Homing Orientation in Salamanders:
A Mechanism Involving Chemical Cues

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THE SALAMANDER *Plethodon jordani* possesses a well-developed homing response that is both highly oriented and direction-independent (refs. 1 and 2). Some individuals have homed following 300-m displacement, a distance 20 times the greatest linear dimension of any home area recorded. The objective of this paper is to report on a series of experiments concerning the senses and cues used by *P. jordani* during homing orientation.

Information on sensory involvement in caudate homing orientation has been obtained mainly by manipulating the experimental subject, either by sensory impairment, conditioning procedures, or rhythm alterations. By such techniques, olfaction (refs. 1, 3 and 4) or photoreception (ref. 5), or both (ref. 6), have been generally shown to be necessary senses. One species of newt (*Taricha rivularis*) homes readily following extirpation of the eyes (ref. 7) but fails to home following severence of the olfactory nerves (ref. 4). However, homing is completed in some cases when the olfactory nerves have regenerated. Studies with a formalin perfusion technique have also shown olfaction to be important to accurate homing orientation in this species (ref. 3). Another newt (*Taricha granulosa*) has been shown to use light cues for spatial orientation under laboratory and field conditions (refs. 5 and 6). Extraoptic photoreception (near the diencephalon) has been demonstrated for the salamander *Plethodon glutinosus* (ref. 8). A similarly located system in a frog (*Acris gryllus*) can even receive directional information to be used in homing orientation (ref. 9). Senses involving other than photoreception and chemoreception have received little attention in caudate homing studies. One exception is Twitty's work which showed that substrate contours were not important for initial homeward orientation in *Taricha rivularis* (ref. 7).

Techniques involving the manipulation of natural cues, which are similar to those methods used by Kramer with starlings (ref. 10), have not been employed in caudate investigations. One advantage of these methods is that the experimental animal can be left in a relatively normal biological state and be less subject to possible experimental trauma. Such

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techniques should be used to supplement the results obtained from sensory impairment studies, particularly when diminished response patterns following sensory impairment are given as evidence of the importance of the sense to the response in question. Both sensory impairment and cue manipulative techniques are used in the following investigation.

GENERAL METHODS

Plethodon jordani Blatchley are terrestrial salamanders of the southern Appalachian highlands that live at high elevations in moist woodland habitats away from aquatic media. They are non-migratory and quite sedentary. Being lungless and depending largely on skin moisture for cutaneous gas exchange, they are vulnerable to dehydration and anoxia. The species is active on the forest floor at night, a time of greater relative humidity, and spends the day under cover usually in burrow systems. An average adult has a total length of 115 mm and a width of 10 mm.

Observations and Subject Handling

Details of the general procedures may be obtained elsewhere (refs. 1 and 2). Briefly, all observations were conducted at night, particularly between 2100 and 2400 hr, the period of greatest subject activity. Each animal when hand captured was uniquely marked by toe-clipping and checked for sex and size. If displaced, the salamanders were denied visual cues. No anaesthesia was used; the animals were retained for typically less than 30 min. Both marking-recapture and radioactive [182]Ta-tagging procedures were used to record the animals' movements. Displacements were made usually of 30 m, a distance twice the greatest home-range dimension yet recorded. This distance reduced the time required for displacement and the time required for relocating the salamanders that were momentar-

ily lost, while still satisfying the requirement of displacement into unfamiliar areas. Almost invariably, displaced salamanders either remained in the vicinity of the release point (within 12 m) or returned close to the initial capture position (within 8 m). The latter animals were considered to have homed. Throughout the studies, wind directions were frequently measured. On a given night wind conditions were usually such that, at one time or another, breezes from most all directions were recorded.

Analytical Procedures

Nonparametric statistics were used throughout, specifically the Mann-Whitney U test and the Chi Square test on 2×2 contingency distributions, where appropriate (ref. 11). Rejection of the null hypothesis was based on the .05 level of significance. Rejection at lower significance levels are so indicated.

SENSORY IMPAIRMENT

Because it was suggested from other experimental work that vision and olfaction may be quite important to homing, these senses were selected for impairment studies. With certain provisions, the impairment of these senses should indicate their relative importance to homing in terms of their necessity. The provisions are that suitable controls for trauma or other subtle effects are instituted and that sensory impairment does not severely disrupt normal locomotion through the environment.

Methods

Impairment procedures were performed in the field just prior to displacement. Salamanders were blinded by extirpating the eyes.

