hood represented less than 2% of the kidney enzymatic capability.

The ontogenesis of GGTP in rat liver was sharply different from that in other tissues. During the 2 days before term, GGTP specific activity was comparable to that of the small intestinal mucosa. However, after birth there was a sharp decline and during the lactation period GGTP levels were almost negligible. Ultimately, adulthood values were about 1000 times lower than in the kidney.

Rat brain GGTP showed still a different pattern to that observed in other tissues. In absolute terms, the activity demonstrated was minimal before birth. At delivery, GGTP became undetectable and a moderate surge followed during the subsequent three weeks, stabilizing, at that point, at levels that persisted through adulthood.

Discussion. The patterns of GGTP ontogenesis in various tissues can provide clues to the importance of GGTP activity for the physiologic function of different organs during development in regard to amino acid exchanges and/or cellular turnover. The steady decrease of placental specific activity during the last third of gestation may suggest a progressive loss of physiologic role as the delivery date approaches. A similar pattern occurs in the brain (figs 1 and 2). The declining trend is shared by the liver. In this tissue, however, GGTP enzymatic activity drops rapidly after the 2nd day of life. By day 6 it is already negligible.

The kidney is the organ with the highest GGTP specific activity. The ascending progression observed early in life continues through adulthood. The levels of renal GGTP by far exceed those of all other organs and has thus received the greatest attention. This phenomenon prevails in all mammals. Physiologically, it provides an effective mechanism for the salvage of amino acids and the production of ammonium ions[2,11].

To an extent 3 orders of magnitude smaller than in the kidney, a steady increase of GGTP is also found in the brain, from birth through the adult stage. The significance of this finding is not yet clear, but may relate to the active translocation of amino acids through the blood-brain barrier[2,12].

The rat small intestinal mucosa presents a peak of GGTP levels at mid-lactation. This is a period of rapid growth, almost continuous feedings and proliferation of the mucosal surface. Afterwards, GGTP specific activity declines sharply and never surpasses one fourth to one half the maximum levels recorded at the 12th day of life.

Different enzymes usually show recognizable developmental characteristics. Some typical patterns have been described in hepatic enzymes of energy metabolism[13,14]. GGTP presents the singularity of possessing tissue-specific isozymes which have varied ontogenic patterns. In general, most enzymes have relatively low activity before birth and show a rapid increase in the postnatal period, as is the case in rat kidney GGTP. Teleologically, tissues may require at various stages of development one or several active translocation mechanisms for amino acids. The orders of magnitude differences existing for GGTP in the organs studied here also suggest that the transport of protein breakdown products may be simultaneously carried out by more than one, unrelated, energy-requiring mechanisms.

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A comment on the estimation of times required for the attainment of equilibrium by noncooperative, single site ligand-receptor systems

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Summary. A table presents the number of hours required for binding to reach 80% and 95% of the equilibrium value for a noncooperative, single site ligand binding system. A 2nd table provides the fraction of binding sites occupied and the fraction of the total ligand bound at equilibrium under the same conditions.

The rate equation for noncooperative, single site ligand binding systems can be represented as follows: $\frac{dB_{sp}}{dt} = k_a (S_o - B_{sp}) (B_{max} - B_{sp}) - k_d B_{sp}$, where B_{sp} is the concentration of specifically-bound ligand, S_o is the total ligand concentration, B_{max} is the total concentration of binding sites, k_a and k_d are the 2nd-order and 1st-order association and dissociation rate constants, and t is the time of incubation. The exact solution to this equation gives the value of B_{sp} as a function of time for the given incubation conditions if the rate constants (or the equilibrium constant, K_d, and one of the rate constants) can be estimated and if the concentrations of ligand and binding sites are known[1,2]. Thus, if nonspecific binding and loss due to inactivation of binding sites may be neglected as an approximation, the solution to the rate equation provides an estimate of the time required for any arbitrary degree of approach to the equilibrium value of specific binding. For example, in recent studies[3,4] the solution to the rate equation has been used to examine the effect of inadequate incubation time (during which equilibrium is not attained under conditions of low ligand

