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A geometric process for spatial reorientation in young children

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DISORIENTED¹⁻³ rats and non-human primates reorient themselves using geometrical features of the environment^{2,4-6}. In rats tested in environments with distinctive geometry, this ability is impervious to non-geometric information (such as colours and odours) marking important locations and used in other spatial tasks⁷. Here we show that adults use both geometric and non-geometric information to reorient themselves, whereas young children, like mature rats, use only geometric information. These findings provide evidence that: (1) humans reorient in accord with the shape of the environment; (2) the young child's reorientation system is impervious to all but geometric information⁸, even when non-geometric information is available and is re-presented by the child—such information should improve performance and is used in similar tasks by the oriented child; and (3) the limits of this process are overcome during human development.

All organisms that navigate must reorient themselves when they lose track of their position and heading. Although young children use non-geometric landmarks to locate objects when their sense of orientation is intact⁹⁻¹², no previous study has examined children's or adults' reorientation by geometric and non-geometric information or has compared these abilities with those of other species. In our experiments, subjects saw an object being hidden in a corner of a rectangular room and then were disoriented. Orientation was partially specified by the room's shape and fully specified in some conditions by non-geometric landmarks. Subjects demonstrated their ability to reorient themselves by locating the hidden object.

In experiment 1, university students were tested in an all-white room and in a room with one blue wall (Fig. 1). Unlike rats, human adults used the non-geometric landmark ($F(1, 14) > 35$,

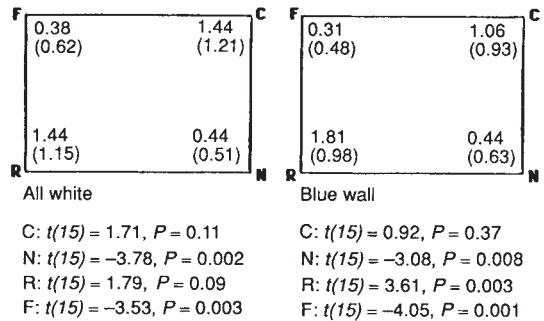
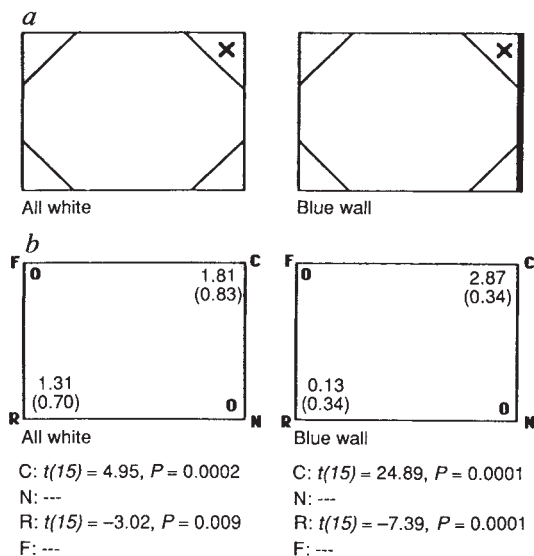


FIG. 2 Search patterns for experiment 2 with young children ($n = 16$, mean age 20.9 months). The experimental design, procedure and analysis were the same as before except that each child's parent (blind to our hypotheses) conducted the experiment from inside the chamber, hiding a toy brought from home. To disorient the children, parents lifted them, covered their eyes, turned at least 4 revolutions, and released them on cue from the experimenter facing a randomly pre-chosen wall. Care was taken to avoid subject dizziness and to ensure that parents did not cue subjects to any location. Only subjects completing 3 or 4 trials were included. Five additional subjects were eliminated for failure to complete 3 trials or for experimenter error; their data were similar to those of the other subjects. Subjects did not search the correct corner in the blue-wall condition more than the correct corner in the all-white condition ($t < 1$). The ANOVA revealed a significant effect of geometry ($F(1, 14) = 31.43, P < 0.001$) but no effect of condition, proximity or sex, and no significant interactions among these factors. No effect of training was found in the blue-wall condition by a Mann-Whitney test comparing subject accuracy in the first and last search trials, $P > 0.20$, despite the fact that children were rewarded for success on their first guess and corrected for failures. This suggests that children's search is not easily modified by feedback. A further experiment (manuscript in preparation) showed that children's failure to use non-geometric information for reorientation does not result from the disorientation procedure itself (Fig. 4 legend).

