verse a neonatal tissue formerly believed to transport only maternal antibodies. Thus, selective transport of IgG-antigen complexes represents a possible mechanism for entry into the neonate of a wide variety of antigens. We must therefore consider the transmission of immune complexes as an extremely important, possibly frequent event that may influence the development of immune capability.

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Strong Electrical Currents Leave the Primitive Streak of Chick Embryos

Abstract. *The electrical fields above chick embryos were explored with a vibrating probe. These fields indicate that steady currents with exit densities of the order of 100 microamperes per square centimeter leave the whole streak and return elsewhere through the epiblast. The epicenter of these strong exit currents lies near Hensen's node. They are probably pumped into the intraembryonic space by the epiblast and then leak out of the streak because it is a zone of junctional disruption.*

Recent explorations with a vibrating probe show that a wide variety of developing systems drive strong steady electrical currents through themselves (*1*). Currents of 1 to 100 μA/cm^2 traverse developing systems from a level as simple as an algal egg (*2*) through one as complex as the regenerating stump of a newt limb (*3*). Moreover, substantial evidence indicates that these currents—or at least some of them—act back to affect development (*4*). However, an important intermediate stage of developing system—which may be roughly called the epithelial one—has not been explored. We now report a first exploration of developmental currents at this stage—specifically, through the early chick embryo. At the primitive streak stages, the embryo consists largely of two flat epithelia separated by a narrow intraembryonic space. The upper sheet, or epiblast, contains a 1- to 2-mm long groove (the primitive streak) through which epiblast cells enter en route to forming all, or almost all, of the internal tissues. We have found that strong steady currents pour out of the whole streak and return elsewhere through the epiblast. In the measurement plane, 0.2 mm above the epiblast, current densities of up to 10 to 20 μA/cm^2 were found; ones on the order of 100 μA/cm^2 are estimated to leave the streak.

Large pieces of vitelline membrane with an adherent embryo were peeled off the yolk and explanted, right side up, into a measurement chamber according to a modification of Nicolet and Gallera's method (*5*) together with Jaffe and Nuccitelli's vibrating probe technique (*6*). The explant was supported on a dense, inert oil (Mediflor, Minnesota Mining and Manufacturing) and covered with a layer of thin albumen (of 92 ohm-cm resistivity) in turn covered with a light nontoxic oil (Klearol, Witco). The probe's meniscus setter was placed at the upper water-oil interface. The preparation was maintained at 38°C. Typical signals were 0.3 to 3 μV; root-mean-square noise levels (with a 10-second time constant), 0.02 μV. We visualized the top surface of the 20- to 40-μm thick vitelline membrane by depositing upon it some 10 μm of crystals of the rare earth oxide, Barnesite (which is sold for lens grinding). We studied a dozen explants and succeeded in exploring the patterns of tangential currents above three of them during streak stages 3 to 5. These all seemed relatively healthy since they later formed several pairs of somites, a well-formed head fold, and a neural tube.

Figure 1 shows a scan of the current component flowing across the streak. The direction of the current reversed sharply above the streak, with current flowing away from both sides of it. This outward current reached a peak density of 8 to 10 μA/cm^2 at 0.1 to 0.2 mm from the streak and then continued, with diminishing intensity, out to 1 mm from the streak. Farther out, toward the edges of the explant, the current reversed direction again, so that it returned from these edges. We obtained similar results from all of the seven similar scans made across various levels of the streak (from front to rear) of the three explants successfully explored. They indicate that current leaves the whole streak (as well as the periphery) and returns elsewhere through the epiblast (Fig. 1C).

Scans of the cross component were also made in several vertical lines extending through various points, particularly the circled point of peak density, shown in Fig. 1A. This curve (not illustrated) fell steadily from 16 μA/cm^2 at 0.15 mm above the embryo's top surface to 11 μA/cm^2 at 0.2 mm, 6 μA/cm^2 at 0.3 mm, and 3 μA/cm^2 at 0.5 mm; this is about the shape predicted by potential theory. Integration of this curve indicates that about 1 μA leaves each centimeter length of the streak. If we assume that current leaves a strip about 0.1 mm wide, it leaves with a density of the order of 100 μA/cm^2.