Table 1. Number of hours required for the concentration of specifically-bound ligand (B_{sp}) to reach 80% and 95% (upper and lower number in each pair, respectively) of true equilibrium for a noncooperative, single site binding system in which the second-order rate constant (k_a) equals 10^5 M^{-1} min^{-1}. For other values of k_a multiply the tabulated values by 10^5 and divide the product by k_a. B_{max} is the total number of binding sites, S_o is the total ligand concentration and K_d is the equilibrium constant

- Log S_o	- Log B_{max} = 7	8	9	10	11	7	8	9	10	11	7	8	9	10	11	7	8	9	10	11
	- Log K_d = 8					- Log K_d = 9					- Log K_d = 10					- Log K_d = 11				
6	0.28	0.27	0.27	0.27	0.27	0.28	0.27	0.27	0.27	0.27	0.28	0.27	0.27	0.27	0.27	0.28	0.27	0.27	0.27	0.27
	0.53	0.50	0.49	0.49	0.49	0.54	0.50	0.50	0.50	0.50	0.54	0.50	0.50	0.50	0.50	0.54	0.50	0.50	0.50	0.50
6.5	0.96	0.83	0.82	0.82	0.82	1.01	0.86	0.85	0.85	0.85	1.02	0.86	0.85	0.85	0.85	1.02	0.86	0.85	0.85	0.85
	1.90	1.56	1.53	1.53	1.53	2.02	1.61	1.58	1.57	1.57	2.03	1.61	1.58	1.58	1.58	2.03	1.61	1.58	1.58	1.58
7	2.74	2.52	2.45	2.44	2.44	4.54	2.79	2.67	2.66	2.66	5.78	2.82	2.69	2.68	2.68	6.35	2.83	2.70	2.68	2.68
	5.96	4.76	4.56	4.54	4.54	12.41	5.30	4.98	4.95	4.94	20.34	5.36	5.02	4.99	4.99	26.62	5.36	5.03	5.00	4.99
7.5	2.70	6.56	6.47	6.45	6.44	3.15	9.55	8.34	8.23	8.22	3.21	10.09	8.59	8.47	8.46	3.21	10.15	8.62	8.49	8.48
	5.29	12.61	12.07	12.00	12.00	6.29	18.97	15.61	15.33	15.31	6.42	20.19	16.08	15.77	15.74	6.43	20.32	16.13	15.82	15.79
8	2.52	11.07	13.24	13.40	13.41	2.79	27.44	25.21	24.47	24.39	2.82	45.37	27.92	26.69	26.57	2.83	57.77	28.23	26.93	26.81
	4.76	21.22	24.74	24.94	24.96	5.30	59.62	47.65	45.61	45.41	5.36	124.1	52.95	49.76	49.47	5.36	203.5	53.56	50.22	49.91
8.5	2.46	12.79	19.41	20.28	20.37	2.70	26.96	65.61	64.66	64.47	2.72	31.48	95.51	83.39	82.34	2.73	32.05	100.9	85.91	84.69
	4.61	24.12	36.23	37.76	37.92	5.05	52.90	126.1	120.7	120.0	5.10	62.86	189.7	156.1	153.4	5.10	64.16	201.9	160.8	157.7
9	2.45	13.24	22.59	24.20	24.37	2.67	25.21	110.7	132.4	134.0	2.69	27.92	274.4	252.1	244.7	2.70	28.23	453.7	279.2	266.9
	4.56	24.74	42.10	45.04	45.35	4.98	47.65	212.2	247.4	249.4	5.02	52.95	596.2	476.5	456.1	5.03	53.56	1241	529.5	497.6
9.5	2.44	13.36	23.79	25.76	25.98	2.66	24.64	127.9	194.1	202.8	2.68	26.97	269.6	656.1	646.6	2.69	27.23	314.8	955.1	833.9
	4.55	24.90	44.31	47.96	48.35	4.95	46.09	241.2	362.3	377.6	5.00	50.49	529.0	1261	1207	5.00	50.98	628.6	1897	1561
10	2.44	13.40	24.20	26.30	26.53	2.66	24.47	132.4	225.9	242.0	2.68	26.69	252.1	1107	1324	2.68	26.93	279.2	2744	2521
	4.54	24.94	45.04	48.96	49.39	4.95	45.61	247.4	221.0	450.4	4.99	49.76	476.5	2122	2474	5.00	50.22	529.5	5962	4765
10.5	2.44	13.41	24.33	26.48	26.71	2.66	24.41	133.6	237.9	257.6	2.68	26.60	246.4	1279	1941	2.68	26.84	269.7	2696	6561
	4.54	24.96	45.28	49.28	49.72	4.94	45.46	249.0	443.1	479.6	4.99	49.54	460.9	2412	3623	4.99	49.99	505.0	5290	12612
11	2.44	13.41	24.37	26.53	26.77	2.66	24.39	134.0	242.0	263.0	2.68	26.57	245.0	1324	2259	2.68	26.81	267.0	2521	11071
	4.54	24.96	45.35	49.39	49.83	4.94	45.41	249.4	450.4	490.0	4.99	49.47	456.1	2474	4210	4.99	49.91	498.0	4765	21217
11.5	2.44	13.41	24.38	26.55	26.79	2.66	24.39	134.1	243.3	264.8	2.68	26.56	244.1	1336	2379	2.68	26.80	266.0	2464	12793
	4.54	24.96	45.38	49.42	49.86	4.94	45.40	249.6	452.8	492.8	4.99	49.44	454.6	2490	4431	4.99	49.89	495.4	4609	24116
12	2.44	13.41	24.38	26.56	26.79	2.66	24.39	134.1	243.7	265.3	2.68	26.56	243.9	1340	2420	2.68	26.80	265.7	2447	13235
	4.54	24.96	45.39	49.43	49.87	4.94	45.39	249.6	453.5	493.9	4.99	49.44	454.1	2494	4504	4.99	49.88	494.7	4561	24743

