terminal tyrosine motifs that are critical for gp130 induction of STAT3 in transfected COS cells (*20*). The Y1-F mutation within the TG chimeric protein contains a substitution of Tyr^{759} with Phe. The EL construct contains wild-type LIFRβ cytoplasmic sequences (aa 834 to 1097) fused to the extracellular domain of the EGFR. The dY3-5 mutation contains a deletion of LIFRβ (aa 980 to 1097) that removes three COOH-terminal tyrosine motifs within LIFRβ that are critical for its ability to activate STAT3 in transfected COS cells (*20*). The EGt chimeric protein contains a truncation of gp130 (aa 758 to 918) and EGtY4 is an EGt protein with an appended tyrosine motif (Tyr-Leu-Pro-Gln) derived from Y4 in gp130. The mutations of gp130 and LIFRβ within the chimeric receptors have no effect on the amount of expression of the chimeric receptors (*23*).

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38. Indirect immunofluorescence was done as described (*27*).
39. Transfections were done as described [Z. Xia *et al.*, *J. Neurosci* **16**, 5425 (1995)].
40. In the experiments shown in Fig. 2A, the β-galactosidase signal was detected with a mouse monoclonal antibody to β-galactosidase (Promega) diluted 1:300, followed by a goat antibody to mouse immunoglobulin G (IgG) conjugated to Cy3 [Biological Detection Systems (BDS)]. The nestin signal was detected with a rabbit antiserum to nestin (1:5000) followed by a goat antibody to rabbit IgG conjugated to Cy2 (BDS). The GFAP signal was detected with a guinea pig anti-GFAP (Advanced ImmunoChemical) diluted 1:500, followed by a donkey antibody to guinea pig IgG conjugated to AMCA diluted 1:200 (Jackson ImmunoResearch).
41. Cortical cultures (E17 + 3 DIV) were transfected with a chimeric protein together with the GFAP luciferase reporter gene [containing 1876 nucleotides of the 5′ regulatory region of the GFAP gene fused to the luciferase gene in pGL3 (Promega)] and the EF-CAT plasmid (containing the bacterial chloramphenicol acetyltransferase downstream of the elongation factor 1α promoter) to serve as an internal control for transfection efficiency. Lysates of transfected cultures were left untreated or stimulated with the appropriate ligand [EGF (30 ng/ml) or NT-3 (50 ng/ml)] for 12 hours and were then analyzed for luciferase (Promega kit) and CAT (Dupont kit) activities. Induction with CNTF treatment was determined after luciferase activity was normalized with CAT activity in all transient expression assays in which the GFAP promoter was tested except in the case of transfections with the TG series of chimeric proteins because NT-3 was found to influence expression of the control EF-CAT gene.
42. Immunoprecipitations were done as described (*26*). Protein lysates were immunoprecipitated with an antiserum to JAK1 [Upstate Biotechnology, Inc. (UBI)], separated by SDS–polyacrylamide gel electrophoresis (PAGE), and immunoblotted with antibodies to phosphotyrosine (PY20) (ICN) and 4G10 (UBI). Antibody binding was detected by ECL (Amersham) with a secondary antibody conjugated to horseradish peroxidase. Protein immunoblot analysis was done as described [A. Bonni *et al.*, *Mol. Cell. Neurosci.* **6**, 168 (1995)].
43. The antibodies to phosphorylated STAT3 were generated as described (*37*).
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45. Similar results were obtained with the antibody to phosphorylated STAT3 (*15*). CNTF also induced STAT tyrosine phosphorylation in E14 + 0 DIV cortical cultures (*15*).
46. Northern blot RNA analysis was done as described [Y. Sun *et al.*, *Mol. Cell. Neurosci.* **7**, 152 (1996)].
47. DNA mobility-shift assays were done as described (*27*).
48. We thank Regeneron for providing recombinant rat CNTF; T. DeChiara, D. Ezzadine, and C. L. Cepko for the LIFRβ knockout mice; Amgen for bFGF and NT-3; R. MacKay for the rabbit antibodies to nestin; A. Frankfurter for the antibody to TuJ1; R. Vallee for the antibodies to MAP2; K. Nakajima and T. Hirano for the STAT3 plasmids; N. Moghal for the EF-CAT plasmid; E. Krebs for the pCDNA-3-MKK_{KA97} plasmid; D. L. Feinstein for GFAP cDNA; C. A. Walsh for the β-galactosidase–expressing retrovirus; T. D. Palmer and F. H. Gage for the GFP-expressing retrovirus; S. Vasquez for technical assistance; and D. Levy, G. Corfas, J. A. Loeb, T. Vartanian, G. D. Fischbach, B. A. Barres, and members of the Greenberg laboratory for helpful discussions and critical reading of the manuscript. Supported by an NIH RO1 grant (CA43855; M.E.G.) and an MRRC grant (NIHP30-HD 18655). Animal care was in accordance with institutional guidelines.