Figure 2 shows a scan of the current component flowing parallel to the streak and within a line just above the streak. Current direction reversed sharply about 0.2 mm behind the front end of the streak, that is, behind Hensen's node. Current flowed away from all sides of this central reversal point or epicenter—forward to the most anterior point explored (0.2 mm in front of the node) and backward to the most posterior point explored (0.6 mm behind the rear end of the streak) as well as laterally. The densest forward current (25 μA/cm^2) lay just posterior to Hensen's node, and two similar peaks of backward current lay just posterior to the epicenter and just posterior to the caudal end of the streak. Figure 2A also shows the parallel component with-

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in two lines that cross the streak: The densities of both forward and backward current fell steadily on both sides of the streak, decreasing by half a few tenths of a millimeter away. We obtained similar results from all of the four similar scans made above the three explants successfully explored. However, in two of these, the scan was extended farther; about 2 mm anterior and posterior to the streak, we found outer reversal points with current returning from the periphery as in the crosscurrent scans. There was also some indication of a forward shift of the epicenter during development. In the stage 3 embryo studied, it lay 0.3 mm behind Hensen's node; in the stage 4 embryo (Fig. 2), 0.2 mm behind the node; and in the stage 5 embryo, 0.1 mm in front of it.

Altogether, these measurements of the parallel component are fully consistent with the main inference drawn from cross-component measurements: The whole streak is a current source. Moreover, the anterior position (and sharpness) of the reversal zone as well as the double peak of backward current all indicate that the strongest current source lies near the node. In other words, one can understand the curve in Fig. 2B as the sum of the currents from a strong point source below the epicenter and a slit source. These inferences are also consistent with some old measurements of Romanoff (*7*), who drained off the albumen, explored the surface potentials at 1 to 2 mm intervals over the blastoderm, and found the nodal region to be most electropositive.

Since the (presumably) loose periphery of the explant was also a current source, we suggest that current leaks out of the embryo and is pumped back into it. This hypothesis is also consistent with the epiblast's structure. Most of it looks like a transporting epithelium (*8*), with a polarized array of organelles within its columnar cells and lanthanum-impermeable, many-ridged zonulae occludens between them. Moreover, these zonulae bear swollen, "pillowlike" compartments, which are reported to accompany osmotic flow through other epithelia (*9, 10*); at least by later stages, the embryo pumps water from the albumen into the space below it (*11*). Within the streak, however, most zonulae must be disrupted as the epiblast cells migrate in to become loosely connected mesenchyme cells; indeed fragments of zonulae are seen on these latter (*9*). Moreover, cell movement along the epiblast, particularly near the node, may well shear tight junctions in or near the streak (*12*). We therefore predict that the chick epiblast, like the rabbit trophectoderm after day 7 (*13*), will prove to maintain a substantial positive voltage within the cavity it covers.

In addition to indicating zones of junctional disruption, these strong outward currents may well act back to control, to further, or even to organize development. As they escape through the streak,