The olfactory nerves were severed by two methods: In the first, two small incisions were made through the skin and cartilage of the cranium anterior to the brain case. A sharp probe was then inserted into the incisions and moved through the nerve axes. Details of this technique have been reported (ref. 1). Sham operations consisted of only the initial incisions.

In the second method, the nerves were severed by making incisions dorsally through the roof of the mouth using delicate, sharp-pointed surgical scissors. For each nerve, one tip of the scissors was placed into the laterally situated internal naris, and the other was inserted adjacent to the medial nasal septum on the same side. A quick snip was then made which severed the cartilage, the dorsal and ventral divergences of the olfactory nerve, and the contiguous tissue in the same nasal area. The cartilage above the nasal chamber was usually left intact, thus reduc-

ing the chance of infection through a direct external wound. Also, the mucous glands and ducts between the cartilage and skin on the dorsal surface of the snout were left intact. The second method was used in place of the first in 1970 after it became apparent that occasionally the olfactory nerves, instead of being severed by the transverse movements of the probe, were only displaced temporarily to one side. Also the second method was more consistent from one operation to the next due to the local anatomical references. Both unilateral and bilateral anosmic operations were performed.

One additional sensory impairment was attempted. The nasolabial grooves, single superficial furrows from the upper lip margin to the external naris on each side, were shaved off by a slender scalpel in an attempt to disrupt a possible avenue of substrate chemoreception (ref. 12).

Results and Discussion

A preliminary study involving marking-recapture methods was conducted in 1965. Unimpaired, blinded, and bilateral anosmic salamanders were displaced 15 m in various directions. The results (ref. 1) indicated that the olfactory sense may have been necessary for successful homing (fig. 1). Blinded animals homed without apparent difficulty.

A second displacement series was conducted during the summer of 1969. Thirty each of four treatment groups (bilateral anosmics, sham anosmics, blinded without the nasolabial grooves, unimpaired) were displaced 30 m. A fifth treatment group of 30 sensory unimpaired animals were left at the point of initial capture as displacement controls. Adult salamanders were selected at random for each treatment. Of all the animals recaptured during 1969, the relative number of anosmics that homed was significantly less
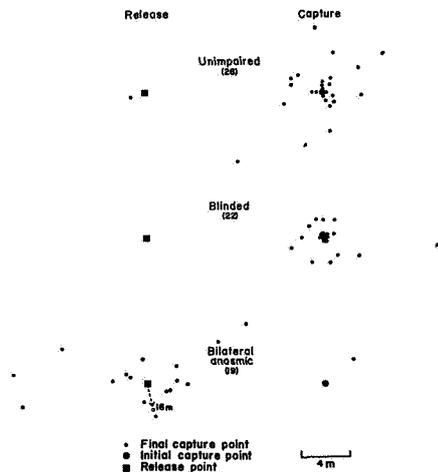

FIGURE 1. Final points of capture of all sensory impaired and unimpaired salamanders displaced 15 m in 1965. Number in parentheses indicates number of adults of each treatment group represented. Actual displacements in each of four directions are combined and included as a single direction. After Madison, 1969.

TABLE 1.—*Comparison of Number of Salamanders Recaptured and Homed for Various Treatment Groups During Summer of 1969 (31 night searches) and Spring of 1970 (3 night searches). UC, unimpaired control; UD, unimpaired displacement; BN, blinded and without the nasolabial grooves; SA, sham anosmic; BA, bilateral anosmic.*

Treatment group	Number marked (1969)	Number recaptured (1969)	Number homed (1969)	Number recaptured (1970) [a]	Additional home (1970)
UC	30	20	. . . .	2(0)	. . . .
UD	30	23	20	7(1)	1
BN	30	27	21	3(0)	0
SA	30	20	17	3(0)	0
BA	30	12	2	4(1)	4

[a] Number in parentheses indicates animals recaptured for the first time.

than the relative number of each of the other treatment groups that homed ($p<.001$) (table 1). The fact that the sham anosmics homed in similar percentages to the unimpaired treatments would seem to indicate that trauma was not primarily responsible for the poorer anosmic returns. In any event olfaction again seemed to be important for the normal homing response.

In the following year (1970) four "anosmic" salamanders were recovered at home for the first time, suggesting the occurrence of homing after regeneration of the olfactory nerves, as has been previously recorded for another salamander species (ref. 4). One of the anosmic *P. jordani* was retained to check on the condition of the olfactory nerves. Both nerves were found intact.

