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Anatomical Distribution of Estrogen, Androgen, Progestin, Corticosteroid and Thyroid Hormone Target Sites in the Brain of Mammals: Phylogeny and Ontogeny

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SYNOPSIS The pattern of the anatomical distribution of estrogen target cells in insectivores, rodents and primates is similar. It shows relationship to the patterns observed in non-mammalian vertebrates. In the forebrain it includes preoptic-septal, central hypothalamic, thalamic and allocortical sites. In neonatal and fetal rodents similar target sites can be demonstrated and evolve during embryonic development; however, the nuclear groups are not as well differentiated and the appearance of steroid hormone receptors does not occur simultaneously in them. Androgen target cells are accumulated at sites that overlap in part with those of estradiol, but in addition are found extensively in areas associated with psychomotor and somatomotor functions, including floor-plate derivatives in the lower brain stem and spinal cord. Glucocorticosteroids show extensive localization in neurons of the allocortex. This indicates a phylogenetically recent forebrain acquisition, compared to the sex steroids. Thyroid hormones show nuclear concentration in many neurons, in addition to selective uptake in tanycytic ependyma, choroid plexus and certain neuropil. The close topographic relationship of hormone target cells to the recess organs of the ventricular system led us to propose the concept of interrelated periventricular secretory units.

INTRODUCTION

The nuclear concentration of ^3H estradiol in neurons and the topographic distribution of such estrogen target neurons was first demonstrated and established through the use of the dry-mount and thaw-mount autoradiographic techniques (Stumpf and Roth, 1976; Stumpf and Sar, 1975*a*). The topographic pattern of estrogen target cells for the rat diencephalon (Stumpf, 1968), the rat forebrain (Stumpf, 1970) and the rat and mouse midbrain, pons, medulla and spinal cord (Stumpf and Sar, 1975*b*; Stumpf *et al.*, 1975) has provided a basis for subsequent studies in this field and has since been largely confirmed by others regarding the estrogen distribution in the forebrain (Anderson and Greenwald, 1969; Attramatal 1970; Tuohimaa 1970; Warembourg 1970; Pfaff, 1973). This hormone architecture for estrogen target cells in the rodent forebrain has subsequently been shown to be paradigmatic not only for mammals but for the non-mammalian vertebrate brain as well (see Stumpf and Grant, 1975; Stumpf *et al.*, 1978). In all of the vertebrate species studied in our laboratory—including lamprey (unpublished), goldfish (Kim *et al.*, 1978*a*), platyfish (unpublished), salamander (unpublished), lizard (Stumpf *et al.*, 1978), turtle (unpublished), ring dove (Martinez-Vargas *et al.*, 1975*b*) opossum (unpublished), tree shrew (Keefer and Stumpf, 1975*a*), mouse (Stumpf and Sar, 1975*b*), rat (Stumpf *et al.*, 1975), guinea pig (Sar and Stumpf, 1975), hamster (unpublished) and squirrel monkey (Keefer and Stumpf, 1975*b*)—estrogen target cells are seen to be accumulated in certain parts of the preoptic-septal area, the central hypothalamus and the thalamus. Certain amygdaloid, hippocampal and related allocortical structures are generally included, with the probable exception of fishes, where such cortical organization is absent or only spuriously developed.

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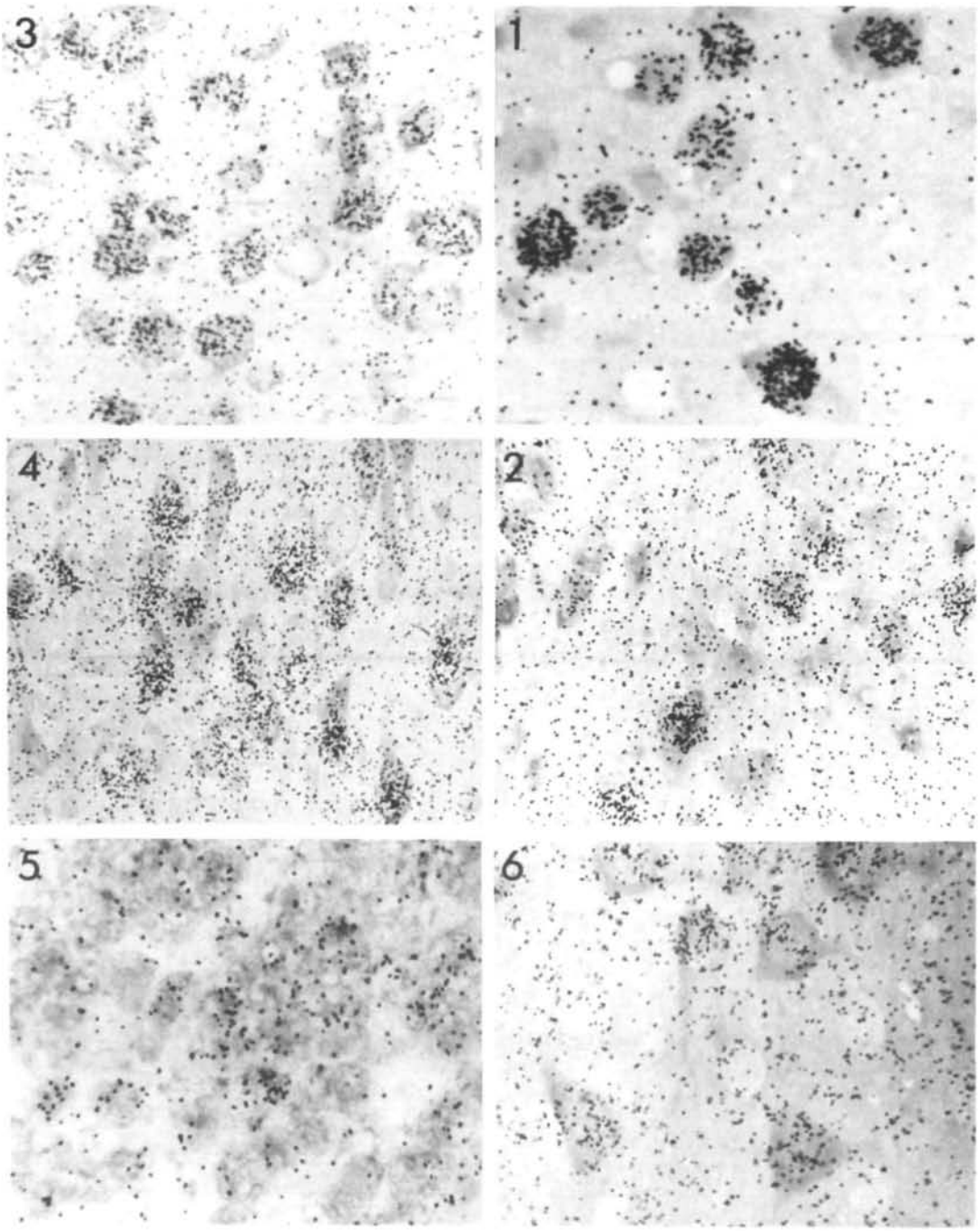