Table 2. Fraction of specific binding sites occupied and the fraction of the total ligand involved in that binding at equilibrium for a noncooperative, single site binding system. Tabulated data are expressed as percentages with B_{sp}/B_{max} ($\times 100$) presented as the upper and B_{sp}/S_o ($\times 100$) as the lower number in each pair. B_{sp} is the concentration of specifically-bound ligand, B_{max} is the total number of binding sites, S_o is the total ligand concentration and K_d is the equilibrium constant

- Log S_o	- Log B_{max} = 7	8	9	10	11	7	8	9	10	11	7	8	9	10	11	7	8	9	10	11
	- Log K_d = 8					- Log K_d = 9					- Log K_d = 10					- Log K_d = 11				
6	98.9	99.0	99.0	99.0	99.0	99.9	99.9	99.9	99.9	99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9
	9.9	1.0	0.1	< 0.1	< 0.1	10.0	1.0	0.1	< 0.1	< 0.1	10.0	1.0	0.1	< 0.1	< 0.1	10.0	1.0	0.1	< 0.1	< 0.1
6.5	95.7	96.8	96.9	96.9	96.9	99.5	99.7	99.7	99.7	99.7	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9	> 99.9
	30.2	3.1	0.3	< 0.1	< 0.1	31.5	3.2	0.3	< 0.1	< 0.1	31.6	3.2	0.3	< 0.1	< 0.1	31.6	3.2	0.3	< 0.1	< 0.1
7	73.0	90.1	90.8	90.9	90.9	90.5	98.9	99.0	99.0	99.0	96.9	99.9	99.9	99.9	99.9	99.0	99.9	> 99.9	> 99.9	> 99.9
	73.0	9.0	0.9	0.1	< 0.1	90.5	9.9	1.0	0.1	< 0.1	96.9	10.0	1.0	0.1	< 0.1	99.9	10.0	1.0	0.1	< 0.1
7.5	27.8	71.0	75.5	75.9	76.0	31.2	95.7	96.8	96.9	96.9	31.6	99.5	99.7	99.7	99.7	31.6	99.9	99.9	> 99.9	> 99.9
	87.8	22.5	2.4	0.2	< 0.1	98.6	30.2	3.1	0.3	< 0.1	99.8	31.5	3.2	0.3	0.1	99.9	31.6	3.2	0.3	0.1
8	9.0	38.2	48.8	49.9	50.0	9.9	73.0	90.1	90.8	90.9	10.0	90.5	98.9	99.0	99.0	10.0	96.9	99.9	99.9	99.9
	90.1	38.2	4.9	0.5	< 0.1	98.9	73.0	9.0	0.9	0.1	99.9	90.5	9.9	1.0	0.1	> 99.9	96.9	10.0	1.0	0.1
8.5	2.9	14.6	22.7	23.9	24.0	3.1	27.8	71.0	75.5	75.9	3.2	31.2	95.7	96.8	96.9	3.2	31.6	99.5	99.7	99.7
