

## TABLE C

### RAT CNS GRAY MATTER REGIONS 4.0BETA5.2

#### (TOPOGRAPHIC HISTOLOGICAL GROUPINGS FOR CEREBRAL CORTEX)

This hierarchical Nomenclature Table provides a set of **standard terms** for describing the **gray matter regions** (Swanson & Bota, 2010) of the adult rat **central nervous system** (Carus, 1814). It is a revised version of Table B in the third edition of *Brain maps: structure of the rat brain* (Swanson, 2004).

In Table B of Swanson (2004) the parts (gray matter regions) were arranged according to the four-systems structure-function network model of Swanson (2003a). Here they are arranged strictly topographically, and in the same order used for the adult human **central nervous system** (Carus, 1814) in *Neuroanatomical terminology* (Swanson, 2015), Appendix Table 3. Both arrangements (functional and topographic) of essentially the same parts are useful for different purposes, as are arrangements based on connections (Bota et al., 2015; Swanson et al. 2016) and other criteria (Swanson, 2000b). It is likely that a strictly topographic ordering is the most straightforward approach to creating a pan-mammalian neuroanatomical terminology. It is purely descriptive of physical structure, and thus more straightforward than the more difficult problem of functional organization.

Highlighted in **bold red text** are gray matter regions as defined by Swanson & Bota (2010): they are recognizable volumes of *gray matter* (Meckel, 1817) that are distinguished by a unique set of neuron types with a unique spatial distribution. In the Table C gray matter regionalization hierarchy here, **gray matter regions** (Swanson & Bota, 2010) occupy the lowest level, equivalent to species in plant and animal taxonomy, except when gray matter subregions (indicated by *italics*, and equivalent to subspecies in biological taxonomy) have been identified, and thus occupy the lowest level. This clarification of regions and subregions was dictated by the emergence of connectomics, where a list of parts is required to create an adjacency (connection) matrix. This approach to choosing a list for a macroconnectome—connections between **gray matter regions** (Swanson & Bota, 2010)—was used systematically by Bota et al. (2015) and Swanson et al. (2015). For example, **field CA3 (Lorente de Nó, 1934)** is a gray matter region at the “species” level whereas its gray matter subregion *pyramidal layer (>1840)* is at the “subspecies” level. The distinction between “species” and “subspecies” levels is not as clear for nonlaminated gray matter regions, and here the basic criterion for distinction lies with the preponderance of current connective evidence to justify inclusion at the “species” level. In animal taxonomy, subspecies is the only taxon allowed below species (International Commission on Zoological Nomenclature, 1999).

The topographic ordering of parts follows the conventions adopted in *Neuroanatomical terminology* (Swanson, 2015), and is based on embryological principles of general developmental sequence: rostral before caudal (cardinal axis), then medial before lateral (first transverse axis), and then ventral before dorsal (second transverse axis).

The naming of parts follows conventions adopted in *Neuroanatomical terminology* (Swanson, 2015). Briefly, all terms listed in Table C are considered standard terms that when used in text have the formal form **term (author, date)**. The definition of all standard terms minimally includes species, sex (if relevant), age, and neuroanatomical method(s) used to define the part. The citation at the end refers to the first use of the term as defined, and is thus not an eponym. If priority for the term has not yet been established the citation is assigned a value of “(>1840)”, that

is, after 1840, for historical reasons explained in *Neuroanatomical terminology* (Swanson, 2015). For standard terms not defined in Table C annotations see *Neuroanatomical terminology* (Swanson, 2015). Non-standard terms that have been defined rigorously in Swanson (2015) or here have the formal form *term (author, date)*, when used in text. Other terms are used without the appended (author, date).

CENTRAL NERVOUS SYSTEM [RAT] (CARUS, 1814)<sup>1</sup> (CNS) or CEREBROSPINAL AXIS [RAT] (MECKEL, 1817) (SPA)

Endbrain (Kuhlenbeck, 1927)<sup>2</sup> (EB) or Cerebrum (Obersteiner & Hill, 1900) (CH)

Cerebral cortex (>1840)<sup>3</sup> (CTX)

Cortical plate (>1840)<sup>4</sup> (CTXpl)

Limbic region (>1840)<sup>5</sup> (LIMB)

Olfactory region (>1840)<sup>6</sup> (OLF)

Olfactory bulb (Weitbrecht, 1751)<sup>7</sup> (OB)

**Main olfactory bulb (>1840)<sup>8</sup> (MOB)**

*glomerular layer (>1840) (MOBgl)*

*outer plexiform layer (>1840) (MOBopl)*

*mitral layer (>1840) (MOBmi)*

*inner plexiform layer (>1840) (MOBipl)*

*granule cell layer (>1840) (MOBgr)*

**Accessory olfactory bulb (>1840)<sup>9</sup> (AOB)**

*glomerular layer (>1840) (AOBgl)*

*mitral layer (>1840) (AOBmi)*

*granular layer (>1840) (AOBgr)*

**Anterior olfactory area (Herrick, 1910)<sup>10</sup> (AOA)**

*molecular layer (>1840) (AOA1)*

*pyramidal layer (>1840) (AOA2)*

Tenia tecta (Swanson, 1992)<sup>11</sup> (TT)

**Ventral part (Swanson, 1992)<sup>12</sup> (TTv)**

*layers 1-3 (Swanson, 1992)<sup>13</sup> (TTv1-3)*

**Dorsal part (Swanson, 1992)<sup>14</sup> (TTd)**

*layers 1-4 (Swanson, 1992)<sup>15</sup> (TTd1-4)*

**Piriform area (Smith, 1919)<sup>16</sup> (PIR)**

*molecular layer (>1840) (PIR1)*

*pyramidal layer (>1840) (PIR2)*

*polymorph layer (>1840) (PIR3)*

Cortical amygdalar complex (Swanson, 2015)<sup>17</sup> (COX)

Cortical amygdalar area (>1840)<sup>18</sup> (COA)

**Anterior part (>1840)<sup>19</sup>** (COAa)  
 Posterior part (>1840) (COAp)  
     **Medial zone (>1840)<sup>20</sup>** (COApm)  
     **Lateral zone (>1840)<sup>21</sup>** (COApl)  
**Nucleus of lateral olfactory tract (Swanson & Petrovich, 1998)<sup>22</sup>** (NLOT)  
     *molecular layer (>1840)* (NLOT1)  
     *pyramidal layer (>1840)* (NLOT2)  
**Piriform-amygdalar area (Canteras et al., 1992)<sup>23</sup>** (PAA)  
**Postpiriform transition area (Canteras et al., 1992)<sup>24</sup>** (TR)  
 Hippocampal formation (Swanson & Cowan, 1977)<sup>25</sup> (HPF)  
     Hippocampal region (Swanson et al., 1987)<sup>26</sup> (HIP)  
     **Indusium griseum (Valentin, 1841)<sup>27</sup>** (IG)  
     **Fasciola cinerea (Arnold, 1838b)<sup>28</sup>** (FC)  
     **Dentate gyrus (>1840)<sup>29</sup>** (DG)  
         *molecular layer (>1840)* (DGmo)  
         *granule cell layer (>1840)* (DGsg)  
         *polymorph layer (>1840)* (DGpo)  
     Ammon's horn (Vicq d'Azyr, 1784)<sup>30</sup> (CA)  
         **Field CA3 (Lorente de Nó, 1934)<sup>31</sup>** (CA3)  
             *stratum lacunosum-moleculare (>1840)* (CA3slm)  
             *stratum radiatum (>1840)* (CA3sr)  
             *stratum lucidum (>1840)* (CA3slu)  
             *pyramidal layer (>1840)* (CA3sp)  
             *stratum oriens (>1840)* (CA3so)  
         **Field CA2 (Lorente de Nó, 1934)<sup>32</sup>** (CA2)  
             *stratum lacunosum-moleculare (>1840)* (CA2slm)  
             *stratum radiatum (>1840)* (CA2sr)  
             *pyramidal layer (>1840)* (CA2sp)  
             *stratum oriens (>1840)* (CA2so)  
     Field CA1 (Lorente de Nó, 1934)<sup>33</sup> (CA1)  
         **Ventral part (Risold & Swanson, 1996)<sup>34</sup>** (CA1v)  
             *stratum lacunosum-moleculare (>1840)* (CA1v-slm)  
             *stratum radiatum (>1840)* (CA1v-sr)  
             *deep pyramidal layer (>1840)* (CA1v-spd)  
             *superficial pyramidal layer (>1840)* (CA1v-sps)  
             *stratum oriens (>1840)* (CA1v-so)

**Dorsal part (Risold & Swanson, 1996)<sup>35</sup>** CA1d)  
*stratum lacunosum-moleculare (>1840)* (CA1d-slm)  
*stratum radiatum (>1840)* (CA1d-sr)  
*deep pyramidal layer (>1840)* (CA1d-spd)  
*superficial pyramidal layer (>1840)* (CA1d-sps)  
*stratum oriens (>1840)* (CA1d-so)

Retrohippocampal region (Swanson et al., 1987)<sup>36</sup> (RHP)  
 Subiculum (>1840)<sup>37</sup> (SUB)

