was weighted near zero, an interpretation that makes no sense. The birds seemed to use the configuration of landmarks both to identify the array and to localize the goal. We believe that subjective discrepancy, this time within a configuration of landmarks, plays an important role again, and we return to this in the Discussion.

**Bayesian Combination of Servomechanisms?**

Navigational mechanisms can be thought of as servomechanisms (Cheng, 2006). The specification of a target location is compared with perceptual input indicating current location, and the animal moves so as to reduce the discrepancy between the two. The simplest are called taxes (Fraenkel & Gunn, 1961). The animal moves in a particular direction relative to sensory cues. Multiple taxes may be combined; for example, millipedes compromise their internal sense of straight ahead and their gravitational sense of up (M. L. Mittelstaedt, Mittelstaedt, & Mohren, 1979). The coastal snail of the genus Littorina provides an excellent illustration (work of Fraenkel in 1927, but translated to English with commentary in Gallistel, 1980, Chapter 6). When submerged in water, Littorina moves away from light (is negatively phototactic) and away from gravity, or up (is negatively geotactic). These servomechanisms function to get the animal out of water and into dark rocky crevices where it prefers to dwell. In the lab, Littorina would move up a vertical glass plate. With a light to one side, however, it moved diagonally, striking a compromise between geotaxis and phototaxis. When a light was overhead, placing light and gravity in direct conflict, the stronger the light, the less likely the animals were to move up. Light was weighted more when it was stronger. If the strength of a signal correlates with its reliability, the pattern of results is consistent with Bayesian principles.

**Path Integration: A Back-Up and Reference System**

As mentioned, path integration is the ability to keep track of the distance and direction one has moved. In some cases, information from path integration appears to be averaged with information from other cues such as visual landmarks and beacons following the principles we have just been reviewing. However, in other kinds of cases, two other things may happen. (a) Path integration acts as a back-up system. Other cues are preferred, but path integration continues to operate obligatorily in the background, keeping track of the animal’s location. If the preferred cues fail to deliver, then path integration can be used again. (b) Path integration acts as a reference system. A cue that is too discrepant with the dictates of path integration may be ignored even though with small discrepancies that cue might be the preferred cue. In the Discussion, we examine to what extent all of these patterns might be accounted for by Bayesian principles.

A recent study illustrating points a and b examined competition between path integration and beacon learning (Shettleworth & Sutton, 2005). Rats searched for food hidden in a large lighted arena and carried it to a home base to eat. In some conditions, a distinctive black panel at the home entrance served as a beacon. Rats provided with a beacon oriented no more accurately than rats homing without a beacon that had to rely solely on path integration. When the beacon was displaced by 45° (i.e., one-eighth of the way around the edge of the arena) nearly all the rats approached it, that is, the beacon was preferred over path integration. Nevertheless, in tests with the beacon absent, these same rats homed as accurately as the rats that had to rely on path integration alone, indicating that path integration functions as a back-up system. This last result also shows that the beacon had not overshadowed path integration.

Further evidence for path integration as a back-up system comes from Whishaw and Tomie (1997; see Etienne & Jeffery, 2004, for other examples), who trained rats to home with food in an arena well-provided with landmarks. When the home cage was then moved to a new location before the rats left on a foraging trip, they headed first toward the old location of the home relative to landmarks. Not finding the home cage there, they then went to the new location by using path integration. Of noted importance, they did not go somewhere in between as if averaging.

Desert ants prefer to follow familiar routes based on a series of recognized landmarks, if such route cues are available (Kohler & Wehner, 2005; Wehner, Michel, & Antonsen, 1996). However, if they are experimentally displaced far from routes, they resort to path integration (Wehner, Boyer, Loertscher, Sommer, & Menzi, 2006). A clear case of the back-up function of path integration is shown in Figure 4. Desert ants were trained to home along a corridor of experimentally provided landmarks along the route on an otherwise open field, their natural habitat (Wehner, 2003). On some tests, the landmarks were rotated about the release point. Some ants followed the route, thus suppressing path integration, but when the landmarks ran out they reverted back to path integration, showing that they had kept the computations of path integration going. In all these cases then, path integration took over when the landmark information failed.

A larger beacon displacement (90°) by Shettleworth and Sutton (2005, Experiments 2 and 3) provided evidence for path integration as a reference system. In this case, a good number of rats no longer followed the beacon, instead reverting to path integration. When a landmark was displaced as far as possible around the arena (180°), hamsters did not follow the landmark at all, every one relying on path integration instead (Etienne, Teroni, Portenier, & Hurni, 1990). Chittka and Geiger (1995) trained honeybees to fly from their hive to a feeder over an open area. Three tents along the route served as landmarks. When the line of tents was rotated by 30° around the hive on a sunny day, they were ignored, and the honeybees relied entirely on their sky compass (Wehner, 1994), the directional compass used for path integration. In all these cases, a large enough discrepancy led animals to ignore the dictates of individual landmarks and rely instead on path integration. They
behaved as if referring to their path integration system initially to
decide whether the landmarks were close enough to the right place
to be relied on and ignoring them when they were too discrepant.

