

Methods

We used standard culture methods for protists to establish simple microbial food chains in microcosms⁴. Treatment of *Colpidium* with a penicillin–streptomycin–neomycin solution eliminated the bacterial assemblage of the stock culture. In experiment 1 we used 12 nutrient levels, ranging from 0.018 to 0.5 g protozoan pellet per litre of well water, evenly spaced on a log scale, with two replicates of each treatment. The ‘*Serratia* alone’ combination ran for 33 days in 15 ml filtered protist pellet medium in 20-ml screw-cap test tubes. *Serratia* was plated every four days during the initial part of the experiment (days 5–17) and every eight days thereafter. Removal and replacement of 4% of the medium every four days renewed nutrients. Counts of *Colpidium* at four-day intervals used a 0.25-ml (± 0.06 ml) subsample from the removed medium. The ‘*Serratia* + *Colpidium*’ combination ran for 25 days, or ~ 100 *Colpidium* generations.

In experiment 2 we used six nutrient levels ranging from 0.0015 to 1 g protozoan pellet per litre of well water, evenly spaced on a log scale, with two replicates of each treatment. Treatment of *Colpidium* with a penicillin–streptomycin–neomycin solution eliminated all but one bacterial contaminant. Antibiotics could not be used to eliminate bacteria from *Didinium* stock cultures because of toxicity. Food-chain combinations ran for 40 days in 100 ml unfiltered protist pellet medium in 250-ml screw-cap Erlenmeyer flasks. Bacteria were plated three times during the experiment for the two- and three-level combinations and four times for the one-level combination. Removal and replacement of 5% of the medium every four days renewed nutrients. Counts of protists at four-day intervals used a subsample of 0.1–3.5 ml (*Colpidium*, subsample size depended upon protist density) or of 0.2–4.6 ml (*Didinium*) from the medium withdrawn for nutrient replacement.

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Terrain influences the accurate judgement of distance

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Mathematically, three-dimensional space can be represented differently by the cartesian, polar, and other coordinate systems. However, in physical sciences, the choice of representation system is restricted by the need to simplify a machine’s computation while enhancing its efficiency¹. Does the brain, for the same reasons, ‘select’ the most cost-efficient way to represent the three-dimensional location of objects? As we frequently interact with objects on the common ground surface, it might be beneficial for the visual system to code an object’s location using a ground-surface-based reference frame². More precisely, the brain could use a quasi-two-dimensional coordinate system (x_s, y_s) with respect to the ground surface (s), rather than a strictly three-dimensional coordinate system (x, y, z), thus reducing coding redundancy and simplifying computations^{2–5}. Here we provide support for this view by studying human psychophysical performance in perceiving absolute distance and in visually directed action tasks^{6–11}. For example, when an object was seen on a continuous, homogeneous texture ground surface, the observer judged the distance to the object accurately. However, when similar surface information was unavailable, for example, when the object was seen across a gap in the ground, or across distinct texture regions, distance judgement was impaired.

The idea of representing space using the ground surface as the reference frame is fundamental to the ‘ecological approach to space perception’ pioneered by J. J. Gibson². A vital prediction of Gibson’s ‘ground theory’² is that, when the common ground surface is disrupted, the visual system is unable to establish a reliable reference frame and consequently fails to obtain correct absolute distance. To test this theory, we placed a target at the other side of a gap in the ground surface (0.5 m deep and 1.3 m wide) from a naive observer, whose task was to judge the absolute distance of the target from himself (Fig. 1a). Then he was blindfolded or asked to shut his eyes, turned 90° away, and instructed to walk a distance equivalent to the remembered absolute distance of the target. Ten observers participated and the average distance walked was 4.60 ± 0.12 m (Fig. 1a), which was significantly farther than the target’s physical distance, 3.66 m ($t(9) = 8.2, P < 0.001$). As a control, we tested five observers over the same physical distance on a continuous surface (with no gap) and found that the average distance walked was 3.69 ± 0.12 m (Fig. 1a), in close agreement with the target’s physical distance from the observer ($t(4) = 0.3, P > 0.05$).