	90.7	46.1	7.2	0.8	0.1	99.9	87.8	22.5	2.4	0.2	99.9	98.6	30.2	3.1	0.3	> 99.9	99.8	31.5	3.2	0.3
9	0.9	4.9	8.4	9.0	9.1	1.0	9.0	38.2	48.8	49.9	1.0	9.9	73.0	90.1	90.8	1.0	10.0	90.5	98.9	99.0
	90.8	48.8	8.4	0.9	0.1	99.0	90.1	38.2	4.9	0.5	99.9	98.9	73.0	9.0	0.9	> 99.9	99.9	90.5	9.9	1.0
9.5	0.3	1.6	2.8	3.0	3.1	0.3	2.9	14.6	22.7	23.9	0.3	3.1	27.8	71.0	75.5	0.3	3.2	31.2	95.7	96.8
	90.9	49.6	8.9	1.0	0.1	99.0	90.7	46.1	7.2	0.8	99.9	99.0	87.8	22.5	2.4	> 99.9	99.9	98.6	30.2	3.1
10	0.1	0.5	0.9	1.0	1.0	0.1	0.9	4.9	8.4	9.0	0.1	1.0	9.0	38.2	48.8	0.1	1.0	9.9	73.0	90.1
	90.9	49.9	9.0	1.0	0.1	99.0	90.9	48.8	8.4	0.9	99.9	99.0	90.1	38.2	4.9	> 99.9	99.9	98.9	73.0	9.0
10.5	< 0.1	0.2	0.3	0.3	0.3	< 0.1	0.3	1.6	2.8	3.0	< 0.1	0.3	2.9	14.6	22.7	< 0.1	0.3	3.1	27.8	71.0
	90.9	50.0	9.1	1.0	0.1	99.0	90.9	49.6	8.9	1.0	99.9	99.0	90.7	46.1	7.2	> 99.9	99.9	99.0	87.8	22.5
11	< 0.1	< 0.1	0.1	0.1	0.1	< 0.1	0.1	0.5	0.9	1.0	< 0.1	0.1	0.9	4.8	8.4	< 0.1	0.1	1.0	9.0	38.2
	90.9	50.0	9.1	1.0	0.1	99.0	90.9	49.9	9.0	1.0	99.9	99.0	90.8	48.8	8.4	> 99.9	99.9	99.0	90.1	38.2
11.5	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	0.2	0.3	0.3	< 0.1	< 0.1	0.3	1.6	2.8	< 0.1	< 0.1	0.3	2.9	14.6
	90.9	50.0	9.1	1.0	0.1	99.0	90.9	50.0	9.1	1.0	99.9	99.0	90.9	49.6	8.9	> 99.9	99.9	99.0	90.7	46.1
12	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	0.1	0.1	< 0.1	< 0.1	0.1	0.5	0.9	< 0.1	< 0.1	0.1	0.9	4.9
	90.9	50.0	9.1	1.0	0.1	99.0	90.9	50.0	9.1	1.0	99.9	99.0	90.9	49.9	9.0	> 99.9	99.9	99.0	90.8	48.8

concentration) on measured 'equilibrium' dissociation constants. The solution to the rate equation can also provide insight into several apparently paradoxical phenomena, including the observation that the degree of approach to equilibrium within a given time is not always a monotonically increasing function of ligand concentration[2].