To measure the course and timing differences in the homing response due to anosmia, a third displacement series was conducted during August 1969. Eight bilateral anosmic (method 1) and 24 unimpaired salamanders were tagged with [182]Ta, displaced 22 to 60 m, and tracked with scintillation equipment. The details of the tracks of the unimpaired salamanders have been reported (ref. 2). Significantly fewer anosmic salamanders homed

(4 of 8) than did unimpaired animals (23 of 24) ($p<.01$). In addition, the total homing times (*THT*, the time from release to arrival back home) and the return trip times (*RTT*, the actual time taken to travel the distance home once directed movement was initiated) of the bilateral anosmic animals were significantly greater than those of the unimpaired salamanders. The median *THT* (20.8 hr) and *RTT* (2.8 hr) values for the unimpaired animals can be compared to the individual values recorded for the anosmics (table 2, 1969). Finally the courses of the anosmics that did home seemed to be more irregular (fig. 2).

A fourth set of impairment displacements was conducted in the spring of 1970 to see what effect more thorough olfactory impairment (method 2) and unilateral anosmia (right side only) might have on homing, and to determine if the homing courses of the blinded salamanders differ from those of the unimpaired animals. The unilateral anosmia treatment was added to see if possible traumatic effects of the olfactory operation might delay homing even though intact olfactory tissue was present. Unilateral and bilateral anosmic, blinded, and unimpaired displace-

Unimpaired
males

Capture   Release

Unimpaired
females

Capture   Release

Bilateral anosmic
females

Bilateral anosmic
males

· Detection point
— Estimated course
⮥ North direction
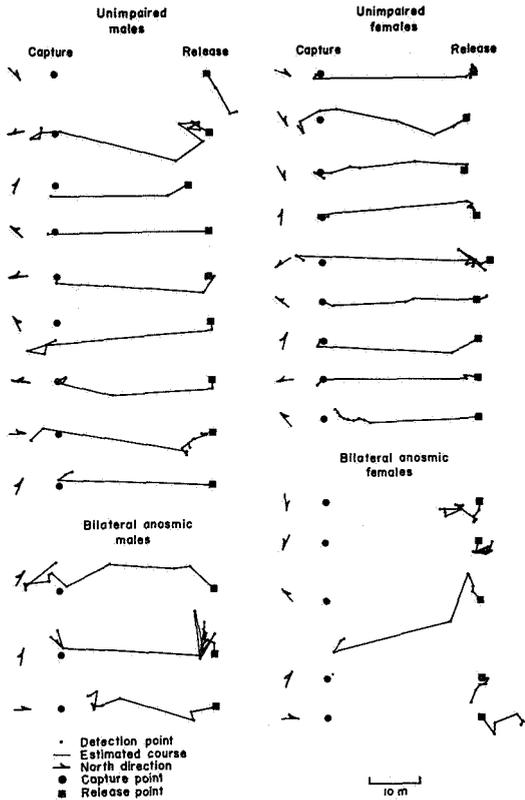● Capture point
■ Release point

10 m

FIGURE 2. Estimated movements of all anosmic and unimpaired salamanders displaced upon initial capture during radioactive tagging study of August 1969.

ments of 24 to 68 m were made in various directions. Except for the different anosmia technique, the same methods and radioactive tracking procedures were used.

The sensory unimpaired salamanders, as in the previous cases, homed more frequently (6 of 8) than did the salamanders with bilateral anosmia (0 of 8) ($p < .01$). The homing performance of the unilateral anosmics (2 of 8) was intermediate to, but not significantly different from, either the bilateral anosmics or the unimpaired treatment groups. The blinded salamanders homed in frequencies (2 of 4) comparable to those of the unimpaired

animals. Except for one unimpaired salamander, the homing times in 1970 were similar (table 2). The courses of the salamanders which homed (10 of 28) showed accurate homeward orientation regardless of treatment (fig. 3). Since the positions of these 10 salamanders were determined on a total of 264 of 267 attempts, these courses are not biased to include only those detection points in the home direction. The movements of the 18 salamanders which failed to home were confined to within 12 m of the release point (fig. 4). The positions of these salamanders were determined on all of the 891 attempts.