**Ventral part (Swanson & Cowan, 1975)<sup>38</sup>** (SUBv)  
*molecular layer (>1840)* (SUBv-m)  
*stratum radiatum (>1840)* (SUBv-sr)  
*pyramidal layer (>1840)* (SUBv-sp)

**Dorsal part (Swanson & Cowan, 1975)<sup>39</sup>** (SUBd)  
*molecular layer (>1840)* (SUBd-m)  
*stratum radiatum (>1840)* (SUBd-sr)  
*pyramidal layer (>1840)* (SUBd-sp)

**Presubiculum (Swanson & Cowan, 1977)<sup>40</sup>** (PRE)  
*layers 1-6 (>1840)* (PRE1-6)

**Postsubiculum (Swanson & Cowan, 1977)<sup>41</sup>** (POST)  
*layers 1-6 (>1840)* (POST1-6)

**Parasubiculum (>1840)<sup>42</sup>** (PAR)  
*layers 1-6 (>1840)* (PAR1-6)

Entorhinal area (Brodmann, 1909)<sup>43</sup> (ENT)

**Medial part (>1840)<sup>44</sup>** (ENTm)  
*layers 1-6 (>1840)* (ENTm1-6)

**Lateral part (>1840)<sup>45</sup>** (ENTI)  
*layers 1-6 (>1840)* (ENTI1-6)

Cingulate region (Brodmann, 1909)<sup>46</sup> (CNG)

**Infralimbic area (Rose & Woolsey, 1948)<sup>47</sup>** (ILA)  
*layers 1-6 (>1840)* (ILA1-6)

**Prelimbic area (Brodmann, 1909)<sup>48</sup>** (PL)  
*layers 1-6 (>1840)* (PL1-6)

Anterior cingulate area (Brodmann, 1909)<sup>49</sup> (ACA)

**Ventral part (Krettek & Price, 1977a)<sup>50</sup>** (ACAv)  
*layers 1-6 (>1840)* (ACAv1-6)

**Dorsal part (Krettek & Price, 1977a)<sup>51</sup>** (ACAd)

*layers 1-6 (>1840)* (ACAd1-6)  
 Retrosplenial area (Vogt & Peters, 1981)<sup>52</sup> (RSP)  
     Ventral part (Swanson, 1992)<sup>53</sup> (RSPve)  
         **Anterior zone (Swanson, BM4)**<sup>54</sup> (RSPv)  
         **Zone a (Brodmann, 1909)**<sup>55</sup> (RSPv.a)  
             *layers 1-6 (>1840)* (RSPv.a1-6)  
         **Zone b/c (Swanson, 1992)**<sup>56</sup> (RSPv.b/c)  
             *layers 1-6 (>1840)* (RSPv.b/c1-6)  
     **Dorsal part (Swanson, 1992)**<sup>57</sup> (RSPd)  
         *layers 1-6 (>1840)* (RSPd1-6)  
     **Lateral agranular part (Risold & Swanson, 1995)**<sup>58</sup> (RSPagl)  
 Insular region (Brodmann, 1909)<sup>59</sup> (INS)  
     Agranular insular areas (Swanson, BM4)<sup>60</sup> (AI)  
         **Ventral agranular insular area (Krettek & Price, 1977a)**<sup>61</sup> (Alv)  
             *layers 1-6 (>1840)* (Alv1-6)  
         **Dorsal agranular insular area (Krettek & Price, 1977a)**<sup>62</sup> (Ald)  
             *layers 1-6 (>1840)* (Ald1-6)  
         **Posterior agranular insular area (Krettek & Price, 1977a)**<sup>63</sup> (Alp)  
             *layers 1-6 (>1840)* (Alp1-6)  
     **Gustatory area (>1840)**<sup>64</sup> (GU)  
         *layers 1-6 (>1840)* (GU1-6)  
     **Visceral area (>1840)**<sup>65</sup> (VISC)  
         *layers 1-6 (>1840)* (VISC1-6)  
 Frontal region (Vicq d'Azyr, 1786)<sup>66</sup> (FRO)  
 Orbital region (Rolando, 1831)<sup>67</sup> (ORB)  
     **Ventral orbital area (Krettek & Price, 1977a)**<sup>68</sup> (ORBv)  
         *layers 1-6 (>1840)* (ORBv1-6)  
     **Ventrolateral orbital area (Krettek & Price, 1977a)**<sup>69</sup> (ORBvl)  
         *layers 1-6 (>1840)* (ORBvl1-6)  
     **Medial orbital area (Krettek & Price, 1977a)**<sup>70</sup> (ORBm)  
         *layers 1-6 (>1840)* (ORBm1-6)  
     **Lateral orbital area (Krettek & Price, 1977a)**<sup>71</sup> (ORBl)  
         *layers 1-6 (>1840)* (ORBl1-6)  
 Somatomotor areas (>1840) (MO)  
     **Primary somatomotor area (>1840)**<sup>72</sup> (MOp)  
         *layers 1-6 (>1840)* (MOp1-6)

**Secondary somatomotor areas (>1840)<sup>73</sup> (MOs)**  
*layers 1-6 (>1840) (MOs1-6)*

Parietal region (>1840)<sup>74</sup> (PTL)  
 Somatosensory areas (>1840) (SS)  
**Primary somatosensory area (>1840)<sup>75</sup> (SSp)**  
*barrel field layers 1-6 (>1840) (SSp-bfd1-6)*  
*lower limb field layers 1-6 (>1840) (SSp-ll1-6)*  
*mouth field layers 1-6 (>1840) (SSp-m1-6)*  
*nose field layers 1-6 (>1840) (SSp-n1-6)*  
*trunk field layers 1-6 (>1840) (SSp-tr1-6)*  
*upper limb field layers 1-6 (>1840) (SSp-ul1-6)*  
**Supplemental somatosensory area (>1840)<sup>76</sup> (SSs)**  
*layers 1-6 (>1840) (SSs1-6)*

**Posterior parietal association areas (>1840)<sup>77</sup> (PTLp)**  
*layers 1-6 (>1840) (PTLp1-6)*

Temporal region (>1840)<sup>78</sup> (TE)  
**Perirhinal area (Brodmann, 1909)<sup>79</sup> (PERI)**  
*layers 1-6 (>1840) (PERI1-6)*

**Ectorhinal area (Brodmann, 1909)<sup>80</sup> (ECT)**  
*layers 1-6 (>1840) (ECT1-6)*

**Temporal association areas (Swanson, 1972)<sup>81</sup> (TEa)**  
*layers 1-6 (>1840) (TEa1-6)*

Auditory areas<sup>82</sup> (>1840) (AUD)  
**Ventral auditory areas (Sally & Kelly, 1988)<sup>83</sup> (AUDv)**  
*layers 1-6 (>1840) (AUDv1-6)*

**Primary auditory area (>1840)<sup>84</sup> (AUDp)**  
*layers 1-6 (>1840) (AUDp1-6)*

**Dorsal auditory areas (Sally & Kelly, 1988)<sup>85</sup> (AUDd)**  
*layers 1-6 (>1840) (AUDd1-6)*

**Posterior auditory area (Doron et al., 2002)<sup>86</sup> (AUDpo)**  
*layers 1-6 (>1840) (AUDpo1-6)*

Occipital region (Vesalius, 1543a)<sup>87</sup> (OCC)  
 Visual areas (>1840)<sup>88</sup> (VIS)  
**Rostrolateral visual area (Thomas & Espinoza, 1987)<sup>89</sup> (VISrl)**  
*layers 1-6 (>1840) (VISrl1-6)*

**Anterolateral visual area (Olavarria & Torrealba, 1978)<sup>90</sup> (VISal)**

*layers 1-6 (>1840) (VISal1-6)*  
**Anterior laterolateral visual area (Thomas & Espinoza, 1987)<sup>91</sup> (VISlla)**  
*layers 1-6 (>1840) (VISlla1-6)*  
**Laterolateral visual area (Espinoza & Thomas, 1983)<sup>92</sup> (VISll)**  
*layers 1-6 (>1840) (VISll1-6)*  
**Intermediolateral visual area (Olavarria & Montero, 1984)<sup>93</sup> (VISli)**  
*layers 1-6 (>1840) (VISli1-6)*  
**Mediolateral visual area (Olavarria & Torrealba, 1978)<sup>94</sup> (VISlm)**  
*layers 1-6 (>1840) (VISlm1-6)*  
**Posterolateral visual area (Thomas & Espinoza, 1987)<sup>95</sup> (VISpl)**  
*layers 1-6 (>1840) (VISpl1-6)*  
**Primary visual area (>1840)<sup>96</sup> (VISp)**  
*layers 1-6 (>1840) (VISp1-6)*  
**Anteromedial visual area (Espinoza & Thomas, 1983)<sup>97</sup> (VISam)**  
*layers 1-6 (>1840) (VISam1-6)*  
**Posteromedial visual area (Espinoza & Thomas, 1983)<sup>98</sup> (VISpm)**  
*layers 1-6 (>1840) (VISpm1-6)*  
 Cortical subplate (>1840)<sup>99</sup> (CTXsp)  
 Basolateral amygdalar complex (Swanson, 2015)<sup>100</sup> (BLX)  
**Nucleus of lateral olfactory tract, dorsal cap (Gurdjian, 1928)<sup>101</sup> (NLOT3)**  
 Basomedial amygdalar nucleus (>1840)<sup>102</sup> (BMA)  
**Anterior part (>1840)<sup>103</sup> (BMAa)**  
**Posterior part (>1840)<sup>104</sup> (BMAp)**  
 Basolateral amygdalar nucleus (>1840)<sup>105</sup> (BLA)  
**Anterior part (>1840)<sup>106</sup> (BLAa)**  
**Posterior part (>1840)<sup>107</sup> (BLAp)**  
**Lateral amygdalar nucleus (>1840)<sup>108</sup> (LA)**  
**Posterior amygdalar nucleus (Canteras et al., 1992a)<sup>109</sup> (PA)**  
 Endopiriform nucleus (Krettek & Price, 1978)<sup>110</sup> (EP)  
**Ventral part (Krettek & Price, 1978)<sup>111</sup> (EPv)**  
**Dorsal part (Krettek & Price, 1978)<sup>112</sup> (EPd)**  
**Clastrum (Burdach, 1822)<sup>113</sup> (CLA)**  
**Isocortical layer 6b (>1840)<sup>114</sup> (6b)**

<sup>1</sup> For definitions and historical usage of these two synonyms in vertebrates generally see Swanson (2015).