FIGS. 1-6. Autoradiograms showing the unclear concentration of radioactivity after injection of ^{3}H estradiol (FIG. 1) and ^{3}H progesterone (FIG. 2) in guinea pig arcuate nucleus; after ^{3}H dihydrotestosterone in rat medial preoptic nucleus (FIG. 3) and ^{3}H corticosterone in rat hippocampus (FIG. 4); after ^{3}H diethylstilbestrol in arcuate nucleus of 16-day mouse fetus (FIG. 5); after ^{125}I triiodothyronin in rat piriform cortex (FIG. 6). Four μ sections, thaw-mounted on emulsion precoated slides; × 670 (Fig. 1), × 480 (Figs. 2-6). Exposure time 3 to 12 months. Reproduced from Sar and Stumpf (1975): Fig. 1; Stumpf and Sar (1975*c*): Fig. 6.

RESULTS AND DISCUSSION

A brief account is given here to demonstrate some of the essential autoradiographic data available to date. Figures 1-6 show representative autoradiograms from different brain regions that depict the typical nuclear concentration of radioactivity after injection of ^{3}H estradiol (Fig. 1) or ^{3}H progesterone (Fig. 2) in guinea pig, ^{3}H dihydrotestosterone (Fig. 3) or ^{3}H corticosterone (Fig. 4) in adult rat, ^{3}H diethylstilbestrol in 16-day mouse fetus (Fig. 5) and ^{125}I triiodothyronin in adult rat (Fig. 6).

The topographic distribution of *estrogen* target neurons is depicted in Figures 7-10, 11A and 12A for the preoptic and central hypothalamic planes of the brain of mouse (Figs. 7A and B), guinea pig (Figs. 8A and B), tree shrew (Figs. 9A and B), squirrel

Abbreviations: AA (aaa), area amygdala anterior; *aa,* area amygdala; *ab,* n. ambiguus; *aba,* n. basalis accessorius amygdalae; *abal,* n. basalis accessorius lateralis amygdalae; *abam,* n. basalis accessorius medialis amygdalae; *abl,* n. amygdaloideus basalis, pars lateralis; *abm,* n. amygdaloideus basalis, pars medialis; *ac,* n. amygdaloideus centralis; *aco,* n. amygdaloideus corticalis; *al,* n. amygdaloideus lateralis; *ala,* n. amygdaloideus lateralis, pars anterior *alp,* n. amygdaloideus lateralis, pars posterior; *am,* n. amygdaloideus medialis; *ar,* n. arcuatus hypothalami; *C,* cingulum; *CA,* comissura anterior; *CAI,* capsula interna; *cci,* cortex colliculi inferioris; *CF,* commissura fornicis; *cl,* claustrum; *CO,* chiasma opticum; *coe,* n. coeruleus; *cov,* n. cochlearis ventralis; *cp,* n. caudatus putamen; *CPF,* cortex piriformis; *CSP,* tractus corticospinalis; *CTH,* commissura thalami; *cu,* n. cuneiformis; *dcmi,* n. dorsomedialis colliculi inferioris; *DCT,* decussatio corporis trapezoidei; *eci,* n. externalis colliculi inferioris; *F,* columna fornicis; *FH,* fimbria hippocampi; *FLM,* fasiculus longitudinalis medialis; *fm,* n. paraventricularis (filiformis) pars magnocellularis; *FMP,* fasiculus medialis prosencephali; *FMT,* fasiculus mammillothalamicus; *fp,* n.