The poorer homing frequency of the unilateral anosmic treatment group (in comparison with the unimpaired group) could have been due to a reduction of the total olfactory input. This reduction to one-half may simulate the results obtained by displacing unimpaired animals twice as far. The reduced homing frequency is probably not the result of inhibitory effects on movement incurred as a result of the operation. This lack of an inhibitory effect is supported by the similar
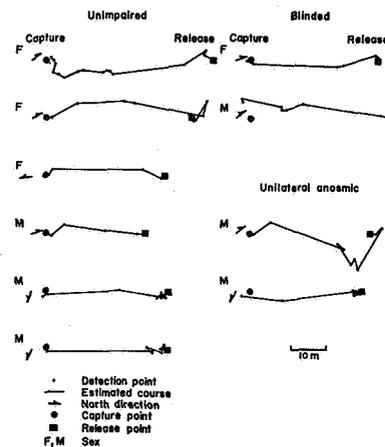
Unimpaired   Blinded

Capture   Release   Capture   Release

Unilateral anosmic

· Detection point
— Estimated course
⮥ North direction
● Capture point
■ Release point
F,M Sex

10 m

FIGURE 3. Estimated courses of all sensory impaired and unimpaired salamanders that homed during the radioactive tagging study of spring 1970.

Unimpaired
M
eif(23)

Blinded
F
41(9)

Unilateral anosmic
M
64(22)

Unilateral anosmic
F
76(20)

Bilateral anosmic
M
73(20)

Bilateral anosmic
F
65(22)

·   Detection point
—   Estimated course
●   Release point
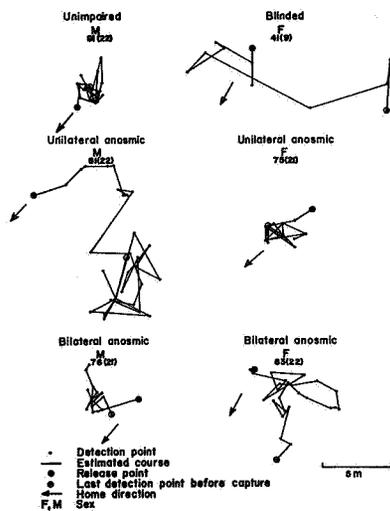●   Last detection point before capture
←   Home direction
F,M Sex

5 m

FIGURE 4. Movements of selected sensory impaired and unimpaired salamanders that failed to home during radioactive tagging study of spring 1970. Salamanders shown are those that had been observed for the longest time following displacement, or which, in addition, had demonstrated greatest amount of movement from the release position. Number of detections and days (in parentheses) are shown for each animal. North direction (top of page) is maintained. Multiple detection points at a given location are not indicated.

degree of movement of the salamanders which failed to home.

CUE DISPLACEMENT

Because it was difficult to assess whether all the provisions mentioned in the previous section had been met, the attempt was made to alter the position of the home odors of the displaced salamander instead of altering the capacity of the animal to detect such odors. It was hypothesized that if an animal were displaced to a totally unfamiliar environment, it would be sufficiently motivated to attempt to return home once left alone. In such a situation any familiar trace of odors

should elicit oriented movements into the wind in the home direction. Successful luring of the animal in a direction opposite the home direction using the displaced home odors would suggest the use of olfactory cues during homing.

Methods

The odor displacement equipment included an intake and a transport unit (fig. 5). The intake unit consisted of a 10-cm diameter galvanized ventilation pipe which had intake openings along its 1.3 m length and a fan blade and shaft mounted inside at one end. The fan was operated by a belt attached to a 12-v d.c. motor. The latter was housed outside the airstream of the pipe in order to avoid scenting the intake air with odors from the motor. The transport unit consisted of 30 m of 10-cm diameter aluminum ventilator pipe. The two units were connected with a 3-m segment of 10-cm diameter flexible plastic tubing that allowed for placement of the intake over the capture points of the resident animals. The two-unit system was set up adjacent to a stream along an abandoned lumber road that had since grown up with trees. The site along the stream was selected because of the consistent wind direction characteristics there (from upstream, SSW)—a mandatory condition for the experiment.
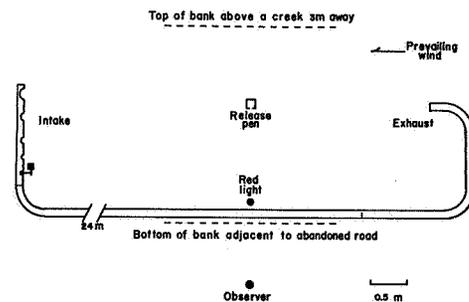

Top of bank above a creek 3m away

Prevailing wind

Intake

Release pen

Exhaust

Red light

Bottom of bank adjacent to abandoned road

Observer   0.5 m

FIGURE 5. Odor displacement apparatus of cue displacement experiment.