Experiments with smaller discrepancies showed that path integra-
tion and landmarks may both be used in combination to deter-
mine a direction in which to travel. In Chittka and Geiger’s (1995)
study, the line of tent landmarks was rotated by 7.5, 15, and 22.5
degree between the dictates of the landmark and of path inte-
gration (Etienne et al., 1990; Figure 3). The European funnel web
spider also combines a landmark cue (a light) and path integration
to home in on their nest (Görner, 1958; for theoretical exposition,
see H. Mittelstaedt, 1983). The spiders relied relatively more on
the light (a) when cues from path integration were made more unreliable by means of a more circuitous outbound trip and (b)
when given longer duration of prior exposure to the light. Both
these patterns are consistent with Bayesian predictions.

In sum, path integration functions as a back-up and a reference
system. Well-learned visual cues are usually given precedence.
However, if those cues do not lead the animal to its goal, or if they
are moved too far from their usual locations, animals resort to path
integration instead. With smaller discrepancies, directional dictates
of landmarks and path integration may be combined, although in
most cases the quantitative data necessary to determine whether
this combination reflects Bayesian weighting remain to be col-
lected.

**Path Integration and Global Landmarks**

When the landmarks are many, path integration is no longer the
reference system, with animals preferring to rely on landmarks in
case of large discrepancies. For example, on a radial maze with
multiple arms radiating out from a central platform, a rat will
retrieve food placed at the end of each arm while avoiding repeat
visits to depleted arms (Olton & Samuelson, 1976; W. A. Roberts,
1984). Rats use both visual cues and internal cues to keep track of
locations (Zoladek & Roberts, 1978). In one study, landmarks
were hung on a circular curtain surrounding the maze (Suzuki,
Augerinos, & Black, 1980). In the middle of a trial, the rats were
enclosed at the central platform, and the landmarks were rotated by
180°, setting the directional dictates of path integration at odds
with the dictates of the landmarks. The rats followed the dictates
of the landmarks. Similarly, when searching for food hidden in a
rectangular arena, rats followed the cues in the arena rather than
using path integration when the arena was rotated (Cheng, 1986).

Von Frisch and Lindauer (1954) pitted landmark cues against
the sky compass in honeybees. The bees were trained to fly to a
feeder along a continuous line of landmarks in one afternoon. The
landmarks included a row of trees and a shore line. Overnight, the
hive was moved and placed at a location at which the line of
landmarks headed off in a different direction from the hive, mak-
ing directional dictates according to landmarks and sky compass
very discrepant. Most bees followed the landmarks.

**Other Topics: Geometry Learning and Cognitive Mapping**

Cue interaction in spatial learning has also been examined with
the geometry or shape of a surrounding enclosure as one of the
cues (for a review, see Cheng & Newcombe, 2005). Evidence for
the use of geometric cues has come from systematic errors made
by rats, monkeys, and human children in which a target location
near a landmark in one corner of a rectangular enclosure is some-
times confused with the diagonally opposite corner. It is as if the
landmark that disambiguates the space was ignored and only the
overall geometry was used. Although the studies reviewed by
Cheng and Newcombe (2005) indicated that geometric cues are
not blocked and overshadowed, two recent studies found overshad-
owing of geometric cues by featural cues (Gray, Bloomfield,
Integration of different sources of spatial information has also been discussed in terms of cognitive mapping (O’Keefe & Nadel, 1978; Tolman, 1948), an idea we do not find necessary for our purposes. A cognitive map is said to integrate all available spatial information, without competition between potentially redundant cues (O’Keefe & Nadel, 1978). It has proven extremely difficult to find unambiguous evidence for cognitive mapping in any animals (Benhamou, 1996; Bennett, 1996; but see Menzel et al., 2005). In practice, to show evidence of a cognitive map an animal must travel a novel route without demonstrably relying on path integration, generalization from familiar to novel views of landmarks or beacons, or any other simpler mechanism. For this reason, we沿 along with others (Giurfa & Capaldi, 1999; Mackintosh, 2002) suggest that more progress will be made by looking at interactions among better specified mechanisms for acquisition and use of spatial information, as we have done throughout this article. Taking another approach, Blaisdell and Cook (2005) suggested that pigeons integrate spatial information across two different learning phases and referred to this as forming a map. However, Sturz, Bodily, and Katz (2006) found an alternative interpretation. Like learning of geometry, this topic is in too much flux currently to be amenable to a Bayesian analysis.