$P < 0.001$). In the white room, subjects exclusively searched the two geometrically appropriate corners, choosing the correct and rotationally equivalent corners equally often ($t(15) = 1.33$). These results indicate that the disorientation procedure was effective and that adults used the metric and sense properties of

FIG. 1 Testing conditions and search patterns for experiment 1 ($n = 16$). **a**, The enclosed rectangular 6.25 × 4 × 6.25-foot testing room was white, with lights centred above each wall, a concealed entry, 4-foot-tall red corner panels, and a bright blue 4 × 6.25-foot cloth covering (bold line). Subjects disoriented themselves by covering their eyes, inertially rotating at least 10 revolutions, and stopping on cue from the experimenter facing a randomly pre-chosen wall. A central overhead video camera recorded subjects' searches for subsequent coding by an observer blind to hiding location. A central overhead white-noise generator prevented subjects from orienting by use of any extraneous sound beacon. Hiding location, side of blue wall, order of search sessions, and subject sex were counterbalanced across subjects. Subjects completed 3 or 4 trials per condition with a single hiding location. **b**, Mean search frequency (and standard deviation) at each corner (C, correct; R, rotationally equivalent; N, near but geometrically inappropriate; F, far but geometrically inappropriate), and summary statistics for search at each position. For the single-sample *t*-tests, chance is 25% of mean search frequency per subject. All *P* values are two-tailed. Search frequencies at each corner were analysed by a 2(sex) × 2(condition: all-white or blue-wall) × 2('geometry': search at C and R versus N and F) × 2('proximity': search at C and N versus R and F) mixed-factor ANOVA. There were significant main effects of geometry and proximity, significant interactions of each of these effects with condition, and a significant three-way interaction of condition, geometry and proximity (all values of $F(1, 14) > 35, P < 0.001$), reflecting subjects' use of both geometric and non-geometric information to guide search in the blue-wall condition. Search at C in the blue-wall condition exceeded search at C in the white room ($t(15) = 4.58, P < 0.001$). For all other effects, including those involving sex, $P > 0.10$.

the room to reorient themselves. With the blue wall, search at the correct corner exceeded search at its rotational equivalent ($t(15) = 16.10, P < 0.001$). Use of this landmark surpassed mature rats' use of olfactory and visual landmarks in a similar study².

In experiment 2, children aged 18–24 months completed the same task (Fig. 2). In the white room, children searched geometrically appropriate corners ($t(15) = 4.77, P < 0.001$) and searched the correct corner and its rotational equivalent equally often ($t(15) < 1$). Unlike adults, children showed the same search patterns with the blue wall (all $F(1, 14)s < 2$). Although they searched geometrically appropriate corners ($t(15) = 3.88, P < 0.001$), they did not search the correct corner more than its rotational equivalent and did not search the two appropriately coloured corners more than the other corners (all $ts < 1$). Children's choice of the correct corner in the landmark condition differed from that of adults in experiment 1 (unpaired $t(30) = -7.05, P < 0.001$) and was comparable to that of rats tested under similar conditions ($\bar{X}_{rats} = 0.35, \bar{X}_{children} = 0.31$) (ref. 2).

Experiment 3 investigated whether children could use solid objects as landmarks and benefit from a more elaborate attention-drawing procedure. Subjects participated in two search sessions with non-geometric landmarks (Fig. 3). Before the first session, the experimenter pointed out the landmark(s) to be used in that session. Before the second session, the child and parent played with the landmarks before placing them in the room together with the experimenter. Again, children failed to use the landmarks to reorient themselves.