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Peripheral and Cerebral Asymmetries in the Rat

Nicholas P. LaMendola and Thomas G. Bever*

Rats learn a novel foraging pattern better with their right-side whiskers than with their left-side whiskers. They also learn better with the left cerebral hemisphere than with the right hemisphere. Rotating an already learned maze relative to the external environment most strongly reduces right-whisker performance; starting an already learned maze at a different location most strongly reduces left-whisker performance. These results suggest that the right-periphery–left-hemisphere system accesses a map-like representation of the foraging problem, whereas the left-periphery–right-hemisphere system accesses a rote path. Thus, as in humans, functional asymmetries in rats can be elicited by both peripheral and cortical manipulation, and each hemisphere makes qualitatively distinct contributions to a complex natural behavior.

Cerebral and peripheral sensory-motor asymmetries in humans have been a central theoretical topic in cognitive neuroscience for more than a century. Today's theories of asymmetries converge on three main ideas. First, asymmetries can involve a general hemisphere dominance for particular skills (*1*) [for example, left hemisphere (LH) specialization for language and right hemisphere (RH) for vision]. Second, asymmetries involve an attentional effect on the contralateral periphery (*2*) (for example, superiority for many language tasks in the right visual field and for many visual tasks in the left visual field). Third, although one hemisphere may be generally dominant for a particular behavioral domain, each hemisphere still contributes a specific kind of processing to it (*3*) (for example, in vision the left hemisphere accesses categorical information, and the right hemisphere accesses metric information). There may be a general computational basis for such functional hemispheric asymmetries. Recent network models have shown that computational systems perform better on complex problems if they segregate them into subproblems that differ in a natural way; this segregation occurs automatically in systems with partially segregated subsystems of different computational configurations (*4*).

The general computational view of the basis for asymmetries suggests that animals other than humans may have behavioral and cerebral asymmetries (*5*). Indeed, some birds and simians have unique mechanisms for specific communicative behaviors in the left hemisphere (*6*). The rat offers a useful case study for research relevant to the general basis for human asymmetries; rats are neither as biologically distant from humans as birds nor as close as simians. Individual rats, in fact, exhibit some neurophysiological and behavioral asymmetries (*7*); however, there is scant evidence that rats as a species have any behavioral asymmetries for natural complex behaviors (*8*).

Our first goal was to establish a popula-

N. P. LaMendola, Department of Psychology, University of Arizona, Tucson, AZ 85721, USA.
T. G. Bever, Program in Cognitive Science, University of Arizona, Tucson, AZ 85721, USA.
*To whom correspondence should be addressed.

tion asymmetry in a peripheral input system that the rat uses in normal behavior. In humans, such investigations typically use unilateral presentation of information to a sensory modality, such as visual field or ear. Whiskers are an important source of information for rats; they use whisker information to learn new pathways and environments, to discriminate textures, and to make depth judgments (9). Accordingly, this study manipulated access to information from the right and left sets of whiskers (RW and LW, respectively).