<sup>2</sup> For definitions and historical usage of these two synonyms in vertebrates generally see Swanson (2015).

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<sup>3</sup> One of the two great divisions of the vertebrate *cerebrum* (**Obersteiner & Hill, 1900**) or *endbrain* (**Kuhlenbeck, 1927**), the other being the *cerebral nuclei* (**Swanson, 2000a**); see Swanson (2000a). In the embryo it develops dorsal to the *cerebral nuclei* (**Swanson, 2000a**) and characteristically displays a laminated cytoarchitecture; see Alvarez-Bolado & Swanson (1996).

<sup>4</sup> In adult mammals, the derivatives of the embryological cortical plate; see Swanson (2000a, pp. 129-131).

<sup>5</sup> See Swanson (2015) for this precise definition in mammals.

<sup>6</sup> See Swanson (2015) for this precise definition in mammals.

<sup>7</sup> The *main olfactory bulb (>1840)* and *accessory olfactory bulb (>1840)* together.

<sup>8</sup> Gurdjian (1925), Ennis et al. (2015).

<sup>9</sup> Gurdjian (1925), Ennis et al. (2015).

<sup>10</sup> It is an olfactory cortical *area*, with a molecular layer (AOA1) and a pyramidal layer (AOA2); see Haberly & Price (1978b), who noted that “the term nucleus is unfortunate since, in spite of the lack of cellular sublamination within these areas [retrobulbar], they are all clearly cortical in organization.” (p. 782). In the Discussion, they refer to “areas within the olfactory peduncle” (Haberly & Price, 1978b, p. 806). In this edition of *Brain Maps*, the name has been changed from anterior olfactory nucleus to anterior olfactory area to emphasize that it is a cerebral cortical area, not a subcortical nucleus. In addition, the five parts of Haberly & Price (1978b) that were listed in previous editions have been eliminated because they are based mostly on relative position, not cytoarchitecturally distinctive parts, except perhaps, for the external part. The detailed description and discussion of the rat AOA in De Olmos et al. (1978) is also quite useful. Neville & Haberly (2004, p. 416) referred to it as the *anterior olfactory cortex* (AOC).

<sup>11</sup> There is little agreement in the literature about the parcelling and nomenclature associated with the tenia tecta and indusium griseum. From examining sections in the three standard planes, it seems clear to us (Swanson, 1992) that the *indusium griseum* (**Valentin, 1841**) in the rat continues uninterrupted around the genu of the corpus callosum to the *septohippocampal nucleus (>1840)* (Atlas Levels 11-13; also see Wyss & Sripanidkulchai, 1983). The part of the *indusium griseum* (**Valentin, 1841**) rostral and ventral to the genu was called the dorsal part of the tenia tecta by Haberly & Price (1978b). The ventral part of the tenia tecta of Haberly & Price (1978b) has a very different structure. They divided it into superior and inferior parts, referred to here as the dorsal and ventral parts of the tenia tecta proper, respectively (Swanson, 1992). The *tenia tecta* (**Swanson, 1992**) reminds one of differentiated parts of the adjacent *anterior olfactory area* (**Herrick, 1910**); see Davis et al. (1978). We recognize three layers in the TTv (as Haberly & Price, 1978b) and four layers in the TTd.

<sup>12</sup> See Swanson (1992) and annotation for *tenia tecta* (**Swanson, 1992**).

<sup>13</sup> See Swanson (1992) and annotation for *tenia tecta* (**Swanson, 1992**).

<sup>14</sup> See Swanson (1992) and annotation for *tenia tecta* (**Swanson, 1992**).

<sup>15</sup> See Swanson (1992) and annotation for *tenia tecta* (**Swanson, 1992**).

<sup>16</sup> See Craigie (1925) and Haberly & Price (1978a), who discuss reasons for not referring to the PIR as “prepiriform”.

<sup>17</sup> See entry in Swanson (2015) for definition and historical background (and Appendix 3).

<sup>18</sup> The traditional cortical nucleus of the amygdala is in fact a cerebral cortical *area* (see Price, 1973, p. 94; Krettek & Price, 1978, p. 264), and was called cortical amygdalar area in Swanson (1998, p. 197) to reflect this fact.

<sup>19</sup> de Olmos et al. (1985); also see Scalia & Winans (1975), Krettek & Price (1978).

<sup>20</sup> Canteras et al. (1992a).

<sup>21</sup> Canteras et al. (1992a).



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<sup>22</sup> It corresponds to layers I & II of McDonald (1983), Millhouse & Uemura-Sumi (1985); their layer III is listed here under **cortical subplate (>1840)**. This assignment of NLOT1 and NLOT2 to the **cortical amygdalar complex (Swanson, 2015)** was first suggested by Swanson & Petrovich (1998) and followed in Swanson (2004, pp. 168-169). Like the COA, PAA, and TR, this is an area of the olfactory cortex, usually grouped with the amygdala, and calling it a nucleus is a misnomer. Following recent trends, perhaps a better term would be *area of lateral olfactory tract* or *lateral olfactory tract area*.

<sup>23</sup> Canteras et al. (1992a).

<sup>24</sup> It was first identified and described by Haug (1976) as the “area interposed between area entorhinalis caudally, and the piriform cortex and the posterior pole of the amygdala rostrally.” (also see Canteras et al., 1992a). It also corresponds roughly to the amygdalopiriform transition area of de Olmos et al. (1985) and amygdalo-entorhinal transition field (AE, field 6) of Insausti et al. (1997), who included it in their definition of the entorhinal area, although it does not project to the **dentate gyrus (>1840)** (see Petrovich, 1997; Dolorfo & Amaral, 1998a; Santiago & Shammah-Lagnado, 2005). Jolkkonen et al. (2001) divided it into medial part that is more densely packed with neurons, and a lateral part where lamination becomes somewhat more clear.

<sup>25</sup> This account closely follows Swanson & Cowan (1977) and Swanson et al. (1987), which are based largely on Blackstad (1956). See Swanson (2015) for this precise definition in mammals.

<sup>26</sup> In the account of Swanson et al. (1987) the **hippocampal formation (Swanson & Cowan, 1977)** has two major divisions, the **hippocampal region (Swanson et al., 1987)**, which is topologically medial, and the **retrohippocampal region (Swanson et al., 1987)**, which is topologically lateral.

<sup>27</sup> See Wyss & Sripanidkulchai (1983), but also see annotation for **tenia tecta (Swanson, 1992)**.

<sup>28</sup> Hjorth-Simonsen (1972).

<sup>29</sup> See Blackstad (1956).

<sup>30</sup> For definition and historical usage in mammals generally see Swanson (2015).

<sup>31</sup> See Swanson et al. (1987).

<sup>32</sup> See discussion in Swanson et al. (1978, p. 684) for definition adopted here, based on Haug (1974); for more recent molecular characterization of pyramidal neurons in this general region, at least in mouse, see Lein et al. (2005).

<sup>33</sup> See Swanson et al. (1987).

<sup>34</sup> A clear difference between connections arising from the dorsal and ventral (also called septal and temporal) parts of **field CA1 (Lorente de Nó, 1934)** and the **subiculum (>1840)** goes back to early findings of Swanson & Cowan (1975, 1977). There are, however, no clear cytoarchitectonic borders, and for descriptive purposes may be divided by a line across the top of functional domain 2 in Figure 6 of Petrovich et al. (2001). In addition, it is often useful to indicate roughly dorsal, intermediate, and ventral (also called septal, occipital, and temporal) parts of **field CA1 (Lorente de Nó, 1934)** and the **subiculum (>1840)**. This distinction goes back to the statement, “In a number of experiments the injections involved a region of the subiculum which, on topographic grounds, could not be described as either ‘dorsal’ or ‘ventral’ subiculum, but rather an intermediate zone...injections involving the dorsal subiculum always give rise to labeling over the dorsal part of the lateral septum, while intermediate and ventrally placed injections respectively labeled intermediate and ventral parts of the lateral septal nucleus.” (Swanson & Cowan, 1977, p. 68). For the name, and other clear dorsal-ventral distinctions of **field CA1 (Lorente de Nó, 1934)** and the **subiculum (>1840)** connections, see Risold & Swanson (1996, p. 1486 & Fig. 1); also see Cenquizca & Swanson (2006).