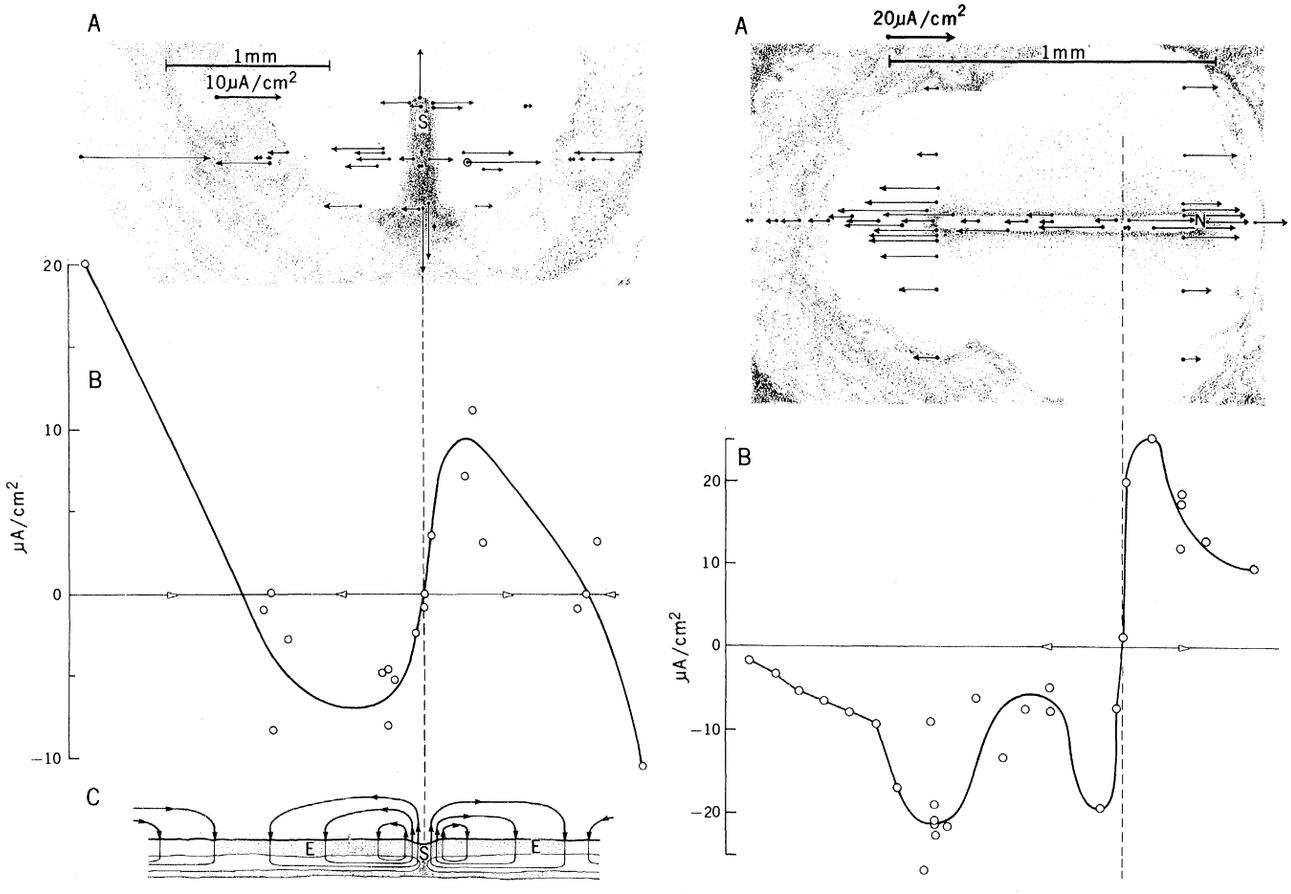

Fig. 1 (left). The pattern of current that flows across the streak (*S*) of embryo 9 during stage 3, measured in a horizontal plane 0.2 mm above the epiblast (*E*). (A) Map of a scan across the middle of the streak together with all measurements made nearby. The sketch of the embryo was made by adjusting the Hamburger and Hamilton (*18*) stage 3 photograph to the dimensions of the living one observed. (B) Graph of the main scan. As the arrowheads on the abscissa indicate, positive values indicate current going right; and negative ones show current going left. (C) Diagram of inferred current pattern in a cross section through the streak. The thickness of the embryo is exaggerated. Fig. 2 (right). The pattern of current that flows along the streak of embryo 4 during stage 4, measured in a plane 0.2 mm above the epiblast. (A) Map of a scan along the streak together with all measurements made nearby. *N*, Hensen's node. (B) Graph of the main scan. Positive values indicate current going right (toward the front end of the embryo) and negative ones, current going left. The dashed line goes through the central reversal point or epicenter.

they probably establish enough voltage across some ingressing cells—only 1 to 10 mV is needed—to redistribute charge components floating in their membranes and markedly affect their behavior (*14*); as they are pumped through the epiblast, they may establish significant transcytoplasmic gradients (*15*); and as they traverse the intraembryonic space, they may establish significant extracellular gradients. With this in mind, certain experiments involving incisions in the epiblast may now be tentatively reinterpreted. Long ago, Morita reported that a cut through the prestreak blastoderm can induce a whole extra embryo to form (*16*). More recently, Lipton and Jacobson reported that appropriate cuts through the stage 5 embryo permit somite and heart formation despite the absence of node and notochord (*17*). Perhaps these cuts act at least in part by artificially producing current leaks.