Further analyses tested whether children failed to use non-geometric information because of a tendency to search corners within their visual field immediately after disorientation. Comparisons of search at either of the two immediately visible corners with search at either of the opposite corners revealed no difference in search rates for either condition (each $t < 1$). After disori-

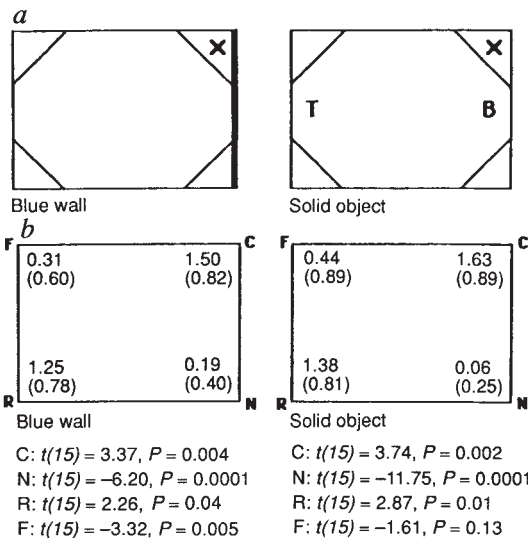


FIG. 3 Testing conditions and search patterns for the children ($n = 16$, mean age 21.2 months) in experiment 3. a, The design, procedure and analyses were the same as in experiment 2 except that children were tested once with the blue wall and once with a toy truck (T) and bear (B) with similar global dimensions, placed in symmetrical locations within the room (see text for description of procedures for drawing children's attention to the landmarks). b, Mean search frequencies (and standard deviations) for each landmark condition, collapsed across attention-drawing procedures. The analysis revealed a significant effect of geometry ($F(1, 14) = 41.34, P < 0.001$), an effect of proximity \times geometry ($F(1, 14) = 6.67, P = 0.02$), and no other effects (all values of $F < 1$). Planned contrasts revealed significant effects of geometry for both attention-drawing procedures (each $t(15) > 5.7, P < 0.001$).

entation, children often looked about the chamber before searching, but their choice was unaffected by non-geometric information.

Finally, in experiment 4 we investigated whether children's search errors resulted from a perceptual salience hierarchy favouring geometric over non-geometric information, by comparing children's performance on two search tasks (Fig. 4). In the reorientation task, two visually distinct containers appeared in diagonally opposite corners of the room, the object was hidden in one container, and the child was disoriented before search. In the other task, the containers were placed at the room's centre, the object was hidden inside one container, the child closed her eyes but remained oriented, and the containers were moved to the corners before search. Both tasks therefore presented the same object search demands in the same environment, but only the first task required that children reorient themselves. Disoriented subjects searched equally at the two corners, but subjects whose orientation remained intact searched the correct corner more often than its rotational equivalent. Performance in the two conditions differed reliably ($F(1, 28) = 17.51, P < 0.001$), suggesting that encapsulation of the favour's reorientation process, and not a salience hierarchy favouring geometric cues, accounts for children's search failures.

In summary, young children oriented themselves by analysing the shape of the environment. They failed to orient themselves in

