ng/ml-hour within 40 minutes. Simultaneously, MAP increased from a control level of 102 ± 6 to a plateau of 134 ± 7 mm-Hg and renal vascular resistance decreased by 11 percent. Administration of 7.5 ml of preimmune serum had no significant effect on these measures. Six units of renin-specific antiserum given 1 hour after constriction caused PRA to fall to control levels in 10 minutes and to 1.3 ± 0.7 ng/ml-hour in 40 minutes. The decrease in PRA was accompanied by a similar reduction in MAP to a nadir of 102 ± 6 mm-Hg and a 40 percent further decrease in renal vascular resistance.

The duration of action of the antibody was at least 21 hours as evidenced by continued suppression of PRA and MAP at or below control levels despite maintenance of renal perfusion pressure at 50 mm-Hg. Beyond this time PRA and MAP slowly approached their postconstriction, preantiserum levels (Fig. 3). This observation regarding duration of action was further supported by the inability of exogenous renin to increase systemic blood pressure for the first 24 hours. Injection of 1 Goldblatt unit of renin thereafter resulted in a pressor response comparable to that obtained before antiserum administration.

Renin-specific antibody completely blocked the pressor action of endogenous and exogenous dog renin, but had no effect on the pressor actions of angiotensin I or angiotensin II. The antibody caused no significant change in mean blood pressure in the sodium-replete state. In the sodium-depleted state, however, with consequent increased renin activity, the binding of the antibody to the enzyme reduced PRA below control levels. This was accompanied by a significant fall in blood pressure. After renal artery constriction, the rise in systemic pressure was associated with an increase in PRA. Renin antibody lowered PRA and restored pressure to normal. The onset of action of the antiserum was prompt (minutes) and the duration of action prolonged (approximately 24 hours). Since the antibody acts by inhibiting renin's enzymatic activity and does not appear to have other pharmacologic actions, these results provide definitive evidence for the role of the renin-angiotensin system in blood pressure homeostasis during sodium-depletion and in the initiation of renovascular hypertension.

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Lateralization of Reward in Rats: Differences in Reinforcing Thresholds

Abstract. *Fourteen rats with bilaterally implanted lateral hypothalamic electrodes were allowed to self-stimulate each side of the brain during daily test sessions. Rotation (circling behavior) during self-stimulation sessions was also recorded. All rats rotated in a preferential direction regardless of the side of the brain stimulated, and, in each case, the direction was the same as that subsequently determined in response to* d*-amphetamine. All rats had asymmetries in self-stimulation thresholds related to the direction of rotation. Thresholds were lower on the side contralateral to the direction of rotation, and entire rate-intensity functions were displaced to the left on that side. The results, discussed in terms of lateralization of affect, suggest a model in which quantitative differences in neuronal firing can be translated into apparent qualitative specialization, with the two sides of the brain appearing to be specialized for high and low mood, respectively.*

Cerebral functional asymmetry, once considered a unique characteristic of the human brain (*1*), has now been demonstrated in the brains of various animal species, including other primates (*2*), cats (*3*), rodents (*4*), and songbirds (*5*). Research conducted in our laboratory has established that normal rats have an asymmetry in nigrostriatal function; asymmetries in striatal dopamine content (*6*), striatal dopamine metabolism, and dopamine-stimulated adenylate cyclase activity (*7*) have been related to spontaneous side preferences (*6*) and to nocturnal (*8*) and drug-induced (*9*) circling behavior. Recently, using labeled deoxy-D-glucose to assess glucose utilization in rats (*10*), we reported evidence of asymmetry in several brain regions (*11*)—the results suggested stronger similarities in lateralization of human and rat brains than had previously been envisioned. We have now investigated the possibility of lateralized affect in rats. Neurological findings indicate that the two sides of the human brain are specialized in this regard, with one hemisphere characterized as more joyful and the other as more depressive (*12*). Reasoning that differences in affect could result from differences in the activity of mechanisms mediating reinforcement, we speculated that the two sides of the rat brain might be differentially sensitive to reinforcing brain stimulation.

The subjects were 14 naïve female Sprague-Dawley rats approximately 3 months old and weighing 250 to 280 g. All rats were initially administered *d*-amphetamine sulfate (1.0 mg per kilogram of body weight, injected intraperitoneally) and placed individually in an automated apparatus (*13*) in which circling behavior (or rotation) was measured for 1 hour. Surgery was performed at least a week later. Bipolar stainless steel electrodes were stereotaxically (*14*) implanted in both lateral hypothalami (*15*) of each rat. Electrode placements were verified histologically after the experiment was completed (*16*).