We then determined whether the common ground surface, in addition to affecting visually directed action, also influences conscious distance perception. We asked five naive observers to judge the absolute distance of a target under similar viewing conditions, and then to perceptually set the distance of a matching target to be at an equal distance. We found that the average matched distance was 4.24 ± 0.6 m when the target was seen across a gap (Fig. 1a) indicating that the observers overestimated the absolute distance ($t(4) = 10.2, P < 0.001$). Conversely, the average matched distance for the continuous surface condition was 3.54 ± 0.07 m (Fig. 1a), which was very close to the physical distance, 3.66 m ($t(4) = -1.44, P > 0.05$). The resemblance between the perceptual matching results and the blindfolded-walking results indicates that the inaccuracy in absolute distance judgement on a discontinuous

surface occurs for both tasks¹². This implies that the internal representation of space, which is based on the common ground surface, is used for both space perception and visually directed performance^{11,13}.

To test the ground theory further, we repeated both the blindfolded walking and the perceptual matching tasks under more stringent conditions. The gap size was now widened to 4.1 m and deepened to 2.0 m (Fig. 1b). Consistent with earlier results, the observers ($n = 8$) also overestimated the distance to target under the gap condition ($t(7) = 5.03$, $P < 0.01$ (walking); $t(7) = 12.4$, $P < 0.01$ (perceptual matching)), and performed quite accurately in the continuous surface condition ($t(7) = -0.32$, $P > 0.05$ (walking); $t(7) = 0.24$, $P > 0.05$ (perceptual matching)).

In all, our results provide evidence for the role of the common ground surface in accurate absolute distance judgement. But what depth cues on the common surface are used to establish its reference frame? As blindfolded walking can be accurate up to 12 m on a continuous ground surface⁷⁻¹⁰, we proposed that the texture gradient of size could be among the likely cues for providing quantitative distance information¹⁴. To test this possibility, we began by consulting a distance/texture model⁵ which states that,

with some approximation, the perceived absolute distance, Z , equals $(H \times G)/3$, where H is the observer's eye height relative to the ground surface, and G is the local texture gradient of size on the ground at the target's location. If the brain uses this strategy, the perceived absolute distance on the common ground surface should depend on both H and G .

To determine the impact of H on perceived absolute distance, our naive observers stood on an elevated ground surface and estimated horizontal distance of a target placed on a lower ground surface (dashed arrow, Fig. 2a). Eight observers performed the blindfolded-walking task while five observers performed the perceptual distance matching task. Their results show overestimation (Fig. 2a, diamond and circle symbols, respectively).

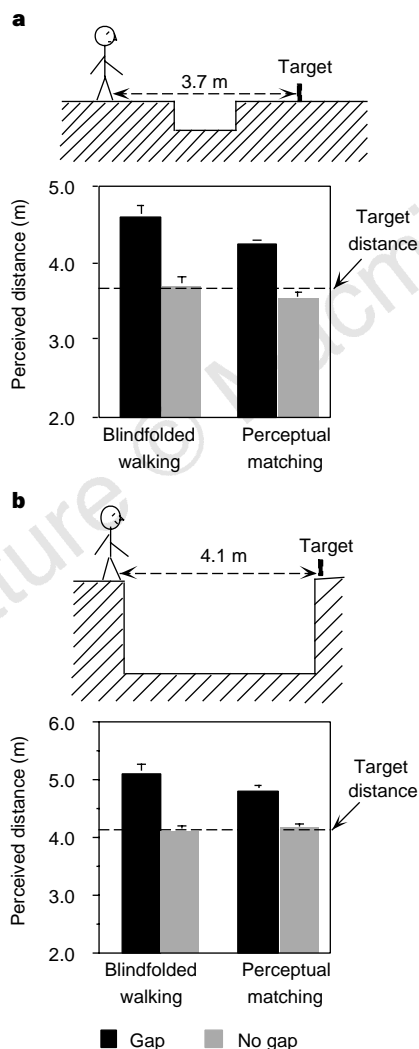


Figure 1 The effect of surface discontinuity (gap) on perceived absolute distance. **a**, A gap in the ground 0.5 m deep and 1.3 m wide separates the target and observer. **b**, The gap was increased to 2.0 m deep and 4.1 m wide. The graph below each illustration plots the average results from the blindfolded-walking and perceptual matching tasks for that condition. The black bars represent the data from the gap condition, and the grey bars data from the control condition, in which the ground surface was continuous (no gap).