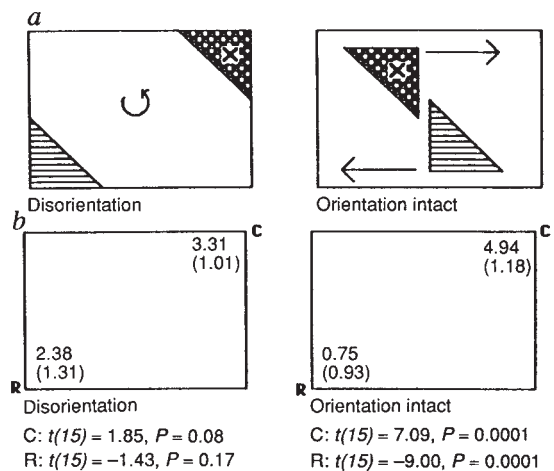


FIG. 4 Conditions and search patterns for the disorientation and orientation-intact tasks (each $n = 16$; mean ages 21.1 and 21.3 months respectively; 5 additional subjects failed to complete the experiment). a, Each child participated in one 4–6-trial search session in the white room with two triangular-solid containers of the same dimensions but different patterns (stripes or dots) and colours. The left diagram depicts the search environment throughout the disorientation task and at the end of each orientation-intact trial. The right diagram depicts the environment at the start of each orientation-intact trial. After the object was hidden, subjects' eyes were closed, facing the same direction as disoriented subjects at the end of disorientation, and the containers were moved to the corners as shown. b, Search patterns as before. The data from experiment 4, analysed using a $2(\text{sex}) \times 2(\text{condition}) \times 2(\text{location})$ ANOVA, revealed a significant interaction of condition and location ($F(1, 28) = 17.15, P < 0.001$) and no other significant effects (all P values > 0.10). Planned comparisons revealed significant effects of choosing $C_{(\text{orientation-intact})}$ more than $R_{(\text{orientation-intact})}$, of choosing $C_{(\text{orientation-intact})}$ more than $C_{(\text{orientation})}$ and of choosing $R_{(\text{disorientation})}$ more than $R_{(\text{orientation-intact})}$ (all values of $t(15) > 4.2, P < 0.001$). In the disorientation condition, choice of C did not exceed choice of R ($P > 0.20$). A further study showed that children can remember and use non-geometric information to find an object after they are disoriented, provided the information does not serve as a cue to reorientation. Subjects were disoriented as in experiment 4, brought outside the testing room with the two containers, disoriented further, and asked to find the object; they reliably chose the container with the appropriate non-geometric markings.

accord with non-geometric landmarks that could have improved their performance, even though most children turned and inspected the room before searching and used the same landmarks in a different search task. These findings provide evidence for a common shape-based orientation mechanism in humans and other mammals and for informational encapsulation⁸ in the child's mechanism.

In contrast to young children and mature rats, human adults conjoined geometric and non-geometric information to reorient themselves. Their performance suggests that some representational systems become more accessible and flexible over development and evolution^{13,14}. Studies of the mechanisms underlying the increase in flexibility for reorientation may shed light on uniquely human capacities for problem solving. □

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An eye-specific G β subunit essential for termination of the phototransduction cascade

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HETEROTRIMERIC G proteins couple various receptors to intracellular effector molecules. Although the role of the G α subunit in effector activation, guanine nucleotide exchange and GTP hydrolysis has been well studied^{1–4}, the cellular functions of the G β subunits are less well understood^{5,6}. G $\beta\gamma$ dimers bind G α subunits and anchor them to the membrane for presentation to the receptor^{7–9}. In specific systems, the G β subunits have also been implicated in direct coupling to ion channels and to effector molecules^{10–19}. We have isolated *Drosophila melanogaster* mutants defective in an eye-specific G-protein β -subunit (G β e), and show here that the β -subunit is essential for G-protein–receptor coupling *in vivo*. Remarkably, G β mutants are also severely defective in the deactivation of the light response, demonstrating an essential role for the G β subunit in terminating the active state of this signalling cascade.

Genetic screening²⁰ for mutations in a photoreceptor-cell-specific G β subunit (G β e)²¹ isolated two alleles, *G β e¹* and *G β e²*. Both alleles have missense mutations which severely reduce the

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levels of the G β subunit (Fig. 1a). *G β e¹* has a tyrosine substituted for a cysteine at amino acid 293 and produces <0.5% of the wild-type levels of the G β subunit, whereas the *G β e²* allele has a glycine substituted for a glutamate at residue 288 and produces ~5% of wild-type protein levels.

