sequence of centrifugations: the homogenate was centrifuged at 30,000g for 15 minutes; supernatant fraction at 78,000g (Spinco Rotor 30) for 30 minutes; and the supernatant fraction at 105,000g (Spinco Rotor 40) for 2 hours. The pellet was resuspended in 1 to 2 ml of media containing sucrose and $MgCl_2$ in phosphate buffer with a motor driven pestle for 10 minutes; it was then clarified at 78,000g for 15 minutes. All isolation steps were carried out at 0°C. The resulting ribosomal suspension (0.5 ml) was placed on linear sucrose gradients prepared in Spinco SW 25.1 rotor tubes by the method of Britten and Roberts [*Science* **131**, 32 (1960)], and the tubes were centrifuged at 24,500 rev/min for 3 to 6 hours. All gradients contained 0.01 M potassium phosphate buffer (pH 6.4) and 6 mM $MgCl_2$ unless otherwise indicated. Optical density at 260 mμ was recorded continuously as the gradient solution was pushed out of the centrifuge tube with a sucrose solution of higher density and through a micro flowcell in a Beckman DU spectrophotometer.

8. We thank Dr. R. Doi and Dr. T. Hsiao for valuable suggestions, Dr. R. Criddle for the ultracentrifugations, J. Pangborn and K. Miyano for electron microscopy, and K. Fisher for technical assistance. This study was supported in part by AEC contract AT(11-1)-34, P.A. 112, Report No. UCD-34P112-27. L(L)K receives a graduate assistantship under the same contract.

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Navigation of Single Homing Pigeons: Airplane Observations by Radio Tracking

Abstract. *Navigation of homing pigeons was investigated by tracking their homeward flights from a light airplane. Released on successive days from a single training point 35 miles (56 kilometers) from home, individual pigeons, each carrying a transmitter, were repeatedly tracked back to their loft. No two tracks covered the same ground for even short distances, yet all tracks were within 10 miles of a straight line. Results from further releases north and south of the training point suggest that pigeons often use three methods in sequence to find home: compass orientation, bi-coordinate navigation, and orientation by familiar landmarks.*

How homing pigeons find their lofts is still obscure despite a long history of investigations (*1*). Since the work of Kramer and Matthews (*2*), it has been widely held that pigeons have the ability to navigate from any release point back to their home loft. Until now, however, there has been little direct information on the behavior of individual pigeons on their homeward flights. The visual following of flocks of pigeons from light aircraft by Griffin, Hitchcock, and Yeagley (*3*) yielded some data, but flock behavior is always some unknown consensus of the reactions of individual birds and is thus difficult to analyze meaningfully. Visual tracking of single pigeons was so difficult that they were not tracked far enough to provide much information. With accumulation of new data and new hypotheses (*4*), it has become increasingly important to know what paths single pigeons follow on their homeward trips. Radio tracking from light aircraft offered a way to obtain this information.