Discussion

To make sense of the diverse phenomena that we have reviewed, we note that the notion of subjective discrepancy is crucial. Discrepancy is found when two cues point to different values on some metric parameter (e.g., direction). Subjective discrepancy is measured not in physical terms but in psychological terms: in units of standard deviation in the subjective measure of a parameter, a measure of subjective uncertainty about the measure. A dual principle we explore is that small discrepancies lead to integration, whereas large discrepancies lead to using one cue or the other, not an averaging of cues. Both sides of this principle may be compatible with Bayesian principles.

Consider first small subjective discrepancies. Psychophysical experiments on humans that have examined Bayesian predictions have largely found confirming evidence. In human locomotion, the change in weighting given to optic flow cues versus a beacon cue accords with ordinal predictions: The more optic flow cues available, the more subjects relied on them (Warren et al., 2001). In animal navigation, we could compare the weighting assigned to landmarks with Bayesian predictions for pigeons in one study (Spetch & Mondloch, 1993). In that case, the averaged results were close to Bayesian predictions. The changes in relative weighting accorded to light versus gravity cues in coastal snails (Gallistel, 1980, Chapter 6) and to inertial versus light cues in funnel web spiders (Görner, 1958) also followed Bayesian principles. In other cases, integration is sometimes found, but how nearly optimal the integration is cannot be evaluated because the requisite data from single-cue conditions are not available. In some cases of cue-conflict situations, the animals rely almost exclusively on one cue. For example, rats rely on a beacon displaced by 45° over path integration (Shettleworth & Sutton, 2005). This pattern may not be contrary to Bayesian principles. The landmark cue might be that much better and receive a strong weighting.

In the case of cue competition during learning, we have supposed that the winning cues specify the target better, either intrinsically (overshadowing) or as a result of prior history (blocking), and thus get weighted more heavily. This view supposes that when the animal learns to use the losing cues through training, their weighting will be increased. Measuring the weights given to winners and losers in cue competition can be done by suitable displacement tests. We also suppose that the weighting affects learning, with cues given higher weights being better learned. Varying the distance between one landmark and a goal and testing how this affects its subsequent control over behavior relative to constant landmarks (as in the studies by Chamizo et al., 2006, and others mentioned) is one example of how weighting might be varied.

Turning to large discrepancies, statistical considerations are important. As Figure 1B shows, if two sample measures are very discrepant, it is statistically highly unlikely that they stem from the same source. Discrepancy is linked to identity: If cues are too discrepant, they are not pointing to the same thing or location, and they should be assumed to stem from two objects rather than one. If one spies a tiger’s stripes straight ahead and simultaneously hears a tiger’s growl 50° to the right, one should assume the presence of two tigers, not one. Indeed, when a sight straight ahead and a sound 50° to the left or right are presented to humans in a lab, they are not perceived as one stimulus (Jack & Thurlow, 1975). If the cues provide dictates for a course of travel (e.g., directional cues), one of the cues should be chosen; averaging is almost guaranteed to be wrong. Thus, averaging the dictates of a route and path integration is a recipe for getting lost.

In animal navigation, large discrepancies typically lead to the use of one cue. Path integration is preferred over isolated landmarks in rats (Shettleworth & Sutton, 2005), hamsters (Etienne et al., 1990), and bees (Chittka & Geiger, 1995). In all these studies, the landmarks were weighted more at smaller discrepancies. This pattern of reversal seems paradoxical. We can explain the reliance on landmarks at small discrepancies by claiming that they make better cues. We are unaware of a direct comparison of single-cue conditions comparing landmarks and path integration. However, across studies, human performance on a beacon-aiming task (e.g., Warren et al., 2001) is much better than performance on a path integration task (e.g., Kearns et al., 2002, or studies reviewed by Klatzky et al., 1997). Taking landmarks to be better cues, why then would animals ever switch to path integration with larger discrepancies?

This pattern of reversal can be understood by considering path integration as a reference and back-up system, as we have done. It sets limits on conditions under which a landmark is still recognized as the same landmark. When the discrepancy with path integration is large, the landmark is no longer viewed as the same landmark as
before. Path integration may be error prone, but it is unambiguous. It does not turn out two different locations as equally good answers. Put more precisely, it delivers a single-peaked probability distribution for the goal location. Landmarks, on the other hand, can be ambiguous, giving rise to what is called in artificial intelligence the problem of perceptual aliasing. Too many trees, stones, and other natural objects are similar (Cheng, 2005). Misidentification systematically misleads the navigator. Path integration, as a reference system, sets limits on what are acceptable landmarks. In natural conditions, when path integration and a landmark are discrepant, it is likely that the landmark is the wrong one. We can consider this as a Bayesian prior found in the natural ecological conditions of most animals. Relying on landmarks at small discrepancies and path integration at large discrepancies, then, might well follow Bayesian principles.