TABLE 2.—*Homing Times of [182]Ta-Tagged Salamanders Displaced During August 1969 (only those of impaired animals shown) and June 1970. DD, displacement distance; DR, displacement direction; THT, total homing time; RTT, return trip time.*

Sex	DD (m)	DR	THT (night hours)	RTT (night hours)	Sex	DD (m)	DR	THT (night hours)	RTT (night hours)
Bilateral anosmics 1969					M	30	SW	44.2	3.3
					M	24	N	63.4	2.0
F [a]	30	SE	111.4	58.3	M	30	W	75.3	2.8
M	30	N	83.9	76.8	Blinded 1970				
M	30	E	113.1	5.2	F	32	N	60.8	0.9
M	30	NE	44.3	5.2	M	34	NE	31.1	5.9
Unimpaired 1970					Unilateral anosmics 1970				
F	42	NE	80.8	42.3					
F	36	N	62.9	1.1	M	30	NE	64.3	2.0
F	30	S	47.1	1.8	M	28	SW	35.3	2.1

[a] Values not included in statistics due to unreliable time estimates resulting from temporary loss of salamander prior to detection at home.

Local wind speeds varied from trace amounts to gusts of 1.2 m/sec, although typically, and during the observations, the speeds were rather consistent around 0.3 m/sec. The wind speed at the exhaust opening due to the intake fan measured 2.5 m/sec. At the screen release pen, 3 m downwind from the exhaust opening, the speed ranged from 0.1 to 0.3 m/sec.

Salamanders were displaced upwind of their home areas but downwind of the exhaust of the transport unit. Non-resident animals were captured on either side of the road more than 10 m downwind of the intake unit. The resident animals were captured on either side of the road near the intake unit which was in turn placed on the surface litter directly over the capture site of the resident. The displaced salamanders were released into the open side of the small release pen, 27 m upwind from the intake unit and 3 m downwind from the exhaust. A small red light (directed away from the observer and the road bank and toward the release pen and

the creek bank) was used for the night observations. The observations began when the salamander voluntarily left the opening of the release pen. Salamanders were scored as moving away from or toward the exhaust relative to a line intersecting the release pen drawn perpendicular to the home-pen-exhaust axis. Movements toward the creek bank or road bank side of the home-pen-exhaust axis were similarly recorded. Seventeen of the 19 salamanders placed in the release pen exited within the alloted time of 10 min. Each of these was continuously observed for at least 10 min or until it went out of sight 2 to 3 m away. Wind direction was monitored continuously throughout the observations 0.5 m above the ground. Although the speed increased with height above the ground, the direction remained the same.

Results and Discussion

Both the resident and non-resident animals were observed to move at random with

respect to directions along the home-pen-exhaust axis (table 3). However, a significant number of salamanders (13 of 16) moved toward the side of the road corresponding to the side on which they were initially captured.

Although these results do not correspond to the expected oriented movements, the results can be accounted for if one accepts the following hypotheses: (1) olfactory cues are relied upon for homing, (2) recognizable home odors were transported successfully in the system above, and (3) a given salamander is able to recognize its position in its home area using only olfactory cues. For example, if a resident's home area was located on the downwind side of the intake, the resident, upon smelling only the odors on that side from the exhaust opening, might well move in a direction which would normally take it to the center of its home area—a direction which at the release pen would be away from the exhaust. By chance, the resident salamanders would be captured with equal frequency in the upwind and downwind halves of their home areas, and thus in the testing situation be expected to move toward the exhaust half the time and away

TABLE 3.—*Direction of Movement of (R) Resident and (NR) Non-Resident Salamanders in the Odor Displacement Study of 1970. Movements (T) Toward or (A) Away from Exhaust Are Indicated. Capture Locations at or Movements Toward (CB) Creek Bank or (RB) Road Bank Also Indicated.*

Date	Animal type	Sex	Capture location	Movements	
				Perpendicular to road	Along road axis
May 26	R	M	RB	CB	T
May 26[a]	NR	F	RB	RB	A
May 26	R	F	CB	CB	A
May 26	NR	F	RB	Along axis	T
May 27	NR	M	CB	CB	T
May 27	R	F	CB	CB	A
May 27	NR	M	CB	RB	A
June 7	R	F	RB	RB	T
June 7	NR	M	RB	RB	T
June 7	R	F	RB	RB	T
June 7	NR	M	?	No pen exit	
June 7	R	F	RB	RB	T
June 7	NR	M	?	No pen exit	
June 14	NR	F	CB	CB	T
June 14	R	F	RB	RB	T
June 14	NR	M	RB	RB	Along axis
June 14	R	M	CB	CB	A
June 14	NR	M	CB	CB	T
June 14	R	F	CB	RB	A