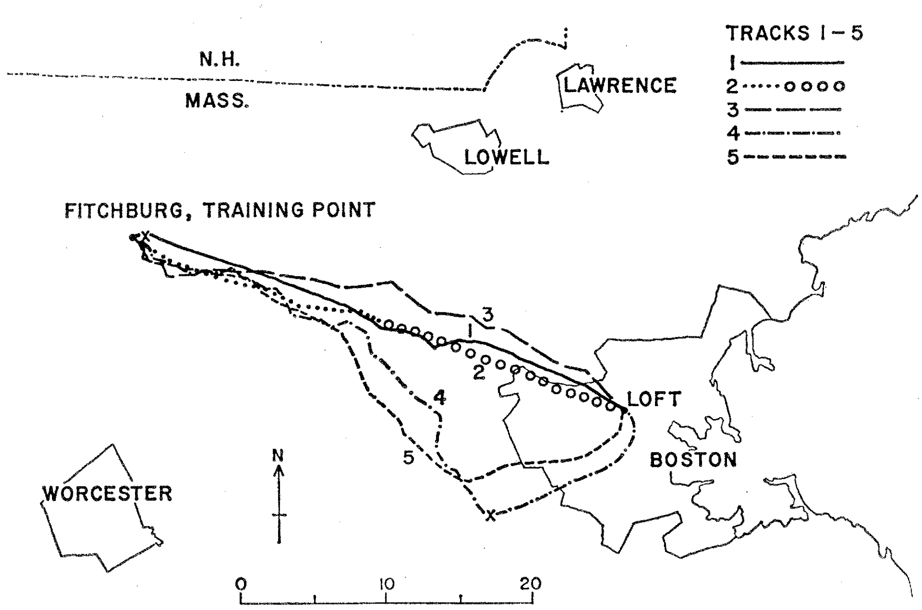

Fig. 1. The five consecutive tracks of Blue from Fitchburg made on the 16th through the 20th releases from the same place. Track No. 6, the 21st release from Fitchburg, was incomplete and is therefore omitted. Releases from Fitchburg in 1964: Track No. 1, 14 June, the 16th release; track No. 2, 18 June, the 17th; track No. 3, 19 June, the 18th; track No. 4, 23 June, the 19th; and track No. 5, 25 June, the 20th release. Sitting places are indicated by ×; open circles indicate area where bird was not followed.

During the summers of 1964 and 1965 we tracked ten individual homing pigeons on 131 flights from various release points to our Cambridge, Mass., loft. Each pigeon carried a 30-g, 52-Mcy transmitter, whose signal was followed with receivers in the airplane (*5*). We initially trained the pigeons by releasing them at increasing distances WNW of the loft until they had been released repeatedly from Fitchburg, Mass., 35 miles (56 km) WNW of the loft; and we compared the returning times of birds in these three categories: (i) birds with no load, (ii) birds with 2-g harness, and (iii) birds with harness plus a 28-g transmitter. On the average, birds wearing harness or harness plus transmitter homed more slowly than those with no load; yet the fastest homing times (when the birds flew home directly) in all three categories were comparable (30 to 40 mi/hr or 48 to 64 km/hr, average airspeed). Birds wearing harnesses were more likely to sit at the release point, but when they flew, their airspeed was the same as that of unharnessed pigeons. Loads up to 40 g seemed to have no effect on the pigeons' behavior aside from that caused by the harness alone.

Figure 1 shows five tracks made by Blue (color of the pigeon) on the 16th through the 20th releases from the Fitchburg training point. These were the only training releases of this pigeon that were followed. Four other birds were tracked on 31 of their releases, and Blue's five tracks are typical examples. The greatest deviation of any of the 36 tracks was 10 miles from a straight line connecting Fitchburg and Cambridge over the 35-mile course. The tracks in Fig. 1 show abrupt turns and the places where Blue sat. In all Fitchburg tracks, each bird seemed to start home most frequently when the airplane was farthest from the sitting place, which suggests that the tracking aircraft was disturbing the pigeon's flight. During these trackings, as with other Fitchburg flights, the airplane frequently came within 1/2 mile, or passed in front, of the pigeons, and, as seen on 20 occasions, the birds tried to avoid the plane by making sharp turns when it came overhead, by prolonged sitting when it was circling in the vicinity, or by stopping or making radical changes in course when it got ahead of them. Subsequently, we always kept the plane more than 1 mile behind the pigeon; although the bird was never seen at this distance, the tracks were straighter and these avoidance reactions were eliminated. Pigeons also spent less time sitting during each flight.

Unfortunately, the effect of the airplane was not discovered until the Fitchburg flights were almost completed, and thus the scatter of the Fitchburg tracks probably represents, in part, this effect. We repeated these releases in 1965 with improved tracking procedure and found that tracks of 13 releases from Manchester, N.H., 41 miles NNW of the loft, were all within 7 miles of a straight line from Manchester to the home loft; of 11 releases from Worcester, Mass., 40 miles WSW of the loft, all were within 3 miles of a straight line. This represents an angular error of less than 9 deg.

In these tracks from the training points, we observed that (i) strong winds did not blow birds to either side of the home course; (ii) tracks were no more scattered on days when atmospheric visibility was limited to 4 miles than when it was 40 miles; (iii) time of day of release did not affect the tracks; and (iv) there were no definite reactions to landmarks more than 5 miles from the loft.

Of 66 tracks made in 1964, 13 were flown under cirrus cloud overcast, through which the sun was visible, but the pigeons' behavior was the same under these conditions as it was when the sky was clear. The sun was not visible on 17 other releases; 6 of these were made from distant points (more than 35 miles from the loft), and, in every case, pigeons perched until the sun was visible again. The other 11 were from a nearer point (Bedford Airport, 10 miles WNW of the loft) from which the pigeons homed as quickly as they did on sunny days. On seven other releases from distant points, the sun was obscured intermittently during the tracks; pigeons flew only as long as the sun was visible and perched whenever the sun was obscured for more than 2 or 3 minutes. Results from a comparable number of flights in 1965 agree closely with those from 1964. Pigeons we studied refused to fly at all, if more than 10 miles from the loft, unless the sun was visible to a human observer. These results with single pigeons are in marked contrast to those of Griffin and Hitchcock (*3*), whose flocks of pigeons routinely homed under total overcast conditions.