We used a laboratory instantiation of a foraging task—learning an eight-arm radial maze, in which the same five arms were always baited (10). The rats first became familiar with learning to find the five rewards in one such maze. After a rest interval of 10 days and with either the left whisker or the right whisker anesthetized, they learned another maze for 4 days. Rats with right whisker intact made fewer learning errors on the new maze than rats with left whisker intact (Fig. 1) (11). This performance asymmetry is an initial demonstration of a right peripheral superiority for a complex natural behavior.

We next used a direct manipulation of the cerebral hemispheres to show that there is a corresponding left hemisphere superiority. Rats were pretrained as before on an initial maze and given the same 10-day rest interval before they learned a new maze over 4 days. Twenty minutes before each daily session on the second maze, we induced a mild cortical spreading depression in one hemisphere. Rats with the left hemisphere intact made fewer errors than rats with the right hemisphere intact (Fig. 1) (12). This difference in errors establishes the fact that for this learning task there is a superiority of the left hemisphere.

The two results together converge on demonstrating a LH-RW system superiority over the RH-LW system for learning a foraging pattern (13). Accordingly, it appears that rat behavior has both a peripheral dominance and a corresponding contralateral cortical dominance (14).

Is the LH-RW system superiority over the RH-LW system merely quantitative or do the two systems access qualitatively different representations? To explore this issue, we adopted a widely accepted distinction between map-based and route-based representations of a learned foraging pattern. In the map representation, an allocentric, declarative map codes goal locations on the basis of their relation to landmarks (15). In the route representation, an egocentric, procedural rote route marks a fixed path from the starting location to each successive goal (16).

One aspect of the learning pattern suggests that the LH-RW system learns a map, whereas the RH-LW system learns a memorized route. The learning inferiority of the RH-LW system is primarily due to the relatively large number of working memory errors—reentering an alley where the reward had already been found and eaten (Table 1). This error pattern follows from the different options the two kinds of maze representations offer to an animal when it misses a baited alley. By hypothesis the LH-RW map system can find the missing alley by accessing a map representation of rewards, but the RH-LW route system can return to its rote path only from the beginning. The result is that the RH-LW system must reenter more alleys to find the missing reward, whereas the LH-RW system can

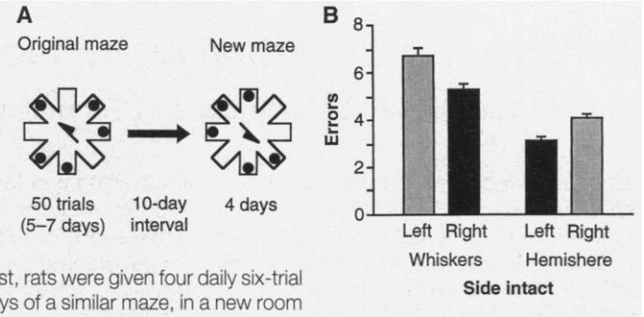

Fig. 1. Paradigm and performance on novel maze learning. (**A**) Rats were run in daily 30-min sessions for a total of 50 trials and were trained to find food in the same five alleys of an eight-arm maze (dots indicate food locations). A given rat was always started pointing at the same alley (indicated by arrow). After 10 days of rest, rats were given four daily six-trial blocks to find food in five alleys of a similar maze, in a new room and with a different baiting pattern. Immediately before each training session on the new maze, one set of 15 rats had the base of either the LW or the RW locally anesthetized (22); another set of 13 rats had either the LH or the RH briefly depressed by KCl (23). (**B**) The interaction of side intact by type of treatment was significant [$F(1,29) = 14.08$, $P < 0.01$] (24).