Testing for self-stimulation was first begun 3 to 4 days after surgery. Rats were placed in a Plexiglas cylinder (30 cm in diameter) containing a single lever and enclosed in a sound-attenuated cubicle. Lever-press responses were continuously rewarded with electrical stimulation to the lateral hypothalamus (one side at a time). The stimulation was a 60-

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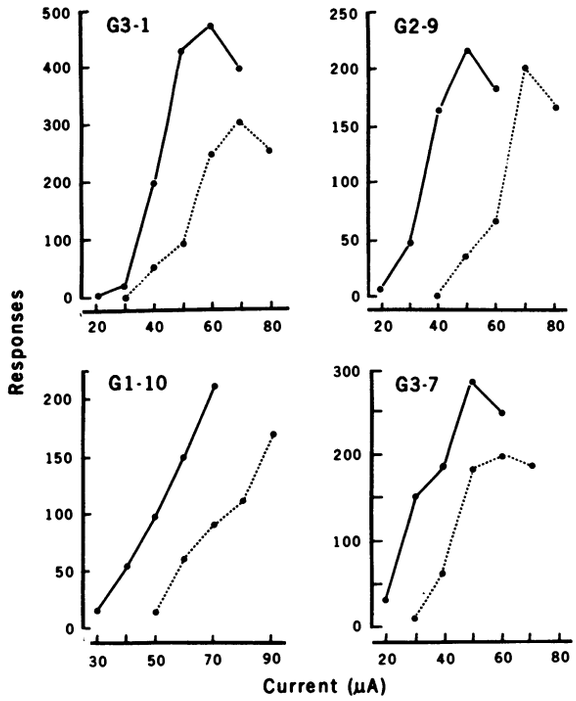

Fig. 1. Rate-intensity functions for four representative rats (averaged data for five sessions). The side of the brain contralateral to the direction of rotation is indicated by a solid line, the ipsilateral side by a dotted line.

Hz sine wave of 10 to 150 μA for 0.5 second. Responses were recorded (Sodeco counters). Rotation was also measured concomitantly during self-stimulation sessions; this was made possible by a commutator arrangement that used the movement of the stimulation cable as the source of input to the rotometer circuitry (*13*).

Availability of brain stimulation was signaled by a light 5 cm above the lever. Test sessions were conducted daily and consisted of ten 5-minute periods during which the stimulation was on, separated by 1-minute time-out (stimulation not available) periods; each side of the brain was stimulated for half of each session with the order (left or right side first) reversed each day. A current range of 10 to 150 μA was first sampled. After finding each electrode's approximate threshold, a rate-intensity function was determined each day, with different current levels presented in a descending series on each side of the brain during each session. Each rat was tested until its performance with each electrode was stable (*17*) across at least 5 days. Upon completion of self-stimulation testing each rat was again administered *d*-amphetamine and its circling behavior measured as it had been before surgery.

All rats had asymmetries in self-stimulation thresholds related to the preferred direction of rotation—thresholds were lower on the contralateral side (mean ± standard error (S.E.), 33.9 ± 6.3 μA contralateral versus 47.7 ± 9.5 μA ipsilateral; paired *t*-test, $P < .01$). In every case the preferred direction of rotation was the same before and after the operation both in response to *d*-amphetamine and during self-stimulation sessions (*18*). The rotation occurring during self-stimulation sessions was not elicited by the stimulation per se, inasmuch as the direction and magnitudes did not differ with the side of stimulation (*18, 19*); rather, such rotation appeared to be the consequence of the nonspecific arousal accompanying self-stimulation behavior, analogous to the rotation normally appearing at night (*8*). Sidedness differences in self-stimulation behavior were not restricted to thresholds—the entire rate-intensity functions were generally higher and displaced to the left on the side contralateral to the direction of rotation (Fig. 1).

It is unlikely that the asymmetries in self-stimulation behavior were artifactual in any way. Electrode placements were symmetrical (Fig. 2), and, most convincingly, the asymmetries were not random, being related in every instance to the direction of rotation. The results therefore indicate that reward processes in the rat are, to some extent, lateralized. The relationship to rotation, a dopamine-mediated behavior (*6–9*), is consistent with other findings implicating dopamine in mechanisms of self-stimulation (*20*).