[a] Only animal to receive occasional wind gusts from the home direction downstream.

from it the other times. The significant correlation observed perpendicular to the home-pen-exhaust axis agrees with this hypothesis; however, one additional fact is necessary. As revealed from radioactive tagging studies, salamanders along trail-bank situations seldom have home areas which cross the trails (only 4 of 562 position points on 11 adult non-displacement animals have been observed either on or across the bordering trail). This condition exists even though there are no apparent barriers to salamander movements on the trails. Thus by the same explanation presented for movements along the home-pen-exhaust axis, one can account for the movements perpendicular to the axis.

One would expect then that salamanders in other displacement situations would have shown more ambiguity in their movements as a result of detecting occasional whiffs of home odors from different areas of the home range. Such ambiguity was not observed. The one important difference in the odor displacement situation was that home odors were picked up from essentially the same microhabitat that the animal was occupying and transported 30 m without dilution. Thus the movements observed by the resident animals may not have been homing movements, but rather movements associated with minor adjustments of position within or immediately adjacent to the home area.

It is still a possibility, and a simpler hy-

FIGURE 6. Olfactometer apparatus of cue identification experiment.

pothesis to propose, that the movements in the home-exhaust axis were random either because the apparatus failed to pick up the essential odor cues, or because home area odors are not used during homing. That the movement was not random as a result of fright or escape behavior is evidenced by the non-random orientation perpendicular to the road. The latter orientation could have been in response to cues obtained from the directionality of the wind or the cooler air near the stream, both of which were similar to conditions at home.

CUE IDENTIFICATION

The possibility of a salamander recognizing its own position relative to a mosaic of site specific odors or odor gradients located throughout the home and contiguous areas raises questions as to the odor sources. To test the possibility that individually recognized conspecifics might be contributing factors in this scheme, an odor discrimination study was initiated in 1969.

Method

An olfactometer was designed and built that would (1) reduce the mixing of two convergent air streams at the point where discrimination would take place and (2) allow easy but thorough cleaning procedures following each individual test (fig. 6). All glass and plastic sections were made in multiple such that all could be soaked in soapy water for 24 hr prior to being used. Compressed breathing air was introduced into the system by way of a constant pressure regulator and then split into two air streams destined to be laden with different test odors within the sample bottles. The wind velocity in the main discrimination tube averaged about 0.2 m/sec. However, momentary velocity increases were occasionally used to stimu-
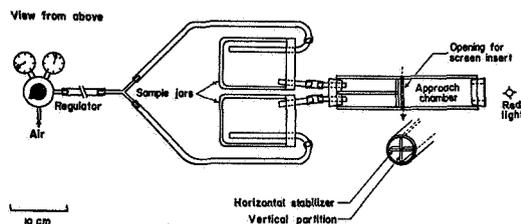
late movement. Prior to testing, the sample jars were moistened with 10 cc of water in order to raise the relative humidity of the air entering the discrimination tube.

Salamanders for testing were collected by searching woodland areas at night until two adult salamanders of the same sex were observed within 3 m of each other. These, classified as familiar with respect to each other, were captured singly and put into separate transport jars. A third conspecific also of the same sex was then captured at least 30 m away (well away from the home areas of the other two) and put into a third jar. This animal was considered to be unfamiliar relative to the first two. The three were then immediately taken to the laboratory where the olfactometer was set up in the dark.

The unfamiliar and one of the familiar salamanders were introduced separately into the sample jars which were arranged at random to the right or left side of the olfactometer. The second familiar salamander became the test subject. This animal was enclosed in the approach section of the discrimination tube between a 3-mm mesh screen partition and a screen-covered hollow plug. When slow investigatory movements were observed away from the partition in front of the divided section of the tube, the partition was lifted and the animal's eventual movement into either side of the tube was recorded. A red light was directed up the discrimination tube and observations were made through a pin hole in the black cloth that covered the entire apparatus.