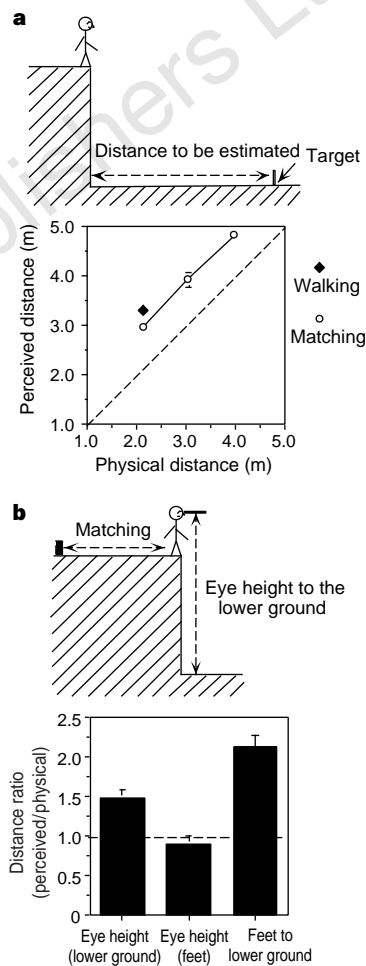


Figure 2 Eye height and surface elevation. **a**, The effect of elevated ground surface on distance perception. The observer stood on the elevated ground surface (2.0 m from the lower ground surface) and estimated the distance of the target, placed on the lower ground surface, from him (arrow). The graph below plots the perceived distance as a function of the target's physical distance from the observers for the blindfolded walking (diamond) and perceptual matching (circle) tasks. Distance overestimation is evidenced by the fact that the data points are located above the dashed line, which demarcates equal physical and perceived distances. The standard error of each data point is represented by the vertical error bar. (Error bars are not shown when they are smaller than the symbol.) **b**, Perception of eye height. The illustration shows the perceptual matching task for measuring the eye height with respect to the lower ground surface. The average result (ratio of matched distance to physical height) is depicted by the left bar in the graph. The middle bar represents the ratio of the eye height with respect to the feet to the physical distance (illustration not shown), and the right bar represents the ratio of the perceived elevated height (feet to the lower ground) to the physical distance (illustration not shown).

A likely source of the overestimation could be related to an exaggeration of the observer's perception of the eye height with respect to the lower ground level, H . To study this possibility, we asked five naive observers to stand on the higher ground surface and to perceptually set the distance of a matching target to equal their perceived eye height to the lower ground surface (Fig. 2b). As predicted, the observers overestimated their eye heights with respect to the lower ground surface (left bar, Fig. 2b, $t(4) = 3.72, P < 0.05$). Then we used the same procedure to measure the observers' perception of their eye height with respect to their feet, and found that their estimations were reasonably accurate (middle bar, Fig. 2b, $t(4) = -0.96, P > 0.05$). We also measured the observers' perception of the distance between their feet level (on the elevated ground) and the lower ground surface (2.0 m), and found that they overestimated the distance (right bar, Fig. 2b, $t(4) = 7.5, P < 0.001$).

These results are consistent with our assumption that the distance overestimation seen in Fig. 2a is due to the observers' overestimation of their eye height with respect to the lower ground surface (H). These observations add support to the idea that the observer's eye height provides information necessary for distance judgement^{5,15,16}. It is likely that the adult observer's eye height with respect to the ground, being a constant most of the time, leads the visual system to internalize it as implicit knowledge (a yardstick).

Finally, we studied the influence of texture gradient information on absolute distance judgement. We used a viewing condition in which the ground surface between the observer and target had two distinct texture regions, namely, concrete and a grass field (Fig. 3). The observer stood on the concrete field and pre-viewed the target on the grass field, and then performed the blindfolded-walking task. We measured four different absolute distances. For each absolute distance, the width of the grass field was kept constant at 3.05 m while the width of the concrete field was varied (0.61–4.56 m). The observers ($n = 10$) tended to underestimate the absolute distance as the distance between the observer and target increased (white

circles, Fig. 3). In separate control experiments, we tested observers ($n = 5$) on a homogeneous (grass only or concrete only) texture surface, and found that their average blindfolded walking performance was quite accurate (squares and black circles, Fig. 3). Indeed, the results of these control experiments are consistent with the ground theory.