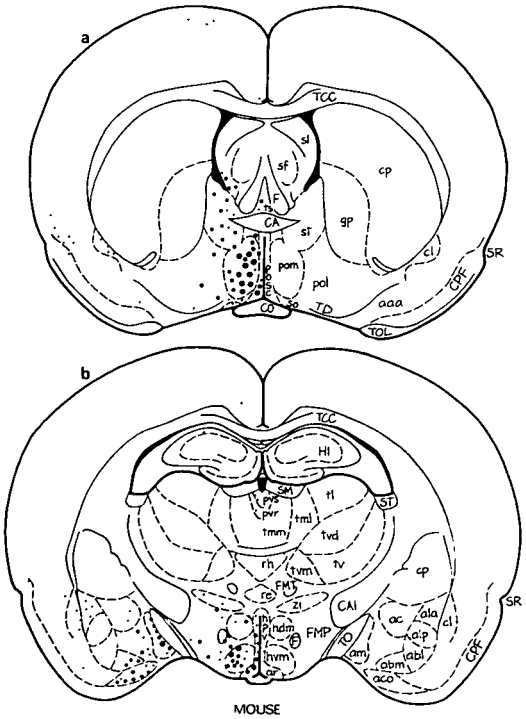


FIG. 7. Localization of estrogen target neurons in preoptic (a) and central hypothalamic (b) levels of the brain of mouse (reproduced from Stumpf and Sar, 1975*b*). Compare with Figures 8-10. The dots on the left half of the schematics represent intensity and frequency of occurrence of estrogen target neurons. Designations of structure on right half.

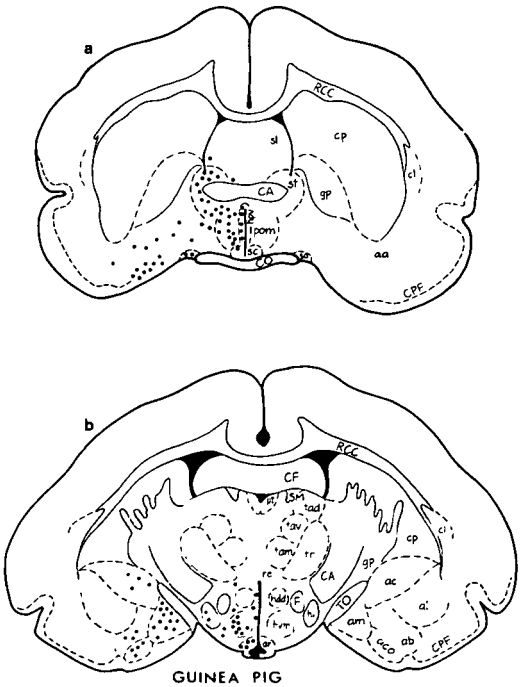


FIG. 8. Localization of estrogen target neurons in preoptic (a) and central hypothalamic (b) levels of the brain of guinea pig—incomplete (modified from Stumpf and Sar, 1975). Compare with Figures 7, 9, 10. The dots on the left half of the schematics represent intensity and frequency of occurrence of estrogen target neurons. Designations of structure on right half.

paraventricularis (filiformis) pars parvocellularis; *g*, n. gelatinosus; *gc*, griseum centrale; *GD*, gyrus dentatus; *gp*, globus pallidus; *ha*, n. anterior hypothalami; *hd*, n. dorsomedialis hypothalami; *hdd*, n. dorsomedialis hypothalami pars dorsalis; *hdm*, n. hypothalamicus dorsomedialis; *hdv*, n. dorsomedialis, pars ventralis; *HI*, hippocampus; *hl (lh)*, n. habenulae lateralis; *hpv*, n. periventricularis hypothalami; *hvm*, n. ventromedialis hypothalami; *hvma*, n. ventromedialis, pars anterior; *hvmp*, n. ventromedialis, pars posterior; *if*, n. infundibularis; *IG*, indusium griseum; *LL*, lemniscus lateralis; *lld*, n. lemnisci lateralis dorsalis; *LM*, lemniscus medialis; *m*, n. mammillaris; *mh*, n. medialis habenulae; *mmm*, n. mammillaris medialis, pars medialis; *OVLT*, organum vasculosum laminae terminalis; *p*, n. pretectalis; *pa*, n. paraventricularis; *pci*, n. principalis colliculi inferioris; *PCM*, pedunculus cerebellaris medius; *PCS*, pedunculus cerebellaris superior; *pd*, n. premammillaris dorsalis; *po*, n. pontis; *pol*, n. preopticus lateralis; *pols*, n. paraolivaris superior; *pom*, n. preopticus medialis; *poma*, n. preopticus magnocellularis; *pome*, n. preopticus medianus; *posc*, n. preopticus, pars suprachiasmatica; *pt*, n. paratenialis; *pvr*, n. periventricularis rotundocellularis; *pvs*, n. periventricularis stellatocellularis; *rad*, n. raphes dorsalis; *RCC*, radiatio corpus callosi; *re*, n. reuniens; *rh*, n. rhomboideus; *rpc*, n. reticularis pontis; *rpo*, n. reticularis pontis oralis; *rtp*, n. reticularis tegmenti; *S*, subiculum; *s*, n. supragenicularis; *sc*, n. suprachiasmaticus; *sf*, n. septalis fimbrialis; *sgco*, substantia gliosa cochlearis; *sl*, n. septi lateralis; *SM*, stria medullaris thalami; *sm*, n. septi medialis; *so*, n. supraopticus; *SR*, sulcus rhinalis; *ST*, stria terminalis; *st*, n. interstitialis striae terminalis; *tad*, n. anterior dorsalis thalami; *tam*, n. anterior medialis thalami; *tav*, n. anterior ventralis thalami; *TCC*, truncus corporis callosum; *TD*, tractus diagonalis; *td*, n. tractus diagonalis (Broca); *tl*, n. lateralis thalami; *tml*, n. medialis thalami, pars lateralis; *tmm*, n. medialis thalami, pars medialis; *TMT*, tractus mam-