Results and Discussion

The results of the 34 salamanders tested indicate that the animals initially preferred to enter the side of the tube corresponding to the side of the system that enclosed the familiar conspecific (fig. 6). Later in the season

the preference was essentially reversed. Before July 9, 15 of 17 salamanders chose the familiar conspecific side; while after July 9, only six of 17 animals chose the familiar side. The difference between the two periods is significant ($p<.01$). No right or left bias (13L:21R) in the system was significant. Of interest to note is the observation that breeding activity increases gradually in July to a peak in the latter part of August (subjective impression from 4 years of observations in the field at night).

During June a different series of tests were also conducted. Salamanders collected in the field were given a choice of odors either from a 10-cm diameter humus sample collected 0.3 m from where the salamanders were captured (familiar sample) or from a sample collected from a similar habitat over 30 m away (unfamiliar sample). Of the 10 salamanders tested, no preference was observed for either the familiar or unfamiliar samples. However, the upward trend generally coincides with the decreasing trend in the cumulative frequency of familiar conspecific choices (fig. 7). Although quite preliminary, these results suggest the possibility that different olfactory cues may be used at different time of the season for identifying the home area.

In any event, the results suggest that the individual odors of conspecifics living in and around the home area of a given salamander may be quite important as site specific odor cues. If the animal were displaced, these odor cues could be used to relocate the home area. The same cues could also be used to adjust both local movements and, perhaps, movements favorable for spacing and reproductive relationships. The climbing behavior exhibited by this species on surface objects and tree trunks at night could easily be a functional part of such a chemical information system (ref. 2). In effect, then, the results of
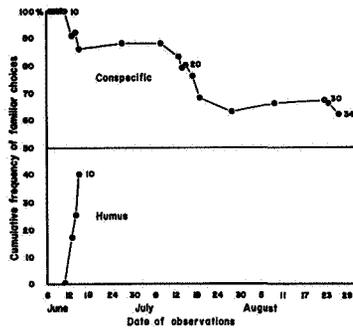
FIGURE 7. Cumulative frequency of familiar choices in the olfactometer apparatus as a function of time. Only the cumulative number of salamanders at intervals of 10 are indicated, with the exception of the last salamander tested. For example, 80 percent of the 20 salamanders tested (16 in number) by July 12 had preferred the familiar conspecific odor.

the olfactometer experiment support the explanation based on olfactory cues given for the results of the odor displacement study. Clearly, however, additional studies are needed before conclusive statements can be made.

HYPOTHESES

In review, the homing ability of *P. jordani* is highly oriented, direction-independent, and distance-dependent. The ability is manifest in salamanders that are displaced into areas that had not been occupied previously. Vision is not required for the response although a functioning olfactory system seems essential. In attempting to relate these characteristics to those of each of the three levels of homing orientation proposed by Griffin (ref. 13), and later clarified by Schmidt-Koenig (ref. 14), I found it difficult to classify the homing response of *P. jordani*. Piloting or type I homing was excluded because *P. jordani* displaced into previously unoccupied areas returned by home-oriented

movements and not by random movements or search patterns. Directional orientation or type II homing was excluded because the homing response was direction independent. Finally bicoordinate or reverse displacement navigation did not seem directly implicated because *P. jordani* probably rely on familiar odor cues emanating from the home area for directional information. Although entirely appropriate for levels of bird orientation for which it was designed, the classification should receive additional emphases if it is to be more broadly applicable to other sensory systems and vertebrate groups.

The modification of the classification would seem to require the following adjustments relevant mainly to piloting. The phrase "familiar landmarks" should be changed to "direct sensory cues." The former words imply mainly visually perceived information, while the latter words include the use of other sensory cues that are specific to and occur in spatial association with the home area or goal. The concept of "familiar territory" should also be considered. The definition of what constitutes such an area is a function of the particular sensory associations considered. The familiar auditory or tactile components of a region may denote an area considerably different in size and meaning from one based on familiar visual or auditory stimuli. In the broadest sense, the area occupied at a given instant can be considered familiar as long as direct sensory cues are still perceivable. Thus *P. jordani* could use familiar olfactory cues to home from areas that had never been occupied previously, and in so doing be "piloting." Random movements or search patterns might be expected then when the salamander is displaced beyond the limits of this direct sensory information.