<sup>35</sup> See annotation for **ventral part of field CA1 (Risold & Swanson, 1996)**.

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<sup>36</sup> In the account of Swanson et al. (1987) the **hippocampal formation (Swanson & Cowan, 1977)** has two major divisions, the **hippocampal region (Swanson et al., 1987)**, which is topologically medial, and the **retrohippocampal region (Swanson et al., 1987)**, which is topologically lateral.

<sup>37</sup> See Swanson et al. (1987).

<sup>38</sup> See annotation for **ventral part of field CA1 (Risold & Swanson, 1996)**.

<sup>39</sup> See annotation for **ventral part of field CA1 (Risold & Swanson, 1996)**.

<sup>40</sup> The **presubiculum (Swanson & Cowan, 1977)** (ventrally) and **postsubiculum (Swanson & Cowan, 1997)** (dorsally) together form a thin longitudinal strip of **cerebral cortex (>1840)** between the **subiculum (>1840)** medially and **parasubiculum (>1840)** laterally; see Swanson et al. (1987), van Groen & Wyss (1990a). The **postsubiculum (Swanson & Cowan, 1997)** is sometimes considered the dorsal part of what others consider the presubiculum as a whole (see Cappaert et al., 2015).

<sup>41</sup> Following Rose & Woolsey (1948, p. 292), who called it the postsubicular area in rabbit and cat, it is distinguished (see Swanson & Cowan, 1977, p. 71) as the dorsal part of what others consider the presubiculum as a whole; see van Groen & Wyss (1990b), Cappaert et al. (2015), and the annotation for **presubiculum (Swanson & Cowan, 1977)**. The retrosplenial area 29e (see Haug, 1976) is included in the **postsubiculum (Swanson & Cowan, 1977)**, following Rose & Woolsey (1948), although others include it in the **presubiculum (Swanson & Cowan, 1977)** (see Vogt & Miller, 1981, p. 622) or even **parasubiculum (>1840)** (see Cappaert et al., 2015).

<sup>42</sup> See Blackstad (1956, p. 432), Swanson et al. (1987), van Groen & Wyss (1990a).

<sup>43</sup> A simple distinction between medial and lateral parts of the **entorhinal area (Brodmann, 1909)** is followed; see Brodmann (1909), Hjorth-Simonsen & Jeune (1972), Swanson et al. (1978), Dolorfo & Amaral (1998b). Insausti et al. (1997) parcelled their entorhinal area into 6 entorhinal fields. The **medial part of entorhinal area (>1840)** contains their caudal (CE, field 1) and medial (ME, field 2) fields; the **lateral part of entorhinal area (>1840)** contains their ventral intermediate (VIE, field 3), dorsal intermediate (DIE, field 4), and dorsal lateral (DLE, field 5) fields; and the **postpiriform transition area (Canteras et al., 1992)** contains their amygdalo-entorhinal transition (AE, field 6) field. **Postpiriform transition area (Canteras et al., 1992)** is not included here in the **entorhinal area (Brodmann, 1909)** because it does not project to the **dentate gyrus (>1840)** (see Petrovich, 1997; Dolorfo & Amaral, 1998a; Santiago & Shammah-Lagnado, 2005). Insausti et al. (1997) did not take into account the rostral extension of the **medial part of entorhinal area (>1840)** called the ventral zone (ENTmv) in Swanson (1992, 1998, 2004); see endnote for **medial part of entorhinal area (>1840)**. The general scheme followed here was also followed for practical purposes by Cappaert et al. (2015, p. 523).

<sup>44</sup> In Swanson (1992) the **medial part of entorhinal area (>1840)** was divided into a dorsal zone (ENTm) and a ventral zone (ENTmv), which is a thin rostroventral extension of the dorsal zone identified and described by Haug (1976). Because this distinction has found little usage in the subsequent literature, it has been dropped for simplicity, and just the ENTm in its entirety is now used.

<sup>45</sup> See endnote for **entorhinal area (Brodmann, 1909)**.

<sup>46</sup> See Swanson (2015) for this precise definition in mammals.

<sup>47</sup> Krettek & Price (1977a), Vogt & Peters (1981).

<sup>48</sup> It was named prelimbic area (area 32) by Brodmann (1909) in guenon and rabbit; for work in the rat see Krettek & Price (1977a, p. 163), Vogt & Peters (1981), Vogt et al. (2013).

<sup>49</sup> It was identified and named thus by Brodmann (1909) in guenon, marmoset, and lemur.

<sup>50</sup> It was named thus in rat by Krettek & Price (1977a, p.163); also see Vogt & Peters (1981).

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<sup>51</sup> It was named thus in rat by Krettek & Price (1977a, p.163 ); also see Vogt & Peters (1981).

<sup>52</sup> See Vogt & Peters (1981, Fig. 1), who divided it into longitudinal *zones a-d*, from ventral to dorsal, in rat. Brodmann (1909) first identified the retrosplenial area, but had a fifth, ventralmost, *zone e* that is now incorporated elsewhere; see annotation for *postsubiculum (Swanson & Cowan, 1977)*. There was ambiguity in Swanson (2004) insofar as the *ventral part of retrosplenial area (Swanson, 1992)* has two clearly differentiable caudal zones, *zone a* and *zone b/c*, whereas the rostral half, where zones were essentially indistinguishable, was simply labeled ventral part (RSPv). Now, the ventral part as a whole has a new abbreviation (RSPve), the rostral half is called *anterior zone of ventral part of retrosplenial area (Swanson, BM4)* (and to avoid confusion remains abbreviated RSPv, as in Swanson, 2004), and the two caudal zones (a and b/c) remain the same.

<sup>53</sup> This is the so-called granular part of the *retrosplenial area (Vogt & Peters, 1981)*, with its zones a-c (Vogt & Peters, 1981, Fig. 1). We could not distinguish clearly zones b and c of Vogt & Peters (1981) on cytoarchitectonic grounds (Swanson, 1992); also see Sripanidkulchai & Wyss (1987) for information about lamination. Swanson (1992) named it ventral part in parallel with the rostrally adjacent *ventral part of anterior cingulate area (Krettek & Price, 1977)*. This basic subdivision has since been recognized by several workers, with RSPv named area 29c, RSPv.b/c named area 29b, and RSPv.a still called area 29a; see Shibata et al. (2009), Vogt (2015) Alternatively, others refer to RSPv as part b of ventral retrosplenial cortex, and RSPv.a and RSPv.b/c together as part a of ventral retrosplenial cortex; see Jones & Witter (2007). To avoid confusion in the comparative literature, we have retained the original lettering scheme of Brodmann (1909) and Vogt & Peters (1981); see annotation for *retrosplenial area (Vogt & Peters, 1981)*.

<sup>54</sup> See annotation for *retrosplenial area (Vogt & Peters, 1981)*.

<sup>55</sup> See annotation for *retrosplenial area (Vogt & Peters, 1981)*.

<sup>56</sup> We could not distinguish clearly zones b and c of Vogt & Peters (1981), hence *zone b/c*.

<sup>57</sup> This is the so-called agranular part of the *retrosplenial area (Vogt & Peters, 1981)*; see Krettek & Price (1977a), Vogt & Peters (1981; *zone a* in Fig. 1). Swanson (1992) named it dorsal part in parallel with the rostrally adjacent *dorsal part of anterior cingulate area (Krettek & Price, 1977)*; also see Jones & Witter (2007)

<sup>58</sup> For this name, in adult rat, see Risold & Swanson (1995a, p. 3899), who distinguished it on cytoarchitectonic and connectional grounds. Also see Risold et al. (1997, p. 209).

<sup>59</sup> See entry in Swanson (2015) for definition and historical background in mammals; also see Appendix 3 there.

<sup>60</sup> Rose (1928) first recognized dorsal, ventral, and posterior parts of the agranular insular cortex in mammals (including rabbit and squirrel), and they were specifically named dorsal, ventral, and posterior areas of agranular insular cortex by Krettek & Price (1977a, p. 166) in rat. It was called the agranular insular area with a dorsal agranular area, a ventral agranular zone, and a posterior agranular strip by Cechetto & Saper (1987), and Swanson (1992) called it the agranular insular area with dorsal, ventral, and posterior parts. Here we specifically refer to *agranular insular areas*.

<sup>61</sup> Krettek & Price (1977a, p. 166).

<sup>62</sup> Krettek & Price (1977a, p. 166).

<sup>63</sup> Krettek & Price (1977a, p. 166).

<sup>64</sup> Kosar et al. (1986). It is the so-called dysgranular insular area; see Cechetto & Saper (1987).

<sup>65</sup> It is the so-called granular insular area; see Cechetto & Saper (1987).

<sup>66</sup> See entry in Swanson (2015) for definition and historical background in mammals; also see Appendix 3 there.