With enough landmarks, however, the hierarchy reverses in case of large discrepancies. Animals prefer to follow an array of landmarks rather than use path integration (Suzuki et al., 1980; von Frisch & Lindauer, 1954). We can again frame this pattern in terms of a priori likelihoods in the natural world. When many landmarks or a whole panorama line up correctly, the probability of perceptual aliasing is vanishingly small, and the odds of mistaken identity is near zero. Entire arrays of landmarks do not often move overnight in the natural world. The odds are thus better that path integration, a single cue, is wrong. Needless to say, this hypothesis can use some more empirical evidence.

A similar analysis accounts for the configurational learning displayed by Sutton’s (2002) pigeons, who ignored any single landmark that was displaced relative to the other three. Sutton’s training conditions, with two configurations composed of the same landmark elements, encouraged the encoding of entire configurations of landmarks. Given configurational learning, the displaced landmark should have been seen as highly discrepant and hence likely to have been wrong and given little weighting.

Relying on a single kind of cue in case of large discrepancies is reminiscent of the “take the best” strategy in human decision making (Hutchinson & Gigerenzer, 2005). In this strategy for making binary decisions, cues or predictors are checked one at a time in some hierarchical order. The first predictor to differentiate between two choices decides the case. The rest of the information in the hierarchy of predictors is ignored. “Take the best” works well in noncompensatory environments, in which each cue is much better than the next one in the hierarchy. In compensatory environments, in which the predictive powers of cues are more even, it is usually better to include all cues in some weighted fashion. Such a strategy is reminiscent of the integration of multiple sources of information. An analogy is clear, but it is unclear how far the parallels can be pushed.

Further Research

It would be overly optimistic to suppose that the Bayesian framework that we have outlined will account for all phenomena of integration of spatial cues. However, it does suggest some lines of research to pursue. As illustrated in the psychophysical experiments described at the beginning of this article, the variance associated with each cue is crucial to a Bayesian analysis. In animal navigation and in human locomotion, systematic data of this kind have rarely been collected alongside data on how different spatial cues are combined at different degrees of discrepancy. For example, desert ants are known to use a sky compass (Wehner, 1994) and landmarks along a route (Kohler & Wehner, 2005; Wehner et al., 1996) to navigate home. If the two cues point to the same direction home, do ants integrate both cues, and is the integration close to optimal? In addition, one can ask similar questions about rats using, for example, landmark and inertial cues for determining direction (see Cheng & Newcombe, 2005, Figure 5). In the case of human locomotion, the advent of virtual technology spells an unparalleled degree of control over visual cues, including dynamic cues. The same technology allows humans to move, using a joystick, without receiving bodily cues. Virtual reality would seem to make an excellent tool for examining the use of multiple cues in human locomotion, including cues from different modalities.

Our review of studies on both animal navigation and human psychophysics highlights the question of what happens when two cues point to very discrepant locations. The role of discrepancy has not been systematically studied in psychophysical experiments. In cases when two cues are perceived as stemming from two stimuli, do the reliability of the cues and the variances associated with them justify the conclusion on statistical grounds, as we have supposed? Encompassing studies that vary discrepancies to examine this issue would make a theoretically important enterprise, for both spatial perception and navigation.

Conclusions

Predictions of Bayesian performance in behavior are functional predictions. Given the reliability of various sources of information, a Bayesian approach prescribes optimal use. As Equations 1 and 2 show, the requisite calculations do not seem demanding computationally, but they do require that spatial parameters of any kind come with measures of both central tendency and variance. The navigational literature concentrates markedly more on central tendency than on variance. In contrast, the field of robotic navigation is seriously concerned with variance and uncertainty (Thrun, 2000). The Bayesian framework, right or wrong, suggests that mechanistic analysis of how variance is perceived and computed would be a worthwhile endeavor. This analysis might give insight into how animals might manage or fail to be optimal in integrating multiple sources of information.

The generality of the Bayesian principles suggests that they might apply to other areas than navigation. Communication is a prime example, far too big to even summarize here. Indeed, some recent theoretical analyses connect with Bayesian principles of maximum likelihood, in foraging (Baddeley, Osorio, & Jones, 2007; Lynn, Cnaani, & Papaj, 2005) and in mate choice (Phelps, Rand, & Ryan, 2006). We suggest that psychology can benefit from taking aboard quantitative functional analyses, Bayesian or otherwise.

References


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