Since our pigeons generally flew at the level of tree tops and since each track followed a different path, we suspect that none of the birds piloted by a fixed sequence of landmarks. Wide variations in atmospheric visibility did not affect the tracks; therefore the birds could not have been relying on distant landmarks (such as tall buildings). The only remaining way pigeons could have used landmarks, over most of the flight, to find the loft was to have known the area between Fitchburg and Cambridge so well that they were able to choose almost any course without losing sight of familiar objects, even when the visibility was less than 4 miles. The tendency, in all the pigeons we tracked, to sit for hours at a time whenever the sun was not visible suggests that the birds could not, in fact, use landmarks alone to find their way home.

Three of the five birds trained from Fitchburg were individually released and tracked from places north and south of Fitchburg. If the birds had learned to fly by landmarks alone, they should have been completely disoriented when released in unfamiliar territory. If they had been flying by some com-

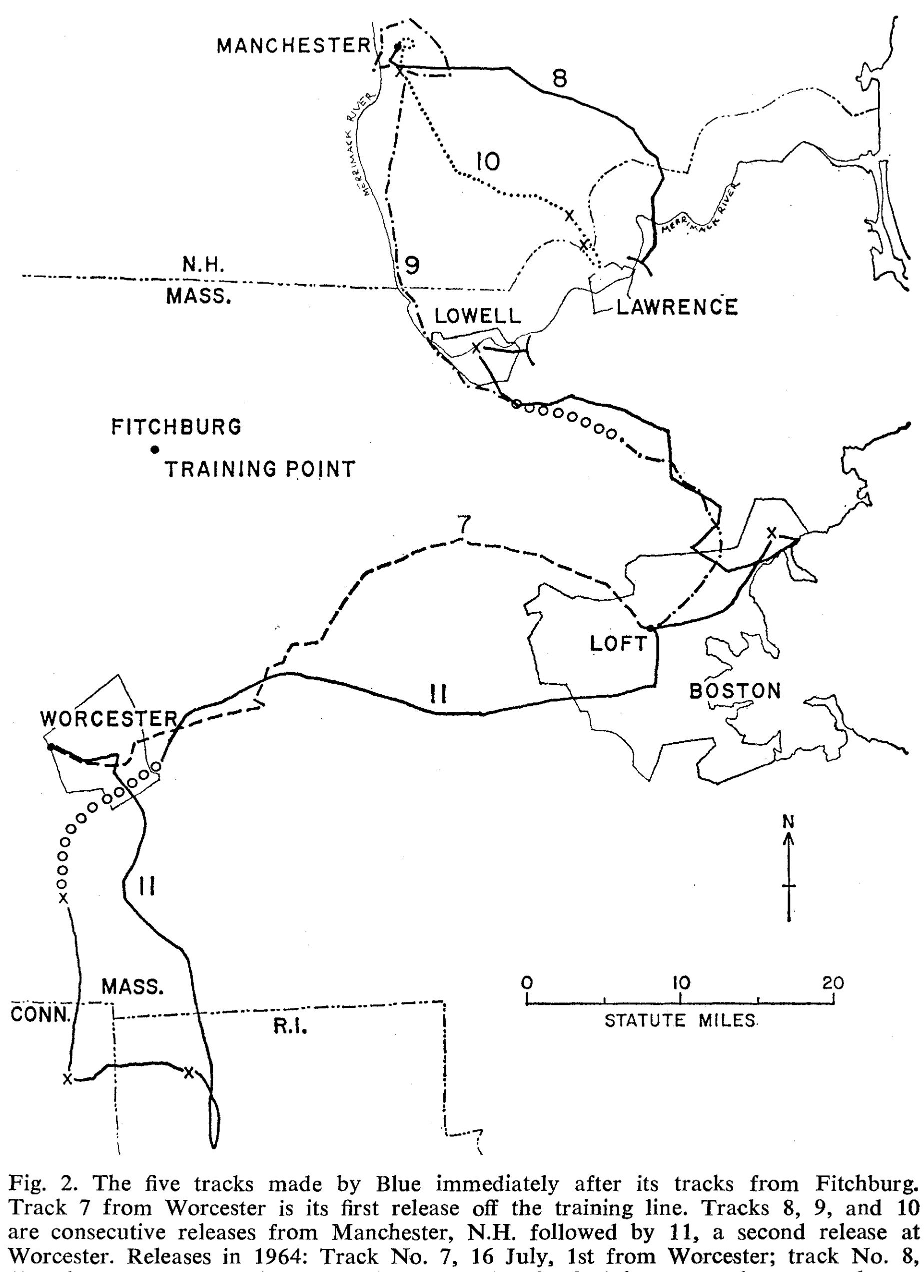

Fig. 2. The five tracks made by Blue immediately after its tracks from Fitchburg. Track 7 from Worcester is its first release off the training line. Tracks 8, 9, and 10 are consecutive releases from Manchester, N.H. followed by 11, a second release at Worcester. Releases in 1964: Track No. 7, 16 July, 1st from Worcester; track No. 8, 17 July, 1st from Manchester; track No. 9, 20 July, 2nd from Manchester; track No. 10, 27 July, 3rd from Manchester; and track No. 11, 30 July, 2nd from Worcester. Symbols are the same as in Fig. 1.