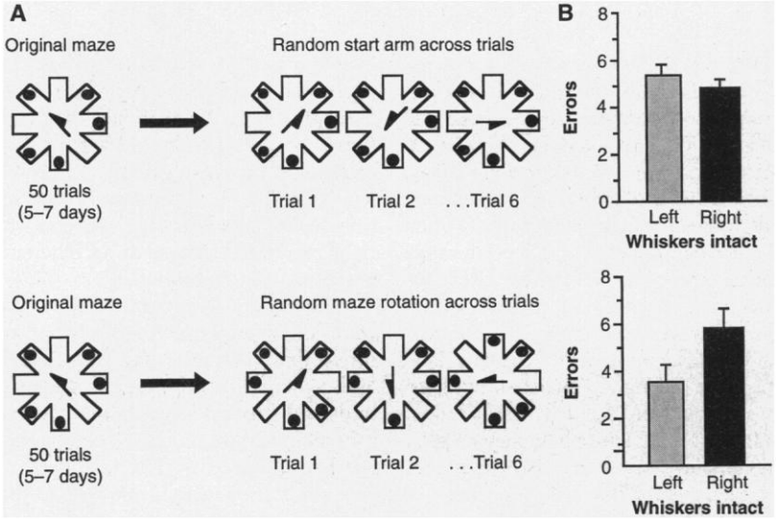

Fig. 2. Paradigm and performance on distorted mazes. (**A**) Intact rats were trained in daily 30-min sessions for 50 trials to find food in the same five alleys of a maze (dots indicate food locations). They were started at the same initial alley on every trial (indicated by arrow) (25). On the day after completion of the 50-trial training sequence, rats were run for a single six-trial session on the same maze, now distorted in one of two ways. For one group of 28 rats, the maze remained the same as it was during training, but the rat was repointed to start facing a different alley on each trial; for another group of 14 rats, the entire maze (and start alley) was pseudo-randomly rotated to a different position before each trial. Immediately before this session, the base of the LW or the RW was anesthetized (21). (**B**) The interaction of type of maze distortion by whisker side was significant [$F(1,40) = 13.85$, $P < 0.001$] (26).

Table 1. Number of different types of errors and adjacent alley choices in learning a new maze described in Fig. 1. Overall error rates were separated into reference memory errors (entering a never baited arm), and working memory errors (reentering an arm that had been baited at the beginning of the trial). The three-way interaction between treatment, side intact, and error type was significant [$F(2,60) = 4.53$, $P < 0.01$] (21).

Group	Reference memory errors	Working memory errors
LW intact	2.14	3.01
RW intact	2.09	2.14
LH intact	1.63	1.08
RH intact	1.87	1.59

more directly locate the missing alley.

We used the whisker-anesthetization technique with a two-part study to directly test the hypothesis that the LH-RW accesses a map and the RH-LW accesses a route. In each case, rats were trained on the same initial maze as before with both whisker sets intact. In the repointing condition, training continued for an additional day on the same maze, but on that day the rat was pointed at a different starting alley on every trial. Rats had their left whisker or right whisker anesthetized just before running on the additional day. Performance on the repointing condition start alley was better with the right whisker intact than with the left whisker intact (Fig. 2). This supports the view that the RH-LW system accesses a rote-route representation, which is more disrupted than a map representation by starting at a new alley.

In the maze-rotation condition, different rats had standard training on the initial maze, and training then continued for an additional day; however, on that day, the entire maze was randomly rotated to a new position before each trial. Rats again had their whiskers unilaterally anesthetized just before running on the additional day. Contrary to the repointing paradigm, performance on the rotated maze was worse in rats with the right whisker intact than in rats with the left whisker intact (Fig. 2). This supports the view that the LH-RW system accesses a map representation, which is disrupted more than a rote-route representation by reorienting the maze in the room space (*17*).

These findings have several implications for current research. At a practical level, they establish the rat as a potentially complete model of cerebral dominance, with contralaterally linked cortical and peripheral qualitative asymmetries that can be easily elicited. Second, although the hippocampus is the most carefully studied structure involved in spatial behavior in rats (*18*), our results demonstrate important differential roles of the neocortical hemispheres as well (*19*). Finally, our results confirm that even spatial behavior in the rat is not uniquely associated with one hemisphere or the other. Rather, the two hemispheres provide different kinds of representations of spatial tasks. This is consistent with the view that the hemispheres make different kinds of computational contributions to many behaviors in humans. It is specifically consistent with a recent differentiation of spatial tasks in humans, which showed that global and metric aspects of a spatial array are accessible in the right hemisphere, and specific local aspects and features are accessible in the left hemisphere (*20*).