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<sup>67</sup> See entry in Swanson (2015) for definition and historical background (and Appendix 3there ). In modern times, Krettek & Price (1977a, p. 163) used this name, in rat; our parcelling of these topologically difficult areas was greatly aided by examining sections cut in the three standard planes. Ray & Price (1992) and van de Werd & Uylings (2008) also delineated a separate dorsolateral orbital cortex or area far rostrally in the frontal pole; their exact parcellations appear to differ slightly although both include parts of the Ald, MOp, and MOs as defined here.

<sup>68</sup> Krettek & Price (1977a, pp. 163-166) provided this name, and a description, in rat. In Swanson (2004), the ORBv was mislabeled ORBvl on Atlas Levels 4-6; thus, the ORBv is found on Atlas Levels 4-9.

<sup>69</sup> Krettek & Price (1977a, pp. 163-166) provided this name, and a description, in rat. In Swanson (2004), the ORBv was mislabeled ORBvl on Atlas Levels 4-6; thus, the ORBvl is found on Atlas Levels 7-9.

<sup>70</sup> Krettek & Price (1977a, pp. 163-166) provided this name, and a description, in rat.

<sup>71</sup> Krettek & Price (1977a, pp. 163-166) provided this name, and a description, in rat.

<sup>72</sup> Donoghue & Wise (1982), Neafsey et al. (1986).

<sup>73</sup> Donoghue & Wise (1982), Neafsey et al. (1986).

<sup>74</sup> See entry in Swanson (2015) for definition and historical background in mammals; also see Appendix 3.

<sup>75</sup> Chapin & Lin (1984), Sanderson et al. (1984), Riddle & Purves (1995).

<sup>76</sup> Welker & Sinha (1972); see also Chapin & Lin (1984). According to Fabri & Burton (1991, pp. 410-412 and Figs. 6, 13), the rat **supplemental somatosensory area (>1840)** has two facing body representations, one dorsally called second somatosensory area (SSII) and one ventrally called parietal ventral area (PV); cytoarchitectonically they are difficult to distinguish. This general organization was confirmed by Remple et al. (2003).

<sup>77</sup> This region appears to lie between the **somatosensory areas (>1840)**, **visual areas (>1840)**, and **auditory areas (>1840)**, and receives inputs from the **lateral posterior thalamic nucleus (>1840)** and **posterior thalamic nuclei (>1840)** to this extent it may correspond to posterior parietal association areas in primates and other mammals; see Hughes (1977), Miller & Vogt (1984), Reep et al. (1994), Olsen & Witter (2016). Olsen & Witter (2016) have divided what appears to correspond rather closely to the PTLp into medial posterior parietal cortex, lateral posterior parietal cortex, and posterior part of parietal cortex based on thalamic connectivity and three staining patterns; not enough information was supplied to distinguish these three zones in the Nissl-stained sections of our atlas.

<sup>78</sup> See entry in Swanson (2015) for definition and historical background in mammals; also see Appendix 3.

<sup>79</sup> Krieg (1946a,b), Deacon et al. (1983). This is area 35 of Brodmann (1909); see Burwell (2001).

<sup>80</sup> Krieg (1946a,b), Miller & Vogt (1984); see annotation for **temporal association areas (>1840)**. Burwell (2001) recognized 5 parts of what is considered here the **ectorhinal area (Brodmann, 1909)** (Brodmann's area 36): the rostral two-thirds or so are divided into dorsal, ventral, and posterior parts of her area 36; and the caudal third is divided into dorsal and ventral parts of what is called the postrhinal area.

<sup>81</sup> We have recognized two distinct fields in the rat **temporal region (>1840)** between the **visual areas (>1840)** and **auditory areas (>1840)** dorsally and the **perirhinal area (Brodmann, 1909)** ventrally; Swanson (1992, p. 196). Krieg (1946a) apparently included both fields in his definition of ectorhinal area. More in keeping with Brodmann (1909), we suggest that the dorsal part of this region (where layer 4 is still recognizable) may correspond to temporal association cortex (perhaps in the dorsal, middle, and inferior temporal gyri of humans), and labeled it TEa (in Swanson, 2004). We have retained ECT for the distinct ventral area, just dorsal to the perirhinal area, where layers 2 and 4 are quite indistinct. The architecture and connections of this whole region require much more analysis.

<sup>82</sup> Sally & Kelly (1988), Kelly & Sally (1988), Arnault & Roger (1990), Doron et al. (2002). These are regions where a frequency map of the cochlea has been established electrophysiologically.

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<sup>83</sup> Sally & Kelly (1988, p. 1627), also see Kelly & Sally (1988). This region was identified electrophysiologically; a detailed structural description remains to appear. Clear cytoarchitectonic differences between areas Te3 and Te2 as defined by Arnault & Roger (1990) were not observed.

<sup>84</sup> Sally & Kelly (1988), Kelly & Sally (1988), Arnault & Roger (1990), Doron et al. (2002).

<sup>85</sup> Sally & Kelly (1988, p. 1627); also see Kelly & Sally (1988) and Azizi et al. (1985).

<sup>86</sup> Doron et al. (2002) carefully remapped the traditional primary auditory area with electrophysiological methods in rat and suggested that a posterior auditory field be recognized in its posterior end, beginning about 5.8 mm posterior to bregma. They did not correlate their results with cytoarchitecture, so comparisons of borders between auditory areas across atlases, rat strains, animal ages, and different histological procedures are crude at best when based strictly on a skull feature like bregma. Clearly, additional characterization of auditory and surrounding cortical areas with both anatomical and physiological methods is needed. Also see Azizi et al. (1985).

<sup>87</sup> See entry in Swanson (2015) for definition and historical background in mammals; also see Appendix 3.

<sup>88</sup> We have followed the parcellation of Thomas & Espinoza (1987), based on regions identified by limited anatomical criteria and the presence of electrophysiologically defined retinotopic maps; see their Fig. 6 and Espinoza & Thomas (1983). Detailed correlations of cellular architecture and electrophysiological mapping have not been carried out in rat, however, leading to some uncertainty. For example, Coogan & Burkhalter (1993) followed the same general scheme but identified fewer specific regions. Montero (1993) carried out a detailed multiple retrograde tracer examination of extrastriate visual region inputs to the primary visual area (VISp) and identified 10 of them with separate, full retinotopic maps. Overall, his scheme was similar to that of Thomas & Espinoza (1987), but differed in that a) he appears to have divided their VISpl into posterolateral and posterior areas, b) he combined their VISll and VISlla into a single laterolateral area, and c) he at least partly divided their VISam into anteromedial and anterior areas (see Fig. 6). We have chosen to retain the Thomas & Espinoza (1987) parceling scheme until definitive cytoarchitectonic-functional analyses are carried out.

<sup>89</sup> Identified and named, in rat, by Thomas & Espinoza (1987, p. 215).

<sup>90</sup> Identified and named, in rat, by Olavarria & Torrealba (1978, p. 388).

<sup>91</sup> Identified and named, in rat, by Thomas & Espinoza (1987, p. 215), who referred to it as laterolateral anterior.

<sup>92</sup> Identified and named, in rat, by Espinoza & Thomas (1983, see Fig. 1).

<sup>93</sup> Identified, in rat, by Olavarria & Montero (1984, see p. 250) who named it laterointermediate visual area and reviewed earlier literature on nomenclature confusion; this variation was introduced by Swanson (1992, p. 196).

<sup>94</sup> Identified, in rat, by Olavarria & Torrealba (1978, p. 388) who named it lateromedial visual area; this variation was introduced by Swanson (1992, p. 196). Also see Montero et al. (1973) for an earlier indication, and Olavarria & Montero (1984) for further clarification of nomenclature.

<sup>95</sup> Identified and named, in rat, by Thomas & Espinoza (1987, p. 221 & Fig. 5).

<sup>96</sup> The primary visual area (>1840) in rat was first clearly identified with neuroanatomical degeneration methods by Lashley (1934) and was carefully mapped electrophysiologically by Adams & Forrester (1968, see p. 327 & Fig. 3), who referred to it as the primary visual area.

<sup>97</sup> Identified and named, in rat, by Espinoza & Thomas (1983, see Fig. 1).

<sup>98</sup> Identified and named, in rat, by Espinoza & Thomas (1983, see Fig. 1).

<sup>99</sup> In adult mammals, the derivatives of the embryological cortical subplate; see Swanson (2000a, pp. 129-131).

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<sup>100</sup> See entry in Swanson (2015) for definition and historical background in mammals. It is included in the **cortical subplate (>1840)** because it develops just superficial to the **external capsule (Burdach, 1822)**, which has often been misidentified near the amygdalar region (see Atlas Levels 24-31). What we have called the **amygdalar capsule (Swanson, 1998)** is a fiber tract along the lateral border of the amygdala, and we suggest it is part of a fiber system within, and external to—for example, the **extreme capsule (>1840)**—the **cortical subplate (>1840)** or deep cortex. Also see Swanson & Petrovich (1998) and Swanson (2003b).

<sup>101</sup> Name based on the cytoarchitectonic description of Gurdjian (1928, p. 265) in rat. It corresponds to layer III of McDonald (1983), Millhouse & Uemura-Sumi (1985). This assignment of NLOT3 to the **cortical subplate (>1840)** was first suggested by Swanson & Petrovich (1998) and followed in Swanson (2004, pp. 168-169).