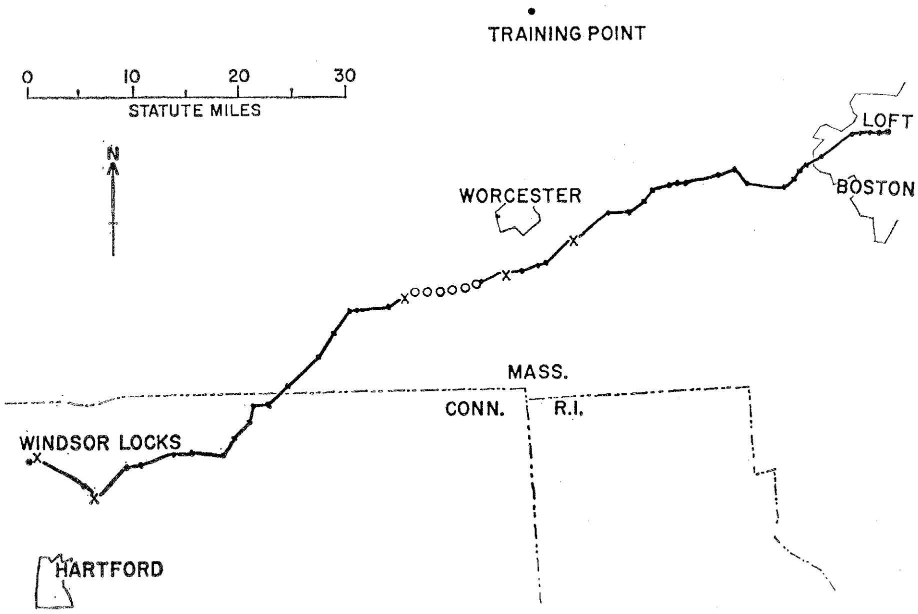

Fig. 3. Map showing track of Silver on its first release from Windsor Locks, Conn. It had previously been trained and released from Fitchburg, and the first 7 miles of this track are in the trained compass direction. Symbols are the same as in Fig. 1.

pass orientation, they should have taken courses parallel to the Fitchburg tracks. If they could truly navigate by some set of coordinates, they should have been able to fly toward the loft from any new release point. The results of such releases are shown in Fig. 2, which depicts the first five tracks of Blue after its training flights from Fitchburg (*6*). The bird's first nontrained release was from Worcester, Mass., 40 miles WSW of the loft (see Fig. 2). The bird started out ESE—the compass direction from Fitchburg to the loft. It flew 6 miles, then turned onto a NE course. This course was directed considerably more northward than the true homeward direction and took the pigeon through the center of the area between Fitchburg and Cambridge, over which it had flown 27 times in the previous 2 months. Blue did not correct its course, but continued on the inappropriate NE course until nearly out of the "familiar" territory and then began to curve southward toward home. Among 20 releases during 1964 from non-Fitchburg points, there were three instances of birds following incorrect courses that traversed this "familiar" region. There were no signs that the birds could correct their courses by recognizing familiar landmarks. These results strengthen the conclusion that pigeons do not pilot most of their courses by familiar landmarks, even over landscape that they cross frequently.