Then to confirm that the underestimation was not due to the viewing direction being from the concrete field, we repeated the experiment with the observers ($n = 5$) standing on the grass field and viewing the target placed 5.79 m away on the concrete field. Here, too, the observers underestimated the absolute distance by almost the same magnitude (triangle, Fig. 3). This indicates that the underestimation errors are not due to the concrete texture region having a different grain size from the grass texture region. Lastly, to determine whether this inaccuracy in absolute distance judgement also occurs in perception, observers ($n = 5$) performed the perceptual distance matching task at an absolute distance of 7.62 m, while viewing from the concrete to the grass field. On average, the observers underestimated the absolute distance (diamond, Fig. 3). Overall, these results indicate that texture discontinuity causes errors in absolute distance judgement, both for perceptual and for visually directed tasks.

In summary, we have found that texture gradient of size, in addition to eye height, can influence judgement of absolute distance. This indicates that texture gradient on the ground surface acts as a depth cue for the visual system to establish a reference frame. However, whether the absolute distance, Z , is determined by the very specific interaction between eye height and texture gradient of size, $(H \times G)/3$, will require more quantitative studies. No doubt, there are other likely depth cues on the ground (for example, the angular declination below the horizon⁵) that can be used by the visual system for absolute distance computation^{2,5,14,17}. It would be interesting to learn how the various depth cues interact when confronted with diverse terrain conditions, such as those in Figs 1 and 3, to cause an observer systematically to overestimate and underestimate absolute distance, respectively.

More generally, our results support the proposal by J. J. Gibson that the common ground surface is used as a reference frame for coding the location of an object². This has significant biological implications because, as noted earlier, there are many ways in which spatial information can be encoded. The question is, which coding mechanism is the most cost-effective? In other words, what type of neural computation can best reduce coding redundancy and enhance overall efficiency²⁻⁵? If the purpose is, ultimately, to ensure the survival of the animal, we are compelled to argue that for terrestrial animals, such as humans, the use of the animal's natural niche, the ground surface, as a reference frame for encoding spatial information is a good start^{2,18}.

Methods

Observers. Twenty-two naive observers (sixteen males and six females) with self-reported normal vision gave informed consent and participated in the experiments on different days.

Viewing environment. All viewing conditions in daylight (parameters described in text) were carefully selected from the natural landscape within the University campus.

The blindfolded walking task. Because of our particular viewing conditions, we could not use the typical blindfolded walking paradigm used by others⁶⁻¹⁰. In a typical walking paradigm, the blindfolded observers would walk directly in the direction of the target, whereas in our modified paradigm the observers were asked to turn 90° away before walking the remembered distance. To establish the validity of our modified paradigm, we first tested ten naive observers (who were either blindfolded or instructed to shut their eyes) in pilot experiments, to compare their performances in both paradigms. For the three distances tested, 6.04 m, 8.08 m and 10.58 m, the corresponding average distances walked were 5.90 ± 0.07 m, 7.85 ± 0.17 m and 9.83 ± 0.16 m, respectively, for the typical blindfolded-walking task, and 5.82 ± 0.10 m,

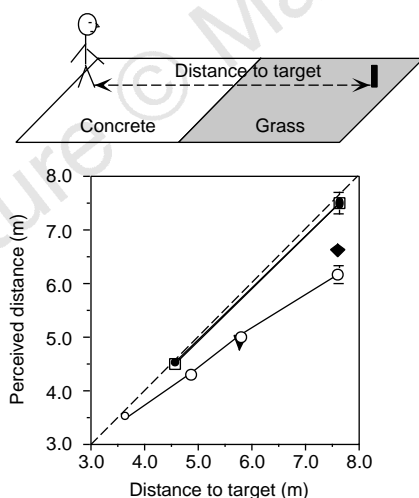


Figure 3 The effect of texture discontinuation on distance perception. White circles represent the distances walked when the observer stood on the concrete field and viewed the target placed on the grass field, as shown in the illustration. The width of the grass field was constant while the width of the concrete field was variable (0.61–4.57 m). The diamond depicts the average result for a perceptual matching task under this viewing condition for a target distance of 7.62 m. The triangle represents the distance walked when the viewing condition was changed so that the observer stood on the grass and viewed the target on a concrete field (viewing distance 5.79 m). In all, the observers showed underestimation of distance (their data being below the dashed line which demarcates equal physical and perceived distances). The filled circles and open squares represent the blindfolded-walking data obtained from the control conditions, under which the common ground surface consisted of homogeneous concrete or grass field, respectively.