When whole-cell patch clamp recordings^{22,23} were used to analyse the electrophysiological response of the *G β e¹* and *G β e²* mutant photoreceptors to light stimuli, both G β alleles showed a dramatic loss of light sensitivity, *G β e¹* mutants showing a reduction of nearly two orders of magnitude (Fig. 1b). The kinetics of their photoresponse also differed markedly from that of wild

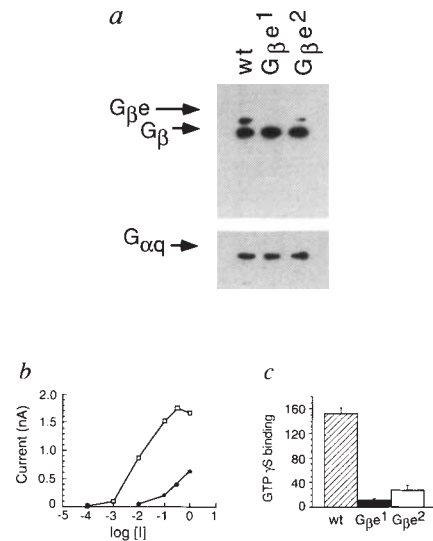


FIG. 1 a, Quantification of G β e protein levels. *G β e¹* = 0.4% \pm 0.2; *G β e²* = 4.6% \pm 5.7 (range 0.8–16%). Similar results were obtained using two different antibodies with two different specificities. G β and G α q refer to a brain-specific isoform of G β ³² and to the photoreceptor-cell-specific G α ²⁷. As neither mutation affected the levels of G β e transcripts (data not shown), the dramatic reduction of G β e levels in these missense mutants is probably due to the synthesis of misfolded or unstable proteins that are rapidly degraded in the cell. Neither G β mutation affected the expression of a photoreceptor-cell-specific G α subunit, or of several other molecules involved in the phototransduction cascade (data not shown). b, Intensity response functions for wild-type (*w¹¹¹⁸*) and mutant photoreceptors. Note that 100-fold stronger light was required to evoke a minimal current from *G β e¹* photoreceptors (closed circles) than from wild-type cells (open squares). Equivalent results were obtained from seven cells from each genotype. Photoreceptors were isolated and patch clamp recordings performed as previously described²². c, Blue-light-stimulated eye-specific GTP- γ S binding. Dark-adapted *Drosophila* head sections were stimulated with blue, 480-nm light (R \rightarrow M conversion) or red, 610-nm light (M \rightarrow R conversion). GTP- γ S binding to eye tissue was determined by autoradiography. In wild-type controls, GTP- γ [³⁵S] binds to target substrates in the compound eyes following blue light illumination which activates Rh1 rhodopsin. However, no retina-specific binding is observed following stimulation with red light (610 nm). *G β e* mutants showed dramatically reduced levels of blue-light-stimulated GTP- γ [³⁵S] eye-specific binding. Values shown indicate per cent of maximal wild-type response at saturating blue light intensity (*w¹¹¹⁸*, *n* = 9; *G β e¹*, *n* = 7; *G β e²*, *n* = 7).

METHODS. Cryostat sections (10 μ m thick), each containing ~40 fly heads on nitrocellulose filters (Schleicher and Schull BA85, 25-mm circles), were pre-flashed for 10 s with red light (Schott RG-610 filter) in 50 mM 4-morpholine propanesulphonic acid, pH 6.7, 5 mM MgCl₂, 2 mM 2-mercaptoethanol, 2 μ g ml⁻¹ pepstatin, 10 μ g ml⁻¹ leupeptin, 2 mM benzamide, 0.2 mM ATP. Sections were then stimulated with red or blue (Schott BG-28) test flashes in the presence of 96 nM GTP- γ S and 4 nM GTP- γ [³⁵S]. After the light flashes, the filters were incubated in the dark for 1 min and washed with 10 mM sodium phosphate, pH 7.5, 150 mM NaCl, 0.1% Tween-20, then with 0.1 \times SSC. Details of the procedure will be published elsewhere.