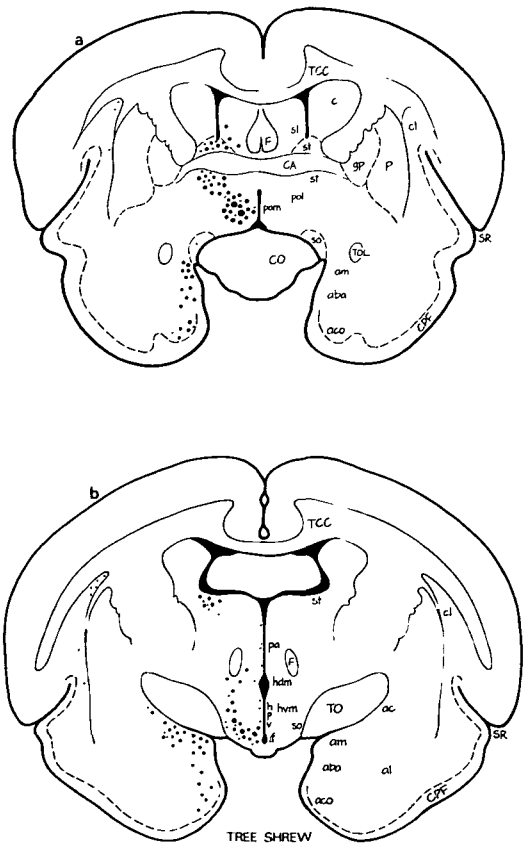


FIG. 9. Localization of estrogen target neurons in preoptic (a) and central hypothalamic (b) levels of the brain of tree shrew (modified from Keefer and Stumpf, 1975*a*, *b*). Compare with Figures 7, 8, 10. The dots on the left half of the schematics represent intensity and frequency of occurrence of estrogen target neurons. Designations of structure on right half.