The third level of homing orientation should receive an additional emphasis in the nature of the coordinates. Instead of using

global coordinate systems, a fairly sedentary animal by similar processes could use local gradients to achieve what I would like to call "local gradient navigation." This type of navigation would require (1) the existence of two or more fairly linear but non-parallel gradients of physical or chemical variables, (2) a region including and extending beyond the home area of the animal through which the slope and direction characteristics of the gradients would be consistent, (3) an animal sensitive to different measures of the physical or chemical variables in question, (4) an animal with the knowledge of the direction of the local gradients, (5) an animal able to "remember" in some way the home values of these measures during displacement, and (6) an animal able to compare the home and release values, either concurrently or alternately, and to move in such a way that the home reference values would be restored.

The degree of displacement necessary before differences in the variable measures could be detected, of course, would be proportional to the slope of the gradients. The maximum effective distance of such a mechanism would be reached when, in other areas, different slope or direction characteristics of the same variables are encountered. In effect, then, the same general characteristics used to define long-range bicoordinate navigation, i.e., the use of bicoordinate information obtained from cues that are not in direct association with the home area of goal, also define the characteristics of this local mechanism. Subtle local gradients of the types just mentioned could have aided *P. jordani* in its homeward movements.

Another type III homing mechanism that *P. jordani* could have used, and one needing some reconsideration on a local scale, is inertial navigation. The potential cumulative error associated with linear and angular acceleration determinations would probably be

less critical during shorter range displacements or homing movements, providing the frequency of these determinations was proportional to distance. In fact the mechanism could be expected to produce the direction-independent and distance-dependent results recorded. Perhaps relevant to the possibility of this mechanism operating in *P. jordani* is the occurrence in this species of a specialized substrate vibration detection system (ref. 15) which could act as an independent sensor of movements imposed upon the whole body. This system includes an opercularis muscle that connects the opercular cartilage of the middle ear to the suprascapular process of the shoulder blade. Also of potential importance to an inertial mechanism is the fact that *P. jordani* moves with the long axis of the body generally aligned in the direction of movement. This alignment would tend to facilitate detection of direction changes because of bending forces along the body axis. Animals moving through less fixed and more homogeneous media (air, water) would not likely have this advantage to the same degree.

In conclusion, the actual homing mechanism in *P. jordani* remains unknown. However, the results recorded to date can best be explained by a mechanism involving oriented movement into the wind when occasional familiar odors from the home area are detected and when environmental conditions are moist enough to allow prolonged surface exposure. That such a mechanism may be supplemented by inertial cues or by local physical or chemical gradients is a reasonable possibility.

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DISCUSSION

QUESTION: Have you any examples of disorientation on longer distances?

MADISON: In a previous study (*Animal Behaviour*, 19(1), 1969), I reported on a series of displacements of 6 to 300 m with the same species. Successful homing seemed to be a function of displacement distance.

EMLEN: Have you done any experiments with displacements in different directions?

MADISON: Yes, in the same study animals were displaced in four directions parallel and perpendicular to a mountain slope. There was no difference between any of the displacement groups. In other studies salamanders homed successfully following displacement in both directions across mountain ridges and streams.

JACOBS: Have you tried displacing them vertically, up in a tree?

MADISON: No. However, I have recorded the frequency of climbing by displaced and control salamanders (Madison and Shoop, 1970). There is a significant correlation between animal displacement and their frequency of occurrence in trees soon after release. This behavior could facilitate the detection of home associated odors.

WILLIAMS: Did you try any work with vibrations? These animals live near a stream which produce characteristic vibrations at various points.

MADISON: Vibration could give one coordinate of a bicoordinate system in terms of a vibration intensity gradient. However, another physical or chemical gradient along a different axis would have to be used before local navigation could be possible.

WILLIAMS: Animals pay attention to more than one cue. It is common that they use a landmark system.

MADISON: *P. jordani* is probably quite sensitive to the physical and chemical environment in which it lives. Removed almost totally from its normal environment, the salamander may very well have but just one sort of direct familiar information about the home area and just one sensory system able to receive the information. I prefer not to regard occasional familiar odors, which are detected in areas removed from the home area, as landmarks. The definition of what constitutes a landmark is quite difficult when considered in terms of the various kinds of sensory input that are possible.

EMLEN: About redundancy of systems: If a blinded animal comes home, that doesn't say that it can't use visual cues. That says that it has enough information available without visual cues. In another situation it may rely heavily upon visual information. Experimental results can be, and have been, misinterpreted by ignoring the redundant nature of orientation systems. That is an important point.

MADISON: That is a good point. One would think, however, that the anosmic animals might home using their visual system—if intersystem redundancy in this species works both ways.

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