After its return from Worcester, Blue was released from Manchester, N.H.; the three consecutive flights from Manchester are shown in Fig. 2. On its first homeward flight, Blue started flying east, then turned south and spent the entire day alternately flying along the Merrimack River and stopping in the industrial cities near it. The bird homed jaggedly the next morning. On the next two flights, Blue flew more direct routes to the south each time.

Blue was again released from Worcester (the second time). On this trip (Fig. 2) it flew east, then turned southward and maintained a course that was within 10 deg of the proper homeward route from Manchester—a very different course from the ENE direction it had flown from Worcester 2 weeks earlier. After flying south for 28 miles, the bird reversed course abruptly and landed at Pascoag, R.I. There are no large cities in this region, and Blue lighted on the only large factory within sight. If the pigeon was looking for the cities it had encountered 20 miles south of Manchester, as this behavior suggests, then not only had it learned the southerly compass orientation in its three releases from Manchester, but it had also learned to depend on the cities along the Merrimack River as checkpoints on its route to Cambridge. Thus, though these birds do not seem to guide their entire course by landmarks, they seem to use some of them as crude checkpoints. From Pascoag, Blue flew west for 8 miles, sat again for an hour, and then flew back toward the release point. Just short of the city of Worcester (while the plane was refueling) the bird turned eastward. It then flew a gradually curving course homeward. When it crossed the rim of hills around Boston, 4 miles south of the loft, it turned abruptly and headed toward the loft. The last part of this flight was probably piloted by familiar buildings in Cambridge, but the curving course between Worcester and the hills around Boston was probably flown by true, bi-coordinate navigation.

An even more striking example of true navigation is Silver's trip from Windsor Locks, Conn., 87 miles SW of the loft. To our knowledge, this pigeon had never been within 40 miles of Windsor Locks, yet it made a very direct flight back to the loft on its first release (Fig. 3). Starting out in the ESE training direction, it crossed the Connecticut River, stopped for 50 minutes, then took off toward home. The track of this flight deviates from a straight line by an average of 1.7 miles out of the total distance of 87 miles ($\pm \sim 1$ deg). While no single flight can prove a pigeon's ability to navigate, we have more than 20 tracks in which pigeons showed clear homeward orientation from release points that were almost certainly unfamiliar. On only two occasions out of the 131 flights tracked did the pigeons fail to return home, and both of these occurred when pigeons trained to fly 30 miles were released 100 miles from home. These two pigeons flew a homeward-directed track but did not continue on it long enough to reach home.

Our results suggest that there are three stages in a pigeon's homing. It starts out first in the trained compass direction, using landmarks as checkpoints. If the compass course proves incorrect, the pigeon generally stops flying or makes an abrupt turn to a well-directed homeward course. Within 10 miles of the loft, we suspect that landmarks play a major role.

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5. These techniques and data will be published extensively in the near future.
6. Blue's sixth track was a flock release from Fitchburg and is not shown. It covered the same ground as the first five tracks shown in Fig. 1.
7. Supported in part by contracts Nonr 1866(12), 1866(46), and 3225(00) between the Office of Naval Research and Harvard University and by NSF grant GB 3403.

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Age of the Ocean Floor

According to Wilson (*1*), the ages of islands increase with distance from an oceanic ridge; recent potassium-argon dating of sea-floor basalts also suggests ages roughly proportional to this distance, which might be interpreted as the consequence of movement of the ocean floor with constant velocity away from the crest of a ridge. On the basis of this assumption, a velocity of 1 cm/yr would lead to an age of 1 million years for a point on the ocean floor 10 km from the axis of the ridge. Accordingly, when Saito, Ewing, and Burckle (*2*) recently discovered Lower Miocene microfossils in two boulders dredged from points 10 and 130 km from the crest of the Mid-Atlantic Ridge, they concluded that, unless patches of old rock were left behind near the crest, "expansion or crustal movement, if any, ceased at least 20 million years ago," and that "The data rule out the possibility of large-scale continental drifting or spreading of the ocean floor since the Lower Miocene."