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10. The maze was modeled after Olton [D. Olton, *Sci. Am.* **236** (no. 6), 82 (1977)]. It was 106.68 cm in diameter with a central area 45.72 cm in diameter; each 12.7-cm wide, 30.48-cm-long arm had 35.36-cm–high opaque walls and a unique cue roughly 58 cm^2 in area suspended about 25.4 cm above its entry, and mazes were located on a table in running rooms (1.83 × 1.83 m) with eccentric lighting sources near the 2.44-m-high ceiling. A baited arm had three Noyes 45-mg pellets in a 3.175-cm-deep, 3.81-cm-wide well at its far end. Thirty-two 90- to 120-day-old male Sprague-Dawley albino rats from Harlan Sprague Dawley, were run at 85 to 90% of their ad lib weight after about a week of daily handling. All animals were individually housed and cared for according to animal care guidelines at the University of Rochester and University of Arizona. A rat's initial response to the maze situation is sometimes emotional. We pretrained animals on an initial maze in part because prior research suggests the emotionality itself may be asymmetrical [V. H. Denenberg, *Behav. Brain Sci.* **4**, 1 (1981)]. We defined completely correct performance as entering each baited alley once and eating the food in it; entering a never-baited arm or reentering any arm was counted as an error. Performance on the initial maze was highly variable, but there were no significant correlations between number of errors on the training maze and on the second maze. The asymptotic error score for the last 10 trials on maze 1 were not significantly different in the four experimental groups. However, to further reduce the effect of interrat variability, we converted rats' performance on the second maze into standardized scores. The last 10 to 15 trials of the training maze determined the baseline mean number of errors and standard deviation for each rat. Each measure of errors on the second maze for the rat was converted to standard scores by using this mean and standard deviation. All statistical analyses of errors were done on these standard scores. Occasionally, rats just sit in a maze, which can distort overall analyses. We excluded the following trials from analysis: in the normal maze learning study, any trial longer than 10 min; in the distorted maze studies, any trial longer than 5 min. In all, fewer than 2% of trials were excluded; there was no relation between the number of excluded trials to unilateral conditions in any study.
11. Rats in each unilateral whisker condition learned the maze to some degree over the 4 days. Linear trend analysis showed improvement across 4 days: $F(1,6) = 16.71$, $P < 0.05$ for LW-intact rats; $F(1,7) = 11.75$, $P < 0.01$ for RW-intact rats. There was considerable variability on the second and third days, but a comparison of performance on the first and fourth days showed significant improvement for both LW-intact rats [$F(1,12) = 7.99$, $P < 0.01$] and RW-intact rats [$F(1,14) = 9.15$, $P < 0.01$].
12. Rats in each unilateral KCl condition learned the maze to some degree over the 4 days. Rats with the LH intact showed a significant descending linear trend [$F(1,6) = 16.71$, $P < 0.001$], as did RH-intact rats [$F(1,9) = 14.20$, $P < 0.001$]. In addition, the fourth-day performance was better than the first-day performance for LH-intact rats [$F(1,12) = 7.02$, $P < 0.01$] and for RH-intact rats [$F(1,18) = 18.51$, $P < 0.001$].
13. We also ran two groups of rats without any unilateral treatment while they learned the second maze. One group of six rats was subjected to the same Halothane procedure (*21*) as rats with anesthetized whiskers, but no lidocaine was administered; the other group of eight rats had cannulae surgically installed (*22*), but only saline-soaked pledgets were placed in both cannulae before each day's training. Both groups learned the second maze significantly better than rats in either anesthetized whisker condition and better than rats in the RH-intact condition. Both groups performed within 10% of rats in the LH-intact condition. These results suggest that the LH-intact rat and the untreated rat are accessing the same level of learning capacity. The very poor overall performance of rats in each anesthetized whisker condition may reflect aversion to having half the whiskers numbed; in contrast, prior research has suggested that KCl-induced cortical spreading depression is not aversive [V. I. Koroleva and J. Bures, *Neurosci. Lett.* **149**, 153 (1993)]. Another informative control condition would be to anesthetize both whisker sets. We tried this with four animals. They could move through the maze but had great difficulty in the last stages of locating the food rewards; the result was that they did not eat the rewards and so cannot be compared with rats in the other conditions.
14. Prior research suggests that rats adopt turning biases, which might interact with our unilateral intervention conditions [M. Ammassari-Teule and A. Caprioli, *Behav. Brain Res.* **17**, 9 (1985)]. About half the rats