7.92 ± 0.12 m and 9.68 ± 0.19 m, respectively, for the modified blindfolded-walking tasks. The similarity between the results obtained from both types of walking task indicates that our modified walking task can also be used to accurately reflect the observer's distance judgement.

The perceptual matching task. The target viewing conditions were similar to those used for the walking task. To obtain the observer's perception of distance, the matching target was placed 90° from the observer. The observer's task was to view the test target, then turn toward the matching target and instruct the experimenter to adjust the location of the matching target until it appeared to be at the same distance from him as the test target.

Each observer underwent a practice session before commencing the experiments. During the proper experiments, the observers were tested under the same condition two to three times, depending on the particular task. When more than one target distance was tested in an experiment, the order of testing was counterbalanced across observers.

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Shape selectivity in primate lateral intraparietal cortex

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The extrastriate visual cortex can be divided into functionally distinct temporal and parietal regions, which have been implicated in feature-related ('what') and spatial ('where') vision, respectively¹. Neuropsychological studies of patients with damage to either the temporal or the parietal regions provide support for this functional distinction^{2–4}. Given the prevailing modular theoretical framework and the fact that prefrontal cortex receives inputs from both temporal and parietal streams^{5,6}, recent

studies have focused on the role of prefrontal cortex in understanding where and how information about object identity is integrated with (or remains segregated from) information about object location^{7–10}. Here we show that many neurons in primate posterior parietal cortex (the 'where' pathway) show sensory shape selectivities to simple, two-dimensional geometric shapes while the animal performs a simple fixation task. In a delayed match-to-sample paradigm, many neuronal units also show significant differences in delay-period activity, and these differences depend on the shape of the sample. These results indicate that units in posterior parietal cortex contribute to attending to and remembering shape features in a way that is independent of eye movements, reaching, or object manipulation. These units show shape selectivity equivalent to any shown in the ventral pathway.

Previous studies of the parietal cortex that demonstrated its sensitivity to object shape have tended to focus on tasks involving hand manipulation of three-dimensional solid objects^{11–14}. Little attention, however, has been paid to the basic question of simple, two-dimensional shape selectivity in the parietal cortex. Here we test directly the extent to which units in the lateral intraparietal area (LIP) in posterior parietal cortex respond to differently shaped, two-dimensional visual stimuli that the animal did not and could not manipulate.

We recorded from 124 isolated neurons in area LIP of two macaque monkeys. The monkeys were trained to perform a simple fixation task. After the animal fixated a central spot, a shape was briefly presented within the receptive field of the unit being recorded. We recorded the activity of 74 of the 124 neurons while the animal performed this fixation task. Surprisingly, many units (42 of 74, 57%) showed a significant difference in activity during the stimulus presentation, which was dependent on which of eight shapes was presented (Fig. 1).

We calculated a shape-selectivity index (SI) for each unit using the average rate of firing for the stimuli that produced the strongest and weakest responses ($SI = (\max - \min)/(\max + \min)$). The histogram in Fig. 2 shows the distribution of indices, with units that show significant differences in responses to different shapes being indicated in black. The median of the indices for these significant units corresponded to a response that was 2.5 times stronger for the most-preferred (best) relative to the least-preferred (worst) shape (median SI = 0.43).

This shape selectivity is unlikely to arise from accidental interactions between shape features and receptive-field profiles, because LIP receptive fields are typically large and homogeneous¹⁵. Nevertheless, to discount such accidental interactions, we tested some units using stimuli in different positions or of different sizes. For 6 of the 42 units with significant differences in response that were dependent on the shape of the stimulus, the same stimuli were presented at the same eccentricity in a second location. The polar angular difference between the first and second location ranged from 25 to 130 degrees depending on the size of the receptive field of the particular unit. There was good agreement between the shape selectivities in the two locations. For three of the units, the preferred shape or preferred two shapes in one location were the same in the second location. For the remaining three units, which were more broadly tuned, at least one or two of the three shapes with the strongest response agreed. In addition, the least-preferred one or two shapes in one location remained the same in the second location. For two units with significant sensitivity to shape, we recorded the activity of each unit when the size of the stimuli was increased by 50%. Each unit maintained its shape preference. These results indicate that shape selectivities in LIP units are not an accidental result of receptive-field profiles.

To test for shape-selective behavioural effects in area LIP, we trained the animals on a delayed match-to-sample task. After the monkey fixated a central spot, a sample shape was briefly presented in one of three eccentric locations. After a short delay (0.5–2.1 s),