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Bees Have Rules

Abstract. *Honey bees frequently dance with some view of the sky, orienting themselves to the sun or natural patterns of polarized skylight. Three new conventions have been discovered in the dance language which are used in these circumstances to eliminate potential ambiguity in the dance message.*

Upon discovering a food source, a foraging honey bee can compute her distance and direction from the hive (*1*). This directional information can be encoded into a dance that specifies the location of the food (*2*). Normally, dances are performed on a vertical comb of the dark hive such that the dance angle with respect to vertical (up) is the same as the horizontal angle between the sun and the food (*3*) (the relative azimuth). The convention of defining "up" as the direction toward the sun permits recruits to decode and use the information. Likewise, distance is specified by the duration of the waggle phase of the dance (*2*). Since the communication system employs "abstract" conventions common to the members of a social group, Frisch and others refer to it as a dance *language*.

Dancing on vertical surfaces is a consequence of living in insulating cavities—a behavioral adaptation that permitted *Apis mellifera* to move out of the tropics and penetrate temperate latitudes (*4*). Tropical honey bees perform their dances on open clusters with a restricted view of the sky (*5*), and thus seem to lack the up-is-the-sun convention. On the surface of swarms (*6*) and at the hive entrance (*3*), temperate zone honey bees often dance on a horizontal surface where the up-is-the-sun rule is useless. Since they are outdoors, the dancers orient directly by cues they see in the sky: the sun and extensive patterns of polarized skylight (*1*, *7*). As long as dancers and dance attenders use the same reference system, the language works. However, bees frequently must dance on cloudy days or in locations where a view of the sky is restricted by trees or other landmarks. In these situations, it may not always be easy for them to agree among themselves whether what they can see is the sun or sky, and, if it is indeed part of the sky, which section it is. Nevertheless, dancers seem to resolve possible ambiguities, and successfully recruit other bees.

To study how bees do this, we turned an observation hive horizontally (so that the bees could not use the "up" rule) and provided an artificial light as the only cue for dance orientation. We could control its elevation, angular size, intensity, wavelength distribution, degree of polarization, and direction of polarization (E-vector orientation) (*8*). Bees were individually numbered at the food source, and danced for distances of 265 to 700 m. Where appropriate, these dances were videotaped and analyzed cycle by cycle.

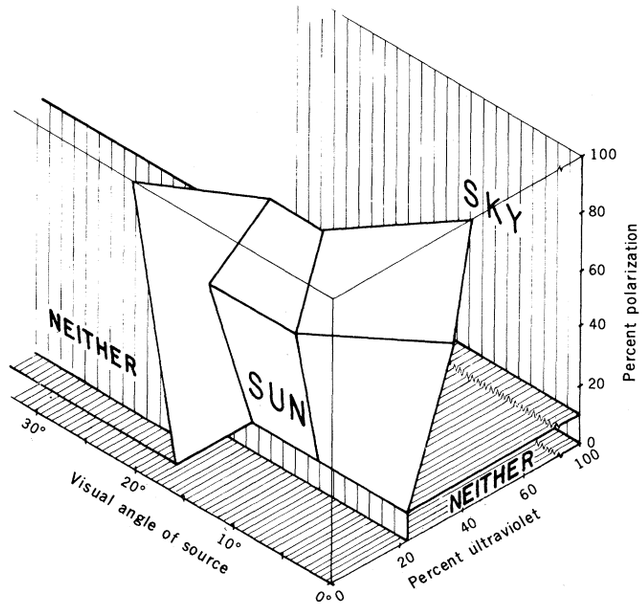

Fig. 1. Distinction between sun and sky. Dancing honey bees were shown one of more than 80 combinations of stimulus angle, spectral distribution, and percentage polarization (*8*). Subsequent dance orientations revealed whether the bees interpreted the pattern as sky or sun, or were disoriented ("neither" in the figure). Approximately 2450 dance cycles were recorded—at least five cycles from each of at least five dances. Near the boundary surface between sun and sky, a bee may exhibit both orientations. The 10 percent polarization boundary is based upon the data of Frisch (*2*, p. 403). Unpolarized UV light often elicited dance orientations 180° from that predicted on the basis of sun orientation, as though this situation was taken as the "antisun."

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