turned predominantly right when they were exiting one alley and going into the next alley on the second maze. The data suggest that the LH-RW superiority is most strongly elicited in those rats that chose to turn right in the second maze. If future research confirms this trend, it will be consistent with our general claims. If the LH-RW system dominates the acquisition of a new maze, the animals are making most critical use of right-peripheral information, information that is most salient when they make a right turn to go to the next baited alley. A related issue is the possibility that each rat has an individual turn-direction bias, which interacts with the unilateral conditions. Our original study was not designed to control for this; rats were assigned to particular unilateral experimental conditions before they ran on the first maze. In fact, on the initial maze the 32 experimental animals exhibited a slight population bias to turn right when exiting from one alley and going into the next. However, there was no correlation between turning bias direction in maze 1 and performance in maze 2 either across all conditions ($r^2 = 0.06$) or within each of the experimental conditions. Also, by using turn bias on the initial maze as a measure, all unilateral conditions had about the same ratio of right-turning versus left-turning rats. The potential importance of a turning-bias confound prompted us to replicate the initial unilateral whisker study with explicit attention to turn bias and performance on the initial maze. We trained 16 rats on the initial maze as before. Then we assigned 8 rats to the LW- and 8 rats to the RW-anesthetized condition, so that each condition had the same proportion of rats showing a right-turn bias on the initial maze; we also arranged the two groups so that their asymptotic performance on the initial maze was within a few percentage points. The maze learning for 4 days showed the same pattern as in our original study. Rats in each condition learned the maze, but rats with RW intact learned the second maze with fewer errors than rats with LW intact. Also, in this study, more animals with LW intact failed to find all five rewards within the allotted time on a given trial.