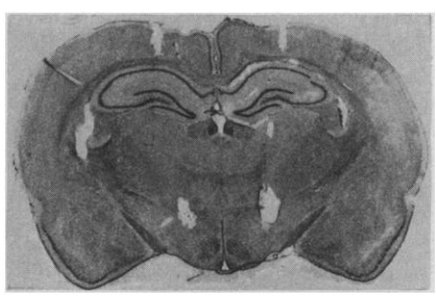

Fig. 2. Representative electrode placements. Lesions were made to facilitate localization (*16*).

Numerous questions remain to be answered, including whether similar effects are apparent in other brain regions and whether pathways mediating aversion also exhibit functional asymmetry. The implications of such findings are manifold. One might hypothesize, for example, that the side of the brain having lower reward thresholds would also have higher aversion thresholds. An individual presented with mood-related material engendering mixed affect might have one side of the brain more receptive to perceiving it as pleasant and the other side more likely to perceive it as unpleasant. In this way, quantitative differences in neuronal mechanisms (for example, rates of firing) could be translated into apparent qualitative specialization, with one side of the brain appearing to be specialized for high mood and the other for low mood. The results might also be relevant to our understanding of how different drugs act as reinforcers and maintain different patterns of addictive behavior. Subtle and not-so-subtle differences in the "highs" produced by different classes of drugs might be related to the different ways in which drugs can differentially influence the two sides of the brain. Regardless of whether these speculations are substantiated by future findings, it is becoming increasingly clear that lateralization is a fundamental aspect of brain function that must now be considered in any attempts to formulate animal models of human brain function.

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15. Coordinates were 0.6 mm posterior to bregma, ± 1.7 mm lateral to the midline, and 8.0 mm from the dura.
16. Before the rats were killed, lesions were made through all electrodes by a direct anodal current of 2 mA for 5 seconds. Rats were then perfused with 0.9 percent saline solution and 10 percent formalin; their brains were removed and immersed in formalin for at least a week before sections (40 μm, stained with Luxol blue and cresyl violet) were made.
17. The threshold for self-stimulation behavior was defined as the lowest current that would maintain a rate of responding higher than the highest rate during any time-out period. Performance was considered stable when the threshold remained constant, and the rates at each current setting varied no more than ± 10 percent from day to day.
18. Eight rats rotated to the left and six to the right. Rotation in response to *d*-amphetamine averaged 39.8 ± 19.8 net rotations per hour preoperatively and 43.6 ± 17.4 net rotations per hour postoperatively (net rotations were determined by subtracting rotations in the nonpreferred direction from those in the preferred direction (*13*). When self-stimulating the side of the brain opposite the preferred direction of rotation, rats averaged 20.3 ± 3.4 net rotations in 25 minutes; when self-stimulating the side of the brain ipsilateral to the preferred direction of rotation, rats averaged 23.2 ± 3.8 net rotations in 25 minutes.
19. If the rotation occurring during self-stimulation sessions had been elicited by the stimulus, the direction would have changed with the side of stimulation; see, for example, G. W. Arbuthnott and T. J. Crow, *Exp. Neurol.* **30**, 484 (1971).
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Anthophora Bees: Unusual Glycerides from Maternal Dufour's Glands Serve as Larval Food and Cell Lining

Abstract. *The Dufour's gland of* Anthophora abrupta, *a solitary bee, secretes a complex mixture of liquid triglycerides containing one long-chain and two short-chain fatty acids. This is applied inside the earthen brood cells and added to the provision, where it is converted, perhaps by enzymes from the bee's saliva or gut, to solid diglycerides that are later eaten by the bee larvae. This use of Dufour's gland secretion as food and its nutritive function are reminiscent of the royal jelly secreted by honey bees.*

Most bees (Apoidea) eat a diet of nectar and pollen exclusively. Exceptions are the well-known but chemically complex salivary royal jelly of honey bees; the host brood commonly eaten by inquiline bees (*1*); and the ingestion of Thysanoptera (*2*) and floral oils (*3*). The function of the Dufour's gland of the sting apparatus in Hymenoptera is incompletely known; however, in ants it secretes pheromones (*4*), and in various families of bees it produces the waterproof cell lining, which, being fragrant, may include pheromones (*5*). Several species of *Anthophora* have white, waxy cell linings with a cheesy odor (*6*), which long have been hypothesized to originate from the Dufour's gland (*7*). In this report we characterize the contents of Dufour's gland as an unusual group of triglycerides, show their conversion to diglycerides for construction of the cell lining, and demonstrate their ultimate use as larval food. This combination of features has apparently not been reported heretofore.