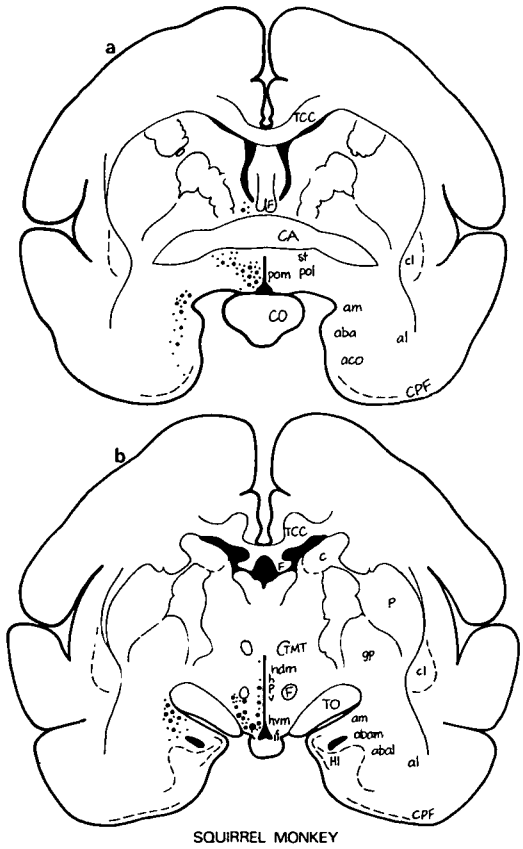
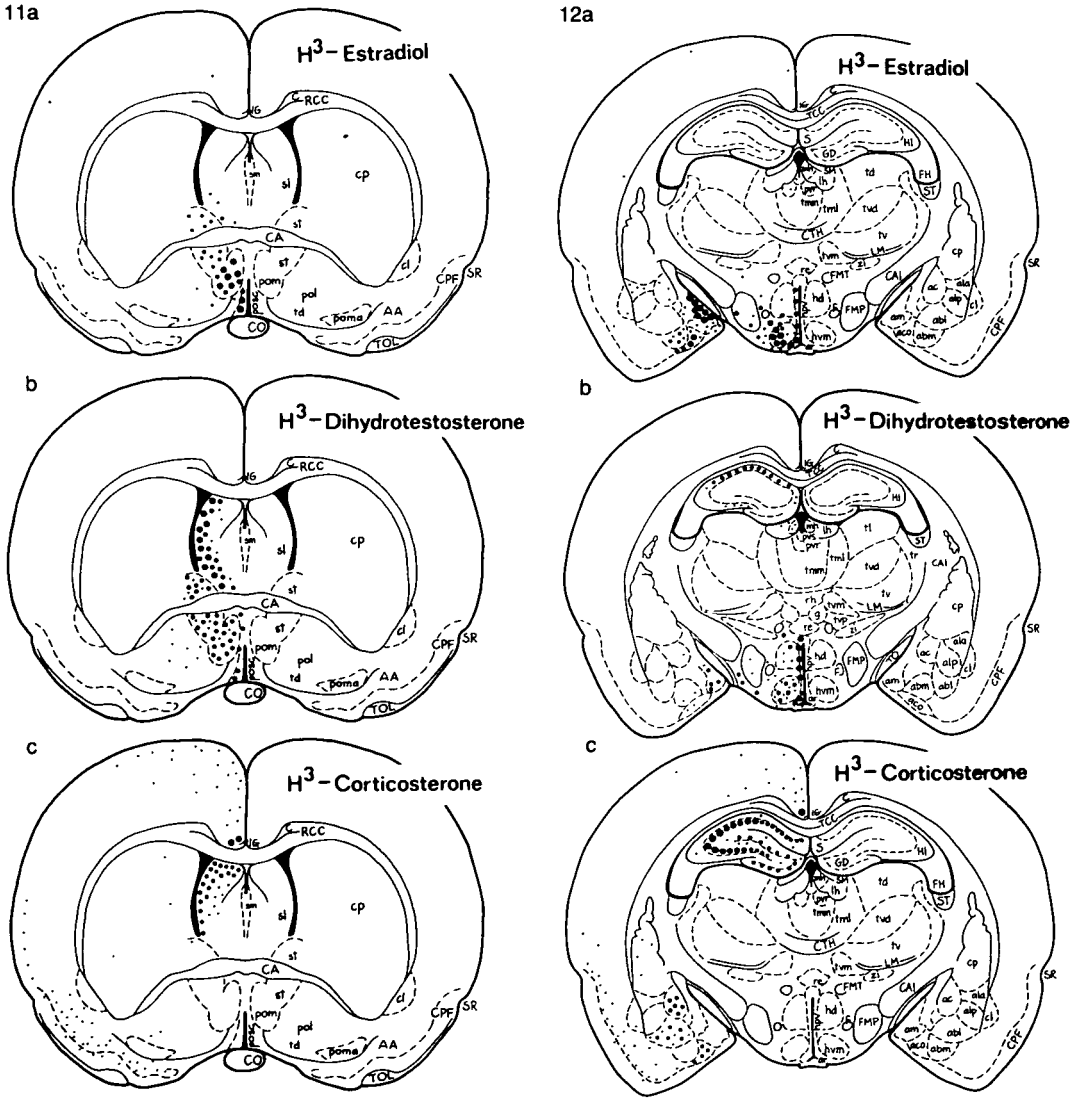
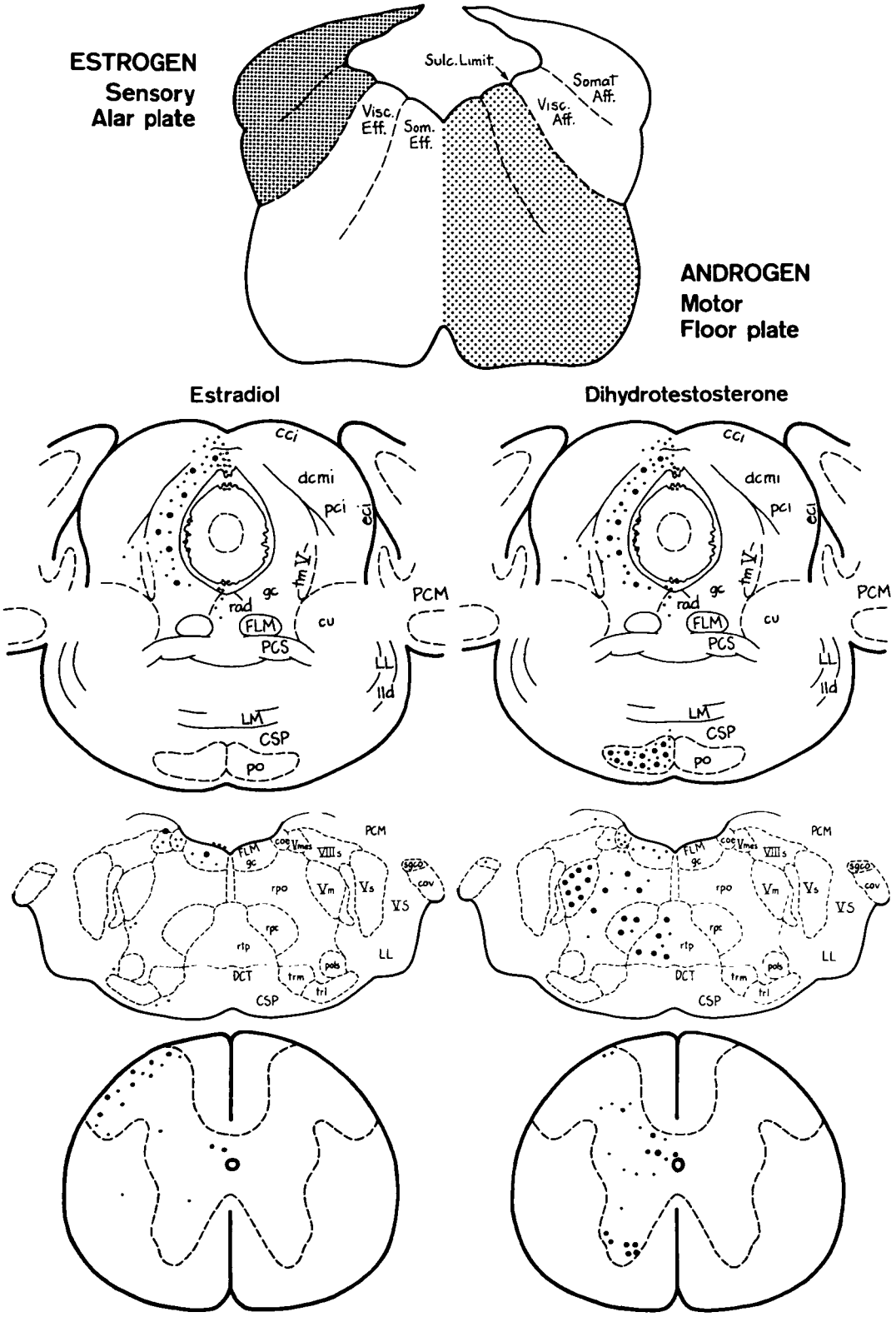