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17. We also ran rats without any whisker anesthesia on the same paradigms. After they learned the initial maze, the rats were subjected to the same Halothane procedure as the whisker-anesthetized conditions (*22*) but without any unilateral anesthesia. In the repointed start alley condition, five bilaterally intact rats then performed better than rats with either unilateral whisker condition; this suggests that rats in both unilateral conditions are somewhat affected by a change in the start alley. In the maze-rotation condition, five bilaterally intact rats performed better than the RW-intact rats, but they performed the same as the LW-intact rats. This suggests that the intact animal can learn to ignore the maze rotation, whereas the isolated LH-RW system cannot.
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19. Many lesion studies support the role of the posterior parietal cortex [B. V. DiMattia and R. P. Kesner, *Behav. Neurosci.* **102**, 397 (1988)] and ventrolateral orbital cortex [J. V. Corwin, M. Fussinger, R. C. Meyer, V. R. King, R. L. Reep, *Behav. Brain Res.* **61**, 79 (1994)] in the processing of allocentric space and the medial agranular cortex [B. Kolb, in *The Cerebral Cortex of the Rat*, B. Kolb and R. C. Tees, Eds. (MIT Press, Cambridge, MA, 1990), pp. 437–458] and prefrontal cortex [R. P. Kesner *et al.*, *Behav. Neurosci.* **103**, 956 (1989)] in egocentric space.
20. M. Banich, *Neuropsychology: The Neural Bases of Mental Function* (Houghton-Mifflin, Boston, 1997), chap. 6; H. D. Brown and S. M. Kosslyn in *Brain Asymmetry*, R. J. Davidson and K. Hugdahl, Eds. (MIT Press, Cambridge, MA, 1995), pp. 77–97. At a general level, prior research suggests that spatial ability is dominant in the RH of humans, which appears to be the opposite of our findings in rats [B. Milner, *Neuropsychologia* **3**, 317 (1965); M. Habib and A. Sirigu, *Cortex* **23**, 73 (1987)]. However, almost all research on humans has been devoted to simple perceptual problems in external space instead of personal way finding. In fact, the LH has been implicated in Euclidian geometrical processing [L. Franco and R. W. Sperry, *Neuropsychologia* **15**, 107 (1977); E. DeRenzi, *Disorders of Space Exploration and Cognition* (Wiley, New York, 1982); Z. Mehta and F. Newcombe, *Cortex* **27** 153 (1991)], and both hemispheres contribute to personal way-finding skills [G. Ratcliff and F. Newcombe, *J. Neurol. Neurosurg. Psychiatr.* **36**, 448 (1973); E. J. Maguire, T. Burke, J. Phillips, H. Staunton, *Neuropsychologia* **34**, 993 (1996)].
21. The left-right contrasts for working memory errors were significant for whiskers [$F(1,13) = 7.94$, $P < 0.01$] and for hemisphere [$F(1,15) = 4.73$, $P < 0.05$] conditions. Contrasts in both conditions for reference memory errors were not significant. Note that reference memory errors plus working memory errors does not add up to the number of overall errors. This is because the overall error measure includes cases when the rat reenters an always unbaited arm; we omitted those from this differential analysis because such errors are simultaneously reference and working memory errors.
22. The procedure was adapted from the technique described in D. H. Thor and W. B. Ghiselli, *Psychol. Rep.* **33**, 815 (1973). The rat was first lightly anesthetized by inhalation of Halothane; then 0.2 ml of 2% lidocaine with epinephrine was subcutaneously injected into the mystacial vibrissal region on one side. The operational test for numbing the whiskers was that they stopped twitching. Each rat was always injected on the same side of the whiskers across all four daily experimental sessions. We unilaterally anesthetized the whiskers instead of shaving them because prior research showed that rats accommodate quickly to a permanent loss of whiskers: H. Milani, H. Steiner, J. P. Huston, *Behav. Neurosci.* **103**, 1067 (1989). We trained rats on the second maze for only 4 days because of concern that repeated injections would cause discomfort.
23. Before rats were trained on the initial maze, 6-mm cannulae with a 4-mm internal diameter were affixed above a 2-mm hole in the skull 3- to 4-mm off the midline, midway between lambda and bregma—roughly above the parietotemporal cortex. Thirty minutes before each daily second maze learning session, a cotton pellet soaked in a 6% KCl solution was placed on the dura in the cannula above one hemisphere, and a pellet with saline solution was placed in the other cannula [A. A. P. Leão, *J. Neurophysiol.* **7**, 359 (1944); B. Grafstein, *ibid.* **19**, 154 (1955)]. Prior studies characteristically used high KCl concentrations, at least 20%. We used a 6% solution to reduce the possibility of a motor hemiplegia or sensory neglect—all animals with KCl administered still performed the edge-paw placement test bilaterally and showed no sign of unilateral dysfunction. Recording of cortical electroencephalograms with two rats suggests that with our procedure the active depolarization period lasts 5 to 10 min. Thus, by the time rats ran in the maze, active depolarization may have been finished; the treated hemisphere may have been in a state of mild edema and consequent mild ischemia.
24. Rats with LW intact made significantly more learning errors than rats with RW intact [$F(1,13) = 8.05$, $P < 0.01$]. Rats with LH intact made fewer errors than rats with RH intact [$F(1,15) = 5.96$, $P < 0.01$]. Each of three distinct normal maze baiting patterns in maze 2 elicited the same overall superiority of the LH-RW system.
25. With the same initial maze as in the previous experiment, we tested 56 male Sprague-Dawley albino rats (90 to 120 days old) on a variation of the selectively baited radial maze task.
26. Rats with LW intact made marginally more errors than rats with RW intact when the starting position was changed on each trial [$F(1,26) = 2.20$, $P < 0.1$]. However, the difference for working memory errors alone was significant [$F(1,26) = 4.20$, $P < 0.05$]. Rats with RW intact made more errors than rats with LW intact when the maze was rotated to a new position before each trial [$F(1,12) = 4.05$, $P < 0.05$].
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