<sup>102</sup> Anterior and posterior parts were recognized by de Olmos et al. (1985), Canteras et al. (1992a), Petrovich et al. (1996), Olucha-Bordonau et al. (2015).

<sup>103</sup> Some authors regard the BMAa as “layer 3” of the **anterior part of cortical amygdalar area (>1840)** (COAa); see Krettek & Price (1977a), Price et al. (1987), Pitkänen (2000).

<sup>104</sup> See annotation for **basomedial amygdalar nucleus (>1840)**.

<sup>105</sup> Krettek & Price (1978).

<sup>106</sup> Krettek & Price (1978).

<sup>107</sup> Krettek & Price (1978).

<sup>108</sup> Krettek & Price (1978).

<sup>109</sup> It was identified and named thus in adult rat by Canteras et al. (1992a, p. 148), based on cytoarchitectonic and connectional criteria. It is similar but not identical to the rat amygdalo-hippocampal transition area; see Yu (1969), Price et al. (1987).

<sup>110</sup> Krettek & Price (1978). This “nucleus” appears to form the olfactory extension of the **claustrum (Burdach, 1822)**, deep to the **piriform area (Smith, 1919)**; see also Gurdjian (1928). Krettek & Price (1978, pp. 693-695) recognized in cat and rat a dorsal division of endopiriform nucleus and a ventral division of endopiriform nucleus, together the **endopiriform nucleus (Krettek & Price, 1978)** of the present account.

<sup>111</sup> Krettek & Price (1978) recognized and named it the ventral division of endopiriform nucleus in rat and cat.

<sup>112</sup> Krettek & Price (1978) recognized and named it the dorsal division of endopiriform nucleus in rat and cat. Behan & Haberly (1999, p. 535) recognized a rostroventrolateral differentiation of the **dorsal part of endopiriform nucleus (>1840)** (EPd) as the pre-endopiriform region, and Ekstrand et al. (2001) called it the pre-endopiriform nucleus (in Atlas Levels 6-9).

<sup>113</sup> For rat see Krettek & Price (1977a, 1978).

<sup>114</sup> Divak et al. (1987), Vandeveldel et al. (1996), and Friedlander & Torres-Reveron (2009) who noted that layer 6b is also referred to as either cortical layer 7 or subgriseal cells. **Layer 6b (>1840)** is apparently unusually well differentiated in adult rat (see Divak et al., 1987). Historically, Rose (1929) named it layer VII in mouse, and Krieg (1946b) recognized the segment of it in rat somatosensory cortex as layer VIb. For its participation in the subplate region see Valverde et al. (1989, 1995).

BIBLIOGRAPHY STARTS ON NEXT PAGE.

## Bibliography for Table C (version 4.0beta5.2)

- Adams, A.D. & Forrester, J.M. (1968) The projection of the rat's visual field on the cerebral cortex. *Quarterly Journal of Experimental Physiology* **53**:327-336.
- Arnault P. & Roger M. (1990) Ventral temporal cortex in the rat: connections of secondary auditory areas Te2 and Te3. *Journal of Comparative Neurology* **302**:110-123.
- Alvarez-Bolado, G. & Swanson, L.W. (1996) *Developmental Brain Maps: Structure of the Embryonic Rat Brain* (Elsevier, Amsterdam).
- Azizi S.A., Burne R.A., & Woodward D.J. (1985) The auditory corticopontocerebellar projection in the rat: inputs to the paraflocculus and midvermis. An anatomical and physiological study. *Experimental Brain Research* **59**:36-49.
- Behan, M. & Haberly, L.B. (1999) Intrinsic and efferent connections of the endopiriform nucleus in rat. *Journal of Comparative Neurology* **408**:532-548.
- Blackstad T.W. (1956) Commissural connections of the hippocampal region in the rat, with special reference to their mode of termination. *Journal of Comparative Neurology* **105**:417-538.
- Bota, M., Sporns, O., & Swanson, L.W. (2015) Architecture of the cerebral cortical association connectome underlying cognition. *Proceedings of the National Academy of Sciences USA* **107**:20610-20617.
- Brodmann, K. (1909) *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien Dargestellt auf Grund des Zellenbaues* (Barth, Leipzig). For English translation see Garey, L.J. (1994).
- Burdach, K.F. (1819, 1822, 1826) *Vom Baue und Leben des Gehirns* (Dyk'schen Buchhandlung, Leipzig).
- Burwell, R.D. (2001) Borders and cytoarchitecture of the perirhinal and postrhinal cortices in the rat. *Journal of Comparative Neurology* **437**:17-41.
- Canteras N.S., Simerly R.B., & Swanson L.W. (1992) The connections of the posterior nucleus of the amygdala. *Journal of Comparative Neurology* **324**:143-179.
- Canteras N.S. & Swanson L.W. (1992a) Projections of the ventral subiculum to the amygdala, septum, and hypothalamus: a PHAL anterograde tract-tracing study in the rat. *Journal of Comparative Neurology* **324**:180-194.
- Cappaert, N.L.M., Van Strien, N.M., & Witter, M.P. (2015) Hippocampal formation. In: Paxinos, G. (Ed.), *The Rat Nervous System*, 4<sup>th</sup> edn. (Elsevier, Amsterdam), pp. 511-573.
- Carus, C.G. (1814) *Versuch einer Darstellung des Nervensystems und Insbesondere des Gehirns nach Ihrer Bedeutung, Entwicklung und Vollendung im Thierischen Organismus* (Breitkopf und Härtel, Leipzig).
- Cechetto D.F. & Saper C.B. (1987) Evidence for a viscerotopic sensory representation in the cortex and thalamus in the rat. *Journal of Comparative Neurology* **262**:27-45.
- Cenquizca, L.A. & Swanson, L.W. (2006) An analysis of direct hippocampal cortical field CA1 axonal projections to diencephalon in the rat. *Journal of Comparative Neurology* **497**:101-114.
- Chapin J.K. & Lin C.S. (1984) Mapping the body representation in the SI cortex of anesthetized and awake rats. *Journal of Comparative Neurology* **229**:199-213.
- Coogan T.A. & Burkhalter A. (1993) Hierarchical organization of areas in rat visual cortex. *Journal of Neuroscience* **13**:3749-3772.
- Craigie E.H. (1925) *An Introduction to the Finer Anatomy of the Central Nervous System based upon that of the Albino Rat* (Blakiston's Son & Co., Philadelphia).
- Davis B.J., Macrides F., Youngs W.H., Schneider S.P., & Rosene D.L. (1978) Efferents and centrifugal afferents of the main and accessory olfactory bulbs in the hamster. *Brain Research Bulletin* **3**:59-72.
- Deacon T.W., Eichenbaum H., Rosenberg P., & Eckmann K.W. (1983) Afferent connections of the perirhinal cortex in the rat. *Journal of Comparative Neurology* **220**:168-190.