FIG. 10. Localization of estrogen target neurons in preoptic (a) and central hypothalamic (b) levels of the brain of squirrel monkey (modified from Keefer and Stumpf, 1975*a*, *b*). Compare with Figures 7-9. The dots on the left half of the schematics represent intensity and frequency of occurrence of estrogen target neurons. Designations of structure on right half.

millothalamicus; *TO*, tractus opticus; *TOL*, tractus olfactorius lateralis; *tr*, n. reticularis thalami; *trl*, n. trapezoides lateralis; *trm*, n. trapezoides medialis; *ts*, n. triangularis septi; *tv*, n. ventralis thalami; *tvd*, n. ventralis thalami, pars dorsomedialis; *tvm*, n. ventralis medialis thalami, pars magnocellularis; *tvp*, n. ventralis medialis thalami, pars parvocellularis; *Vm*, n. motorius nervi trigemini; *Vmes (tmV)*, n. tractus mesencephali nervi trigemini; *VS*, tractus spinalis nervi trigemini; *Vs*, n. sensibilis nervi trigemini; *VIIIs*, n. vestibularis superior; *zi*, zona incerta.



FIGS. 11-12. Comparison of estrogen, androgen and glucocorticosteroid distribution in rat brain at preoptic-septal levels (FIG. 11) and central hypothalamic-hippocampal levels (FIG. 12). In the lateral septum and hippocampus, androgen and corticosterone target cells are numerous, while estrogen target cells are only few. In contrast, estrogen and androgen localize in the preoptic and basal tuberal regions, where no cellular localization of corticosterone can be demonstrated. Note also the difference in amygdaloid and cortical regions. Glucocorticosteroid localization is absent in most of the medial amygdaloid nucleus, but present in the lateral part of the amygdaloid basal nucleus, contrary to estradiol. The strong representation of corticosterone in the cerebral cortex suggests a phylogenetically more recent acquisition, compared to the sex steroids. Reproduced from Stumpf *et al.* (1975): Figs. 11-12, top; from Sar and Stumpf (1977*b*): Figs. 11-12 center; from Stumpf and Sar (1975*c*):Figs. 11-12, bottom.



monkey (Figs. 10a and b) and rat (Figs. 11a and 12a). A comparison of the individual planes shows great similarity among the different mammalian species. Apparently, in all mammals, the preoptic nuclei, the bed nucleus of the stria terminalis, the medio-cortical amygdaloid nuclei and the infundibular (arcuate)-premammillaris ventralis-ventromedialis (pars ventrolateralis) nuclear groups are involved. Existing variations, for instance, in the thalamus, allocortex and claustrum may represent true differences, but may also relate to variations in technique, dose, exposure time, or hormonal state of the animal.

A comparison of *estrogen, androgen* and *glucocorticosteroid* target cells in the mature rat brain is shown in Figure 11 for the preoptic-septal level and in Figure 12 for the central hypothalamic level. From this comparison it is apparent that there exists a characteristic "hormone architecture" for each hormone with some overlap in certain regions. In contrast to estrogen, androgen target sites are extensively represented in the lateral septum, the hippocampus, and the hypothalamic ventromedial nucleus. In the septo-hippocampal region androgen and corticosteroid concentrating cells are found in identical sites. However, the medial nucleus of the amygdala and the basal hypothalamic nuclei contain androgen and estrogen target cells, and apparently have no corticosteroid receptor cells. These topographical differences as well as the results from competition studies support the interpretation that receptors are specific for each hormone and that a single cell may have receptors for not only one but several steroid hormones.