The implications of this conclusion may be appreciated if one remembers that the mean annual displacement along the major seismic faults currently amounts to several centimeters per year (the maximum rate along the San Andreas fault is assumed to be 5 or 6 m/100 yr). Since earthquakes are caused by relative movement of continental or oceanic blocks adjacent to the seismic fault, the velocity of drift of these blocks also must amount to several centimeters per year. Evidently, neither contraction nor expansion of the earth can be responsible for the movement. Oceanic ridges would demand expansion; the Gutenberg-Richter seismic shear bands, on the other hand, require contraction if they are essentially thrust faults complicated by later strike-slip movements. If the belief of most geologists in the existence of genuine orogenic compression (different from mere folding of surface veneers by gravity sliding) is well founded, there can be no global expansion of tectonic significance. Finally, the observed (seismic plus aseismic) fault displacements around the Pacific add up to relative movements of diametrically opposite continents, probably by some 5 or 10 cm/yr; if these were due to expansion or contraction, the radius of the earth would increase or decrease at a rate no less than about 1 cm/yr—that is, by 1000 km in 100 million years.

Naturally, the currently observed drift velocity of crustal blocks, although of the magnitude assumed by Wegener, does not mean evidence for his scheme of continental movements. However, the results of the recent International Indian Ocean Expedition (*3*) constitute overwhelming support for what seemed the riskiest element in Wegener's theory—the long-range drift of India [see, in particular, Heezen and Tharp's fig. 2 (*3*)].

How then can the findings of Saito, Ewing, and Burckle be fitted into this framework of seismologic and oceanographic facts? Their conclusions are based, as I have mentioned, on the assumption of constant horizontal velocity of the ocean floor, with a discontinuous jump from positive to negative value at the axial line of the ridge. The flow pattern adopted to obtain this velocity distribution is shown in Fig. 1 (*4*). The upwelling beneath the ridge is assumed to consist in vertical rise of a rigid block between rigid walls; the direction of the velocity changes discontinuously from vertical to horizontal in two 45° planes (dashed lines), and the horizontal flow also is represented by the sliding of rigid blocks on a rigid base, *A–A*.

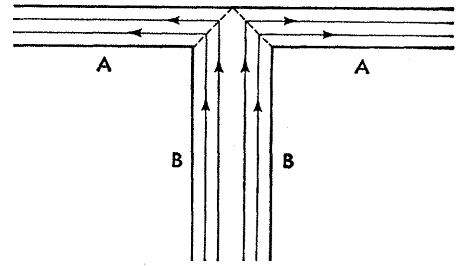

Fig. 1. Discontinuous-flow pattern of upwelling, giving constant velocity at the surface.

In general this flow pattern is not mechanically possible for several reasons: The discontinuity of velocity at the 45° planes amounts to a shear strain of 200 percent occurring in an infinitesimally short time if the velocity of flow is finite. With Newtonian viscosity this would imply an infinitely high shear stress; with the Andradean viscosity of crystalline materials in the hot-creep range (*5*), the shear stress would be very high at the 45° planes and very low (below the creep limit) at an infinitesimally small distance from them. Velocity discontinuities of this kind are possible only in the hypothetical "ideally plastic" material, which has a sharp yield point, no strain hardening, and no velocity dependence of the deformation (no viscosity); moreover, the deformation must be a matter of plane strain (discontinuities caused by the yield phenomenon, as in steel, can be disregarded here).

Furthermore, if any shear stress is transmitted in the horizontal planes *A–A*, it produces compressive stresses in the horizontally sliding slabs, increasing with distance from the crest. Onward from a certain distance, thrust faulting would occur, of which no indication has been observed.

Finally, the flow pattern of Fig. 1 requires that the width of the rising vertical slab be exactly twice the thickness of the horizontally sliding slabs, which thickness is presumably determined by a soft layer in the upper mantle [the thickness of the horizontal slabs is supposed to be of the order of 100 km (*4*)]. If the vertically rising slab is thicker, as is suggested by the width of the oceanic ridges, which have to be floated by lighter material below, use of the 45° shear plane would lead to the flow pattern of Fig. 2. A plateau would rise in the center of the vertical slab; it would gradually flow apart, but no major rift would arise in its center because of no horizontal spreading below the ridge to produce the tensile stress needed for rifting at the surface.

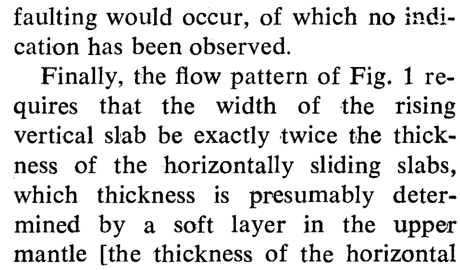

Fig. 2. Discontinuous-flow pattern corresponding to Fig. 1 but for a thicker vertical column.