- de Olmos, J., Alheid, G.F., & Beltramino, C.A. (1985) Amygdala. In: Paxinos, G. (Ed.), *The Rat Nervous System, Vol. 1, Forebrain and Midbrain* (Academic Press, New York), pp. 223-334.
- de Olmos, J., Hardy, H., & Heimer, L. (1978) The afferent connections of the main and the accessory olfactory bulb formations in the rat: an experimental HRP-study. *Journal of Comparative Neurology* **181**:213-244.
- Divac I., Marinkovic S., Mogensen J., Schwerdtfeger W., & Regidor J. (1987) Vertical ascending connections in the isocortex. *Anatomy and Embryology* **175**:443-455.
- Dolorfo, C.L. & Amaral, D.G. (1998a) Entorhinal cortex of the rat: topographic organization of the cells of origin of the perforant path projection to the dentate gyrus. *Journal of Comparative Neurology* **398**:25-48.
- Dolorfo, C.L. & Amaral, D.G. (1998b) Entorhinal cortex of the rat: organization of intrinsic connections. *Journal of Comparative Neurology* **398**:49-82.
- Donoghue J.P. & Wise SP (1982) The motor cortex of the rat: cytoarchitecture and microstimulation mapping. *Journal of Comparative Neurology* **212**:76-88.
- Doron N.N., LeDoux J.E., & Semple M.N (2002) Redefining the tonotopic core of rat auditory cortex: physiological evidence for a posterior field. *Journal of Comparative Neurology* **453**:345-360.
- Ekstrand, J.J., Domroese, M.E., Johnson, D.M.G., Feig, S.L., Knodel, S.M., Behan, M., & Haberly, L.B. (2001) A new subdivision of anterior piriform cortex and associated deep nucleus with novel features of interest for olfaction and epilepsy. *Journal of Comparative Neurology* **434**:289-307.
- Ennis, M., Puche, A.C., Holy, T., & Shipley, M.T. (2015) The olfactory system. In: Paxinos, G. (Ed.), *The Rat Nervous System*, 4<sup>th</sup> edn. (Elsevier, Amsterdam), pp. 761-803.
- Espinoza, S.G. & Thomas, H.C. (1983) Retinotopic organization of striate and extrastriate visual cortex in the hooded rat. *Brain Research* **272**:137-144.
- Fabri M. & Burton H. (1991) Topography of connections between primary somatosensory cortex and posterior complex in rat: a multiple fluorescent tracer study. *Brain Research* **538**:351-357.
- Friedlander, M.J. & Torres-Reveron, J. (2009) The changing roles of neurons in the cortical subplate. *Frontiers in Neuroanatomy* doi: [10.3389/neuro.05.015.2009](https://doi.org/10.3389/neuro.05.015.2009).
- Gurdjian, E.S. (1925) Olfactory connections in the albino rat, with special reference to the stria medullaris and the anterior commissure. *Journal of Comparative Neurology* **38**:127-163.
- Gurdjian, E.S. (1928) The corpus striatum of the rat. *Journal of Comparative Neurology* **45**:249-281.
- Haberly L.B. & Price J.L. (1978a) Association and commissural fiber systems of the olfactory cortex in the rat. I. Systems originating in the piriform cortex and adjacent areas. *Journal of Comparative Neurology* **178**:711-740.
- Haberly L.B. & Price J.L. (1978b) Association and commissural fiber systems of the olfactory cortex in the rat. II. Systems originating in the olfactory peduncle. *Journal of Comparative Neurology* **181**:781-808.
- Haug, F.-M.S. (1974) Light microscopical mapping of the hippocampal region, the pyriform cortex and the corticomedial amygdaloid nuclei of the rat with Timm's sulfide silver method. *Zeitschrift für Anatomie und Entwicklungsgeschichte* **145**:1-27.
- Haug, F.-M.S. (1976) Sulphide silver pattern and cytoarchitectonics of parahippocampal areas in the rat. Special reference to the subdivision of area entorhinalis (area 28) and its demarcation from the pyriform cortex. *Advances in Anatomy, Embryology and Cell Biology* **52**:1-73.
- Herrick, C.J. (1910) The morphology of the forebrain in amphibia and reptilia. *Journal of Comparative Neurology and Psychology* **20**:413-547.
- Hjorth-Simonsen A. (1972) Projection of the lateral part of the entorhinal area to the hippocampus and fascia dentata. *Journal of Comparative Neurology* **146**:219-232.
- Hjorth-Simonsen, A. & Jeune, B. (1972) Origin and termination of the hippocampal perforant path in the rat studied by silver impregnation. *Journal of Comparative Neurology* **144**:215-232.



- Hughes H.C. (1977) Anatomical and neurobehavioral investigations concerning the thalamo-cortical organization of the rat's visual system. *Journal of Comparative Neurology* **175**:311-336.
- Insausti, R., Herrero, M.T., & Witter, M.P. (1997) Entorhinal cortex of the rat: cytoarchitectonic subdivisions and the origin and distribution of cortical efferents. *Hippocampus* **7**:146-183.
- International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature* (International Trust for Zoological Nomenclature, London).
- Jolkkonen, E., Miettinen, R., & Pitkänen, A. (2001) Projections from the amygdalo-piriform transition area to the amygdaloid complex: a PHA-L study in rat. *Journal of Comparative Neurology* **432**:440-465.
- Jones, B.F. & Witter, M.P. (2007) Cingulate cortex projections to the parahippocampal region and hippocampal formation in the rat. *Hippocampus* **17**:957-976.
- Kelly J.B. & Sally S.L. (1988) Organization of auditory cortex in the albino rat: binaural response properties. *Journal of Neurophysiology*, **59**:1756-1769.
- Kosar E., Grill H.J., & Norgren R. (1986) Gustatory cortex in the rat. I. Physiological properties and cytoarchitecture. *Brain Research* **379**:329-341.
- Krettek J.E. & Price J.L. (1977a) The cortical projections of the mediodorsal nucleus and adjacent thalamic nuclei in the rat. *Journal of Comparative Neurology* **171**:157-192.
- Krettek J.E. & Price J.L. (1978) A description of the amygdaloid complex in the rat and cat with observations on intra-amygdaloid axonal connections. *Journal of Comparative Neurology* **178**:255-280.
- Krieg W.J.S. (1946a) Connections of the cerebral cortex. I. The albino rat. A. Topography of the cortical areas. *Journal of Comparative Neurology* **84**:221-276.
- Krieg W.J.S. (1946b) Connections of the cerebral cortex. I. The albino rat. B. Structure of the cortical areas. *Journal of Comparative Neurology* **84**:277-324.
- Kuhlenbeck, H. (1927) *Vorlesungen über das Zentralnervensystem der Wirbeltiere* (Fischer, Jena).
- Lashley, K.S. (1934) The mechanism of vision. VIII. the projection of the retina upon the cerebral cortex of the rat. *Journal of Comparative Neurology* **60**:57-80.
- Lein, E.S., Callaway, E.M., Albright, T.D., & Gage, F.H. (2005) Redefining the boundaries of the hippocampal CA2 subfield in the mouse using gene expression and 3-dimensional reconstruction. *Journal of Comparative Neurology* **485**:1-10.
- Lorente de Nó, R. (1934) Studies on the structure of the cerebral cortex. II. Continuation of the study of the ammonic system. *Journal für Psychologie und Neurologie (Leipzig)* **46**:113-177.
- McDonald, A.J. (1983) Cytoarchitecture of the nucleus of the lateral olfactory tract: A Golgi study in the rat. *Brain Research Bulletin* **10**:497-503.
- Meckel, J.F., the Younger (1817) *Handbuch der Menschlichen Anatomie*, Vol. 3 (Buchhandlung des Hallischen Maisenhauses, Berlin).
- Miller M.W. & Vogt B.A. (1984) Direct connections of rat visual cortex with sensory, motor, and association cortices. *Journal of Comparative Neurology* **226**:184-202.
- Millhouse O.E. & Uemura-Sumi M. (1985) The structure of the nucleus of the lateral olfactory tract. *Journal of Comparative Neurology* **233**:517-552.
- Montero, V.M. (1993) Retinotopy of cortical connections between the striate cortex and extrastriate visual areas in the rat. *Experimental Brain Research* **94**:1-15.
- Montero, V.M., Rojas, A., & Torrealba, F. (1973) Retinotopic organization of striate and peristriate visual cortex in the albino rat. *Brain Research* **53**:197-201.
- Neafsey E.J., Bold E.L., Haas G., Hurley-Gius K.M., Quirk G., Sievert C.F., & Terreberry R.R. (1986) The organization of the rat motor cortex: a microstimulation mapping study. *Brain Research Reviews* **11**:77-96.

- Neville, K.R. & Haberly, L.B. (2004) Olfactory cortex. In: Shepherd, G.M. (Ed.), *The synaptic organization of the brain*, 5<sup>th</sup> edn. (Oxford University Press, New York), pp. 415-454.
- Obersteiner, H. (1888) *Anleitung beim Studium des Baues der Nervösen Centralorgane: Im Gesunden und Kranken Zustände* (Toeplitz & Deuticke, Vienna).
- Olavarria, J. & Montero, V.M. (1984) *Experimental Brain Research* **54**:240-252.
- Olavarria, J. & Torrealba, F. (1978) The effect of acute lesions of the striate cortex on the retinotopic organization of the lateral peristriate cortex in the rat. *Brain Research* **151**:386-391.
- Olsen, G.M. & Witter, M.P. (2016) Posterior parietal cortex of the rat: architectural delineation and thalamic differentiation. *Journal of Comparative Neurology* **524**:3774-3809.
- Olucha-Bordonau, F.E., Fortes-Marco, L., Otero-García, M., Lanuza, E., & Martínez-García, F. (2015) Amygdala: structure and function. In: Paxinos, G. (Ed.), *The Rat Nervous System*, 4<sup>th</sup> edn. (Elsevier, Amsterdam), pp. 441-490.
- Petrovich, G.D. (1997) *Organization of Amygdalar Projections in the Rat*. Ph.D. Thesis (University of Southern California, Los Angeles).
- Petrovich G.D., Canteras N.S., & Swanson L.W. (2001) Combinatorial amygdalar inputs to hippocampal domains and hypothalamic behavior circuits. *Brain Research Reviews* **38**:247-289.
- Petrovich G.D., Risold P.Y., & Swanson L.W. (1996) Organization of projections from the basomedial nucleus of the amygdala: a PHAL study in the rat. *Journal of Comparative Neurology* **374**:387-420.
- Pitkänen, A. (2000) Connectivity of the rat amygdaloid complex. In: Aggleton, J.P. (Ed.), *The Amygdala: A Functional Analysis*, 2<sup>nd</sup> edn. (Oxford University Press, Oxford), pp. 31-115.
- Price, J.L. (1973) An autoradiographic study of complementary laminar patterns of termination of afferent fibers to the olfactory cortex. *Journal of Comparative Neurology* **150**:87-108.
- Price J.L., Russchen F.T., & Amaral D.G. (1987) The limbic region. II. The amygdaloid complex. In: Hökfelt T., Björklund, A., & Swanson L.W. (Eds.), *Handbook of Chemical Neuroanatomy, Vol. 5: Integrated Systems of the CNS, Part I* (Elsevier, New York), pp. 279-388.
- Ray, J.P & Price, J.L. (1992) The organization of the thalamocortical connections of the mediodorsal thalamic nucleus in the rat, related to the ventral forebrain-prefrontal cortex topography. *Journal of Comparative Neurology* **323**:167-197.
- Reep, R.L., Chandler, H.C., King, V., & Corwin, J.V. (1994) Rat posterior parietal cortex: topography of corticocortical and thalamic connections. *Experimental Brain Research* **100**:67-84.
- Remple, M.S., Henry, E.C., & Catania, K.C. (2003) Organization of somatosensory cortex in the laboratory rat (*Rattus norvegicus*): evidence for two lateral areas joined at the representation of the teeth. *Journal of Comparative Neurology* **467**:105-118.
- Riddle D.R. & Purves D. (1995) Individual variation and lateral asymmetry of the rat primary somatosensory cortex. *Journal of Neuroscience* **15**:4184-4195.
- Risold, P.Y. & Swanson, L.W. (1995) Evidence for a hypothalamocortical circuit mediating pheromonal influences on eye and head movements. *Proceedings of the National Academy of Sciences USA* **92**:3898-3902.
- Risold, P.Y. & Swanson, L.W. (1996) Structural evidence for functional domains in the rat hippocampus. *Science* **272**:1484-1486.
- Risold, P.Y., Thompson, R.H., & Swanson, L.W. (1997) The structural organization of connections between hypothalamus and cerebral cortex. *Brain Research Reviews* **24**:197-254.
- Rose, M. (1928) Die Inselrinde des Menschen und der Tiere. *Journal für Psychologie und Neurologie (Leipzig)* **37**:467-624.
- Rose, M. (1929) Cytoarchitektonischer Atlas der Grosshirnrinde der Maus. *Journal für Psychologie und Neurologie (Leipzig)* **40**:1-51.