Considerable differences—but also overlap—between estrogen and DHT target cells in the lower brain stem and spinal cord have been recognized (Fig. 13). Estrogen concentration appears to prevail in sensory areas and cells that are known to modulate sensory perception, contrary to DHT, which prevails in neurons that are associated with somato-motor functions, (for detail see Sar and Stumpf, 1977*a*; Stumpf and Sar, 1977). In addition to these "selective" androgen and estrogen sites, combined androgen and estrogen target cells are found in juxtaventricular regions, including the central gray, locus ceruleus and n. tractus solitarii. From an anatomical viewpoint, the preponderance of androgen for somatomotor neurons in the brain stem and spinal cord appears to be paralleled by a preponderance of androgen for pyschomotor-aggression related neurons in the telencephalon. The latter is suggested, for instance, by the extensive and heavy androgen concentration in the lateral septum and the structures closely associated with it. It is tempting to propose that through the selective action of male hormone(s), certain behavioral patterns are activated, which fall under the categories of territorial defense, "leadership" and war. Since glucocorticosteroid receptors are also abundant in the dorso-lateral septum in mammals, these adrenal hormones may be essential for the full activation and expression of the above mentioned behavioral patterns.

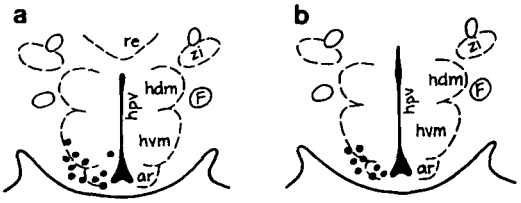


FIG. 14. Hypothalamic distribution of radioactivity in nuclei of cells after ^{3}H estradiol injection in 2-day neonatal rat (a) and after ^{3}H diethylstilbestrol in 16-day fetal mouse (b). Figure 14a reproduced after Sheridan *et al.* (1974).

FIG. 13. Comparison between localization of estrogen and androgen target neurons in pons, medulla and spinal cord of rat. The androgenic metabolite dihydrotestosterone characteristically localizes in neurons related to somatomotor function, while estrogen localization seems more related—although not exclusively—to sensory afferent structures (for detail see Sar and Stumpf, 1977*a*; Stumpf and Sar, 1977). A developmental corresponding relationship to the floor and alar plate derivatives is therefore suggested. Overlap between androgen and estrogen target cell localization exists in juxtaventricular nuclei.