Anthophora abrupta Say is a univoltine solitary bee that usually nests gregariously in clay banks (*8*), and its subterranean cells are lined internally by a layer (0.1 mm) of waxy, white, waterproof substance. A group of females constructed 36 such cells in narrow, clay-filled, acrylic plastic chambers where their behavior was observed. During cell construction, the bees moistened the clay with regurgitated water, manipulated it by the mandibles and legs, and compacted it by the pygidial plate to form a smooth-walled earthen cell. A colorless, oily, faintly fragrant liquid was secreted onto the compacted soil from the sting chamber. Provisioning with pollen and nectar with addition of a transparent liquid from the sting chamber, oviposition, and cell capping followed. A few hours after provisioning began, the cell lining became opaquely white and developed a cheesy odor. The provisions also developed this odor and contained white flocculi. Larvae consumed the provisions within 3 weeks, and for the next 2 days they ate the cell lining (Fig. 1) before transforming into diapausing prepupae. Cells (500) opened in the field revealed that those with prepupae lacked the white lining but those with young larvae retained it, an indication that cell lining is normally eaten by larvae.

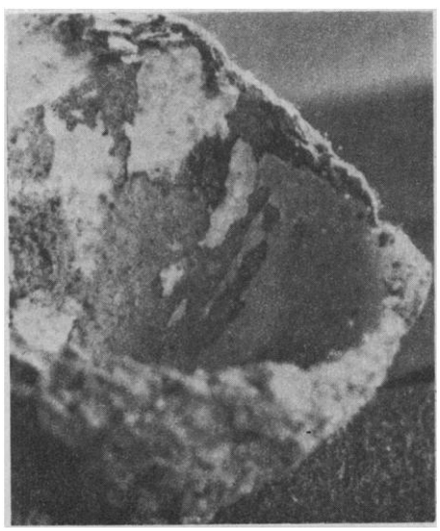

Fig. 1. Brood cell of *A. abrupta* showing grooves in the white lining that were made by the feeding larva.

The hypertrophied Dufour's gland of this bee occupies about half of the abdomen (Fig. 2). It is surrounded by numerous tracheoles, indicating a high metabolic rate. The lumen contains a copious, transparent oily liquid that solidifies after several weeks to a white, waxy, microcrystalline solid when smeared on glass and exposed to air.

The fresh Dufour's gland secretion (3.4 mg) was collected by capillary tube and dissolved in 1 ml of methylene chloride, and 1 μl was injected onto a 3-m column (packed with 1 percent Hi-Eff 3BP; Applied Sciences) of an LKB-9000 gas chromatograph–mass spectrometer system. Five main components eluted at 250°C (Fig. 2). Their electron ionization mass spectra show many ions related by a 2-carbon homology (*m/z* 43, 71, 99) suggesting acetyl, butyroyl, and hexanoyl groups, and all show a common palmitoyl ion at *m/z* 239. Unfortunately, no molecular ions (MH^+ ions) were observed, even with the use of chemical ionization with isobutane (Finnigan 4023). However, with the latter technique, all chromatographic peaks do show abundant ions for the loss of various acids from hypothetical MH^+ ions. Thus, in the mass spectrum of peak 4, assuming an MH^+ ion at *m/z* 499, fragment ions appear at *m/z* 243 (MH^+ − palmitic acid, 100 percent), 383 (MH^+ − hexanoic acid, 12 percent), and 411 (MH^+ − butyric acid, 8 percent). Subtraction of the acids from the molecular weight (498) leaves only 38 atomic mass units (C_3H_2), and hence the compound is simply the triglyceride butyroylhexanoylpalmitin. Its electron ionization mass spectrum shows ions as expected (*9*) at *m/z* 243 (M − palmitoyloxy), *m/z* 383 (M − hexanoyloxy), and *m/z* 411 (M − butyroyloxy). Spectra of the other chromatographic peaks show homologous ions that allow assignment of their structures as isomers of the re-

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