- Rose, J.E. & Woolsey, C.N. (1948) Structure and relations of limbic cortex and anterior thalamic nuclei in rabbit and cat. *Journal of Comparative Neurology* **89**:279-347.
- Sally S.L. & Kelly J.B. (1988) Organization of auditory cortex in the albino rat: sound frequency. *Journal of Neurophysiology* **59**:1627-1638.
- Sanderson K.J., Welker W. & Shambes G.M. (1984) Reevaluation of motor cortex and of sensorimotor overlap in cerebral cortex of albino rats. *Brain Research* **292**:251-260.
- Santiago, A.C. & Shammah-Lagnado, S.J. (2005) Afferent connections of the amygdalopiriform transition area in the rat. *Journal of Comparative Neurology* **489**:349-371.
- Scalia, F. & Winans, S.S. (1975) The differential projections of the olfactory bulb and accessory olfactory bulb in mammals. *Journal of Comparative Neurology* **161**:31-56.
- Shibata, H., Honda, Y., Sasaki, H., & Naito, J. (2009) Organization of intrinsic connections of the retrosplenial cortex in the rat. *Anatomical Sciences International* **84**:280-292.
- Smith, G.E. (1919) A preliminary note on the morphology of the corpus striatum and the origin of the neopallium. *Journal of Anatomy* **53**:271-291.
- Swanson, L.W. (1992) *Brain Maps: Structure of the Rat Brain* (Elsevier, Amsterdam).
- Swanson L.W. (1998) *Brain Maps: Structure of the Rat Brain. A Laboratory Guide with Printed and Electronic Templates for Data, Models and Schematics*, 2<sup>nd</sup> revised edn. with 2 CD-ROMs (Elsevier, Amsterdam).
- Swanson, L.W. (2000a) Cerebral hemisphere regulation of motivated behavior. *Brain Research* **886**:113-164.
- Swanson, L.W. (2000b) What is the brain? *Trends in Neuroscience* **23**:519-527.
- Swanson, L.W. (2003a) *Brain Architecture: Understanding the Basic Plan* (Oxford University Press, Oxford).
- Swanson, L.W. (2003b) The amygdala and its place in the cerebral hemisphere. *Annals of the New York Academy of Science* **985**:1-11.
- Swanson, L.W. (2004) *Brain Maps: Structure of the Rat Brain. A Laboratory Guide with Printed and Electronic Templates for Data, Models and Schematics*, 3<sup>rd</sup> revised edition (Elsevier, Amsterdam), 215 pp. with CD-ROM, *Brain Maps: Computer Graphics Files 3.0*.
- Swanson, L.W. (2015) *Neuroanatomical Terminology: A Lexicon of Classical Origins and Historical Foundations* (Oxford University Press, New York).
- Swanson, L.W. & Bota, M. (2010) Foundational model of nervous system structural connectivity with a schema for wiring diagrams, connectome, and basic plan architecture. *Proceedings of the National Academy of Sciences USA* **107**:20610-20617.
- Swanson, L.W. & Cowan, W.M. (1975) Hippocampo-hypothalamic connections: origins in subicular cortex, not Ammon's horn. *Science* **189**:303-304.
- Swanson, L.W. & Cowan, W.M. (1977) An autoradiographic study of the organization of the efferent connections of the hippocampal formation in the rat. *Journal of Comparative Neurology* **172**:49-84.
- Swanson, L.W., Köhler, C., & Björklund, A. (1987) The limbic region. I: The septohippocampal system. In: Björklund, A., Hökfelt, T., & Swanson, L.W. (Eds.) *Handbook of Chemical Neuroanatomy*, Vol. 5, *Integrated Systems of the CNS*, Part I (Elsevier, Amsterdam), pp. 125-277.
- Swanson L.W. & Petrovich G.D. (1998) What is the amygdala? *Trends in Neuroscience* **21**:323-331.
- Swanson, L.W., Sporns, O., & Hahn, J.D. (2016) Network architecture of the cerebral nuclei (basal ganglia) association and commissural connectome. *Proceedings of the National Academy of Sciences* **113**:E5972-E5981.
- Swanson, L.W., Wyss, J.M., & Cowan, W.M. (1978) An autoradiographic study of the organization of intrahippocampal association pathways in the rat. *Journal of Comparative Neurology* **181**:681-716.
- Terminologia Anatomica* (1998) (Thieme, Stuttgart).

- Thomas H.C. & Espinoza S.G. (1987) Relationships between interhemispheric cortical connections and visual areas in hooded rats. *Brain Research* **417**:214-224.
- Valentin, G.G. (1841) *Hirn- und Nervenlehre*. In: Soemmerring, S.T., et al. (Eds.), *Vom Baue des Menschlichen Körpers*, Vol. 4 (Voss, Leipzig).
- Valverde F., Facal-Valverde M.V., Santacana M., & Heredia M. (1989) Development and differentiation of early generated cells of sublayer VIb in the somatosensory cortex of the rat: a correlated Golgi and autoradiographic study. *Journal of Comparative Neurology* **290**:118-140.
- Valverde F., Lopez-Mascaraque L., Santacana M., & De Carlos J.A. (1995) Persistence of early-generated neurons in the rodent subplate: assessment of cell death in neocortex during early postnatal period. *Journal of Neuroscience* **15**:5014-5024.
- Vandeveldel I.L., Duckworth E., & Reep R.L. (1996) Layer VII and the gray matter trajectories of corticocortical axons in rats. *Anatomy and Embryology* **194**:581-593.
- Van De Werd, H.J.J.M. & Uylings, H.B.M. (2008) The rat orbital and agranular insular prefrontal cortical areas: a cytoarchitectonic and chemoarchitectonic study. *Brain Structure and Function* **212**:387-401.
- van Groen, T. & Wyss, J.M. (1990a) The postsubicular cortex in the rat: characterization of the fourth region of the subicular cortex and its connections. *Brain Research* **529**:165-177.
- van Groen, T. & Wyss, J.M. (1990b) The connections of presubiculum and parasubiculum in the rat. *Brain Research* **518**:2270-243.
- Vogt, B.A. (2015) Cingulate cortex and pain architecture. In: Paxinos, G. (Ed.), *The Rat Nervous System*, 4<sup>th</sup> edn. (Elsevier, Amsterdam), pp. 575-599.
- Vogt, B.A., Hof, P.R., Zilles, K., Vogt, L.J., Herold, C., & Palomero-Gallagher, N. (2013) Cingulate area 32 homologues in mouse, rat, macaque and human: cytoarchitecture and receptor architecture. *Journal of Comparative Neurology* **521**:4189-4204.
- Vogt, B.A. & Peters, A. (1981) Form and distribution of neurons in rat cingulate cortex: areas 32, 24, and 29. *Journal of Comparative Neurology* **195**:603-625.
- Weitbrecht, J. (1751) De vera significatione processuum mamillarum cerebri. *Commentarii Academiae Scientiarum Imperialis Petropolitanae*, Vol. 14 for 1744-1746 (published in 1751), pp. 276-285.
- Welker C. & Sinha M.M. (1972) Somatotopic organization of SmlI cerebral neocortex in albino rat. *Brain Research* **37**:132-136.
- Wyss J.M. & Sripanidkulchai K. (1983) The indusium griseum and anterior hippocampal continuation in the rat. *Journal of Comparative Neurology* **219**:251-272.
- Yu, H. (1969) *The Amygdaloid Complex in the Rat*. Master's Thesis (University of Ottawa, Ottawa).