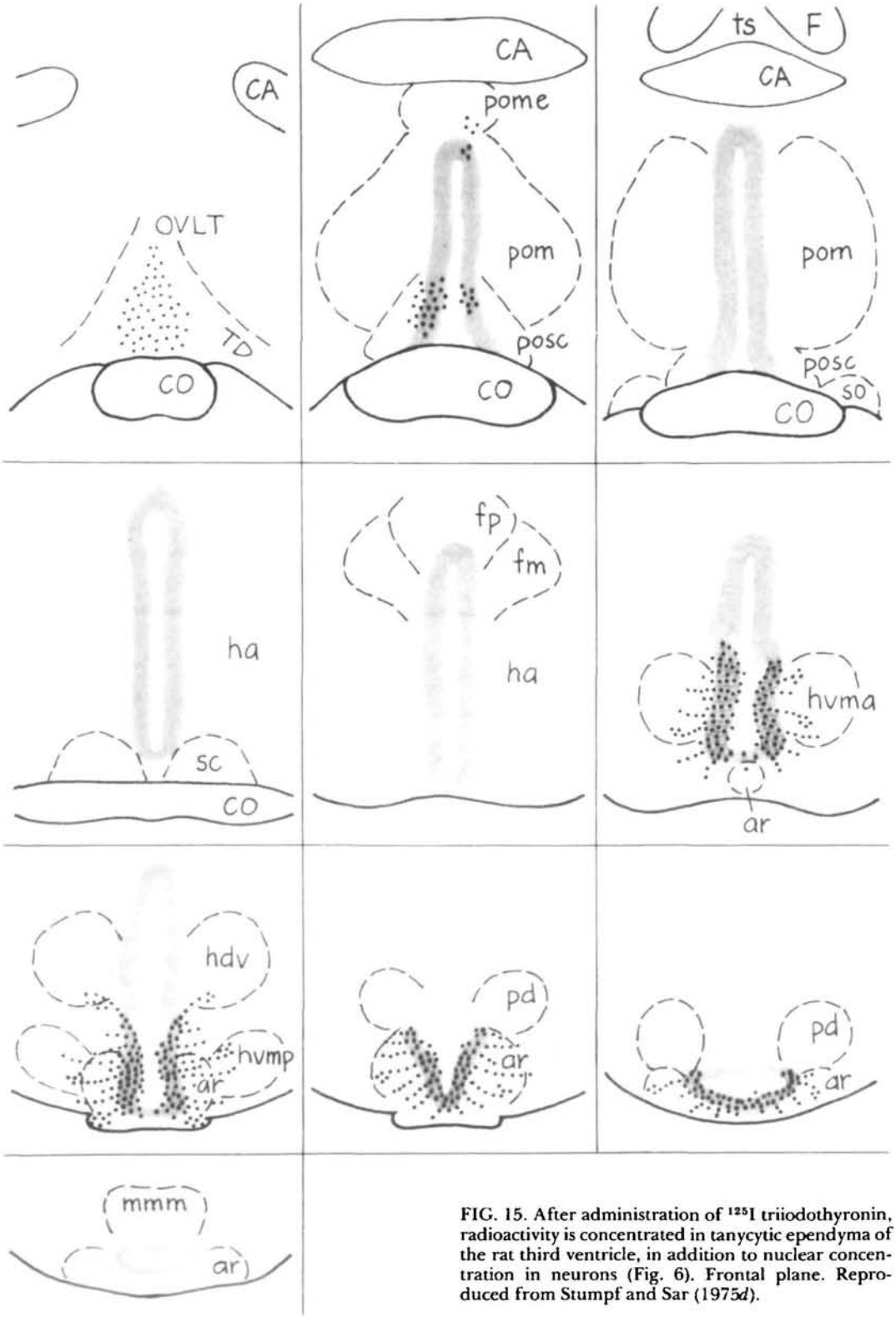


FIG. 15. After administration of ^{125}I triiodothyronin, radioactivity is concentrated in tanycytic ependyma of the rat third ventricle, in addition to nuclear concentration in neurons (Fig. 6). Frontal plane. Reproduced from Stumpf and Sar (1975*d*).

Estrogen target cells in developing animals have been identified first in our laboratory in the 2-day neonatal rat (Fig. 14A) and in the 10-day chick embryo (Martinez-Vargas *et al.*, 1975*a*). In the rat preimplantation blastocyst, suggestive evidence was obtained for ^{3}H-estradiol localization in cells of the inner cell mass (Stumpf and Sar, 1976). Recently we observed nuclear concentration of ^{3}H DES (or metabolites of it) in the arcuate nucleus of a 16-day mouse fetus (Figs. 5 and 14B).

Information on the brain distribution of *progestational* compounds is still sparse. Sar and Stumpf (1973) first demonstrated localization in the preoptic and basal tuberal region of the guinea pig hypothalamus. More recently Kato and Onouchi (1977) were able to provide positive biochemical evidence for the rat, while other investigators were unsuccessful (Atger *et al.*, 1974; McEwen *et al.*, 1976).

The first demonstration of selective cellular and subcellular retention of radioactivity after injection of ^{125}*I triiodothyronine* was provided from our laboratory (Stumpf and Sar, 1975*d*). Prevailing nuclear concentration, in addition to cytoplasmic radioactivity, is seen in a widespread population of neurons. Figure 6 shows an example from the rat piriform cortex. In addition, prevailing cytoplasmic uptake exists in specific regions of the ependyma that lines the third ventricle in the vicinity of the optic and infundibular recess (Fig. 15). The results suggest that thyroid hormones affect neuronal and ependymal functions in the mature central nervous system.

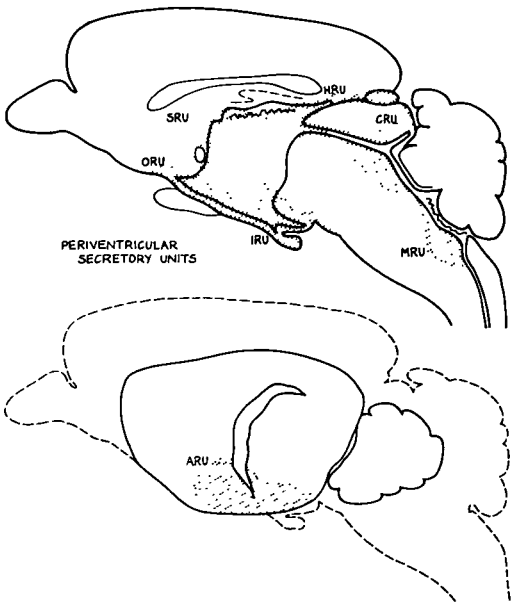


FIG. 16. Periventricular secretory recess-units at sex steroid hormone target sites in and around ventricular recess organs. The existance of several such recess units (RU)—similar to the well recognized infundibular hypothalamic unit—has been proposed (Stumpf *et al.*, 1977). Periventicular units are interlinked by secretory pathways. ARU = amygdaloid, CRU = collicular-pontine, HRU = habenular-epithalamic, IRU = infundibular hypothalamic, MRU = area postrema-medullary, ORU = optic recess-preoptic, SRU = subfornical-septal.

CONCLUSIONS

In all mammalian vertebrates studied to date, estrogen target cells have been found in specific regions of the central nervous system. Evidence for target cells for other steroid hormones as well as for thyroid hormones exists in some animals.

The topographic distribution of estrogen target cells is similar in mammalian and non-mammalian species (Kim *et al.*, 1978*b*; Stumpf *et al.*, 1978), with certain exceptions that appear related to the phylogenetic development and differentiation of encephalic structures.

During embryonic development estrogen receptor cells are present at similar sites as in the adult. However, the nuclear groups are not as well differentiated and, ontogenetically, steroid receptors in them do not occur simultaneously.

The vertebrate pattern of sex steroid hormone target sites shows a close topographic relationship to the ventricular system, with circumventricular organs forming nodal points (Fig. 16). Therefore, and because of additional evidence, such as presence of secretory granules, neurotransmitters and neuropeptides, and specializations of the vascular system and ependyma, we have advanced the concept of *periventricular secretory units* (Stumpf *et al.*, 1977).

The extensive distribution of steroid hormone receptor sites in the brain reflects the significance of gonadal and adrenal activation not only for feedback control of endocrine gland secretions, but for many, if not all, of the brain-regulated functions, such as, alteration of threshold to sensory perception and motor response, memory, and behavior.

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