To facilitate estimation of the times required for the attainment of equilibrium under a variety of conditions we offer in table 1 a short summary of solutions to the rate equation for various useful combinations of the relevant variables B_{max}, S_o and K_d (i.e. k_d/k_a). The initial condition is simply that $B_{sp}=0$ at $t=0$, and the solution is presented as a table of pairs of numbers representing the time (in h) required for B_{sp} to attain 80% and 95% of the equilibrium value. The times were generated (by a very simple Fortran program) for $k_a = 10^5\ M^{-1}\ min^{-1}$. For other values of k_a one simply multiplies the tabulated values by 10^5 and divides the resulting product by k_a. In table 2 we provide estimates of the fraction of binding sites occupied and the fraction of the total ligand bound at equilibrium under the same hypothetical conditions as in table 1. (These percentages apply to all values of k_a.)

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Locomotor behavior in relation to octopamine levels in the ant *Lasius niger*

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Summary. The heads and bodies of hyperactive and hypoactive ants, selected on the basis of motor activity, were tested for their octopamine content. The level was found to be significantly higher in hyperactive animals. A possible involvement of octopamine in locomotor behavior is discussed.

Since highly sensitive and specific determination techniques[1-4] for the non-catecholic amine octopamine have been developed, it has been found in a wide range of vertebrates and invertebrates (see reviews by Robertson and Juorio[5] and by Robertson[6]). This amine is found to be associated with behavior in the rat[7,8] and in the locust *Locusta migratoria*[9]. In these 2 animals, high octopamine levels are associated with avoidance conditioning[8] and with the solitary phase status, respectively[9]. These observations suggested a correlation between the amine and the animal's activity, and led us to study the octopamine levels in ants in parallel with their degree of activity.

Methods. 40 worker individuals from *Lasius niger* were selected on the basis of locomotor activity[10]. This activity, in constant fluctuation, is estimated by the frequency of similar scores (or activity levels) given by the number of circular tracks run in 1 h in repeated tests. Thus animals were separated into groups of hypermotors or hypomotors.

Locomotor activity is characterized by a coefficient (k_a) computed from the indices (0 to 6) attributed to different levels of activity and noted at the tops of each column (table 1).

The coefficient k_a is the quotient of the sum S (sum of the products of the indices 'i' and the corresponding frequencies 'fi') by the total number of tests N. Example for the individual A:

$$k_a = \frac{S\,(2\times 1)+(3\times 3)+(4\times 9)+(5\times 5)+(6\times 6)}{24} = 4.5$$

This coefficient permits us to consider different levels of activity: very high, high, median, low, and very low. Animals used for this work were selected on a severe criterium with a coefficient ka higher than 4.42 (very high) for individuals named 'hyperactive' and lower than 1.42 (very low) for those considered as 'hypoactive' (table 2).

The animals were killed immediately after locomotor testing and heads and bodies were separately kept frozen at −70 °C. Tissues were analyzed within a week for their octopamine content according to the method described by Molinoff and Axelrod[1] as modified by David[4].

Tissues were homogenized with a Potter homogeniser in 10 vol. of tris-HCl buffer 0.05 M (PH 8.6) containing 1 mM pargyline. Extracts were kept in a boiling water bath for 5 min and centrifuged for 5 min at 20,000 × g; 150 µl of supernatant were incubated at 37 °C with 37.5 µl of PNMT (phenyl-ethanolamine N-methyl-transferase) partially purified according to Saelens et al.[11], and 0.04 nmole of [^{3}H]-

Table 1. Example of locomotor activity levels in the ant *Lasius niger*

Activity level	→ 15	16-49	50-89	90-129	130-169	170-189	190→	Activity coefficient
Index	0	1	2	3	4	5	6	k_a
Animal								
A	0	0	1	3	9	5	6	4.50 very high
B	0	0	1	4	12	3	0	3.85 high
C	0	4	12	6	2	0	0	2.25 low
D	6	8	5	5	0	0	0	1.37 very low