Complete 3D Visualization of Primate Striosomes by KChIP1 Immunostaining

SHAWN MIKULA,1 SARAH K. PARRISH,1 JAMES S. TRIMMER,1,2 AND EDWARD G. JONES1*
1Center for Neuroscience, University of California–Davis, Davis, California 95618
2Department of Neurobiology, Physiology and Behavior, University of California–Davis, Davis, California 95618

ABSTRACT
High-resolution 3D reconstruction and morphometric analysis of striosomes was carried out in macaque monkeys by using immunocytochemistry for the Kv4 potassium channel subunit potassium channel interacting protein 1 (KChIP1), a novel marker. The striosomes form a connected reticulum made up of two distinct planar sheets spanning several millimeters in the putamen, and long finger-like branches in the caudate nucleus and putamen. Although their spatial organization is variable, morphometric analysis of the striosomes, utilizing skeletonizations, reveals several quantitative invariant measures of striosome organization, including the following findings: 1) individual bifurcation-free striosome branches are $355 \pm 108.5 \mu m$ in diameter and $1,013 \pm 751 \mu m$ in length, and are both log-normally distributed; and 2) striosome branches exhibit three pronounced orientation preferences that are approximately orthogonal. The former finding suggests a fundamental anatomical and functional component of the striatum, whereas the latter indicates that striosomes are more lattice-like than their spatial variability suggests. The perceived variable spatial organization of the striosomes in primates belies many invariant features that may reflect striatal function, development, and pathophysiology. J. Comp. Neurol. 514: 507–517, 2009. © 2009 Wiley-Liss, Inc.

Indexing terms: potassium channel subunit; putamen; caudate nucleus; basal ganglia; matrix

Modularity and chemical compartmentalization are prevalent throughout the brain, and are present in primate cortical areas such as V1 and V2, the barrel cortex of rodents, the presubiculum, and the entorhinal cortex, as well as the superior colliculus, thalamus, and striatum. Chemical compartments and modules are often associated with segregation of function. Well-known examples in the primate visual cortex are the V1 blobs, which are organized as a lattice of patches in tangential sections and are known to be involved in color vision (Livingstone and Hubel, 1984). One of the most striking examples of chemical compartmentalization occurs in the striatum, in structures called the striosomes (Graybiel and Ragsdale, 1978).

The striatum is implicated in a wide range of functions from motor control to addiction, and although appearing as a generally homogeneous cell mass in Nissl-stained material, is strikingly organized into two complementary chemical compartments known as the matrix and the striosomes when visualized by staining for markers such as acetylcholinesterase (Graybiel and Ragsdale, 1978), enkephalin, substance P, limbic system-associated membrane protein (LAMP) (Prensa et al., 1999), AMPA receptor subunit 1 (GluR1) (Martin et al., 1993), dopamine receptor subunits, and calcium-binding proteins (O’Kusky et al., 1999). Striosomal abnormalities have been associated with neurological disorders, such as mood dysfunction in Huntington’s disease (Tippett et al., 2007). Previous studies of the 3D organization of the striosome system in cats and rats concluded that striosomes are organized as a reticulum (Groves et al., 1988; Desban et al., 1989, 1993; Manley et al., 1994). The detailed structure of primate striosomal organization has not been described.

In the current study, we used immunocytochemical localization of voltage-gated potassium channel interacting protein 1 (KChIP1), a calcium-binding protein that interacts with transient voltage-gated potassium channels, localized in neuronal somata and dendrites (Rhodes et al., 2004), to modulate neuronal excitability (An et al., 2000; Beck et al., 2002). This gave a high-contrast view of the striosomes in Old World monkeys that permitted more accurate reconstruction than hitherto possible.

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*Correspondence to: Edward G. Jones, M.D., Ph.D., Center for Neuroscience, University of California Davis, Davis CA 95618.
Email: ejones@ucdavis.edu

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MATERIALS AND METHODS

Antibody characteristics

Anti-calbindin. A rabbit anti-calbindin antibody, kindly
provided by Dr. P.C. Emson (Brabraham Institute, Cambridge,
UK), was used to stain the matrix compartment in the striatum.
The antiserum was produced against calbindin, MW 28,000,
purified by high-pressure liquid chromatography after iso-
lation from chick intestine (Spencer et al., 1978); Western blot-
ing has shown that the antiserum specifically recognizes
calbindin of MW 28,000 in macaque brain (Graziano and
Jones, 2004). Immunostaining patterns obtained in the
present study were consistent with those previously reported
in previous studies using this antibody in Old World monkeys
(e.g., Jones and Hendry, 1989; Graziano and Jones, 2004).

Anti-KChIP1. Purified mouse monoclonal anti-KChIP1
antibody, K55/7 (available from the University of California,
Davis NeuroMab Facility; www.neuromab.org), was used to
stain striosomes. This monoclonal antibody was generated
against a recombinant fusion protein containing full-length
purified by high-pressure liquid chromatography after iso-
lation from chick intestine (Spencer et al., 1978). Western blot-
ing has shown that the antiserum specifically recognizes
rat KChIPs 2–4 expressed in heterologous cells
(Menegola et al., 2008; Rhodes et al., 2004). In immunofluorescence and immunoblot
assays, K55/7 specifically recognizes recombinant rat KChIP1
but not rat KChIPs 2–4 expressed in heterologous cells
(Rhodes et al., 2004). The rat KChIP1 sequence is 98% iden-
tical to Macaca mulatta KChIP1 and 99% identical to Homo sapiens KChIP1; the Macaca fascicularis KChIP1 sequence is not available.

Immunocytochemistry

Four cerebral hemispheres from three male cynomolgus
monkeys (M. fascicularis) were used. The brains were fixed by
perfusion with 4% paraformaldehyde in 0.1 M phosphate-
buffered saline (PBS; pH 7.2), frozen in dry ice, and sectioned
on a sliding microtome. Both hemispheres from one monkey
cases 91L and 91R) were cut coronally at 25 μm. The right
hemisphere of a second monkey (case 76R) was cut coronally
at 30 μm. The left hemisphere of a third monkey (case 111R)
was blocked just posterior to the anterior commissure, and
was cut at 30 μm in an oblique plane parallel to the internal
capsule, approximately midway between the sagittal and hori-
zonal planes. The 3D reconstruction for case 111R was lim-
ited to the head of the caudate nucleus and was used to
confirm the qualitative and quantitative results from the three
complete reconstructions (cases 76R, 91L, and 91R); how-
ever, this case is not included in the Results section because
the striosomes and striatum are incompletely reconstructed.
The section thickness does not factor into the various mor-
phometric calculations, and is only used for correctly scaling
the 3D reconstructions and skeletonizations (see below).

Sections were preincubated for 10 minutes in a 1:1 mixture of
0.1 M PBS (pH 7.2) and ethanol containing 1% hydrogen peroxide to block endogenous peroxidase that might contribute to background staining, followed by three rinses through
PBS, and then 1 hour in blocking solution (BS) containing 3% normal serum and 0.25% Triton X-100 in 0.1 M PBS. Every
sixth regularly spaced section was incubated for 48 hours at
4°C in BS containing KChIP1 monoclonal antibody at 1:1,000.
Adjacent sections were incubated for 48 hours at 4°C in BS
containing D-28k calbindin rabbit polyclonal antibody at
1:2,000; calbindin immunoreactivity is a known marker for the
complementary matrix compartment. After three washes in
PBS, the sections were incubated in BS containing biotinyl-
ated secondary antibody (1:200) for 1–2 hours, washed three times in PBS, and transferred to PBS containing the peroxi-
dase conjugate from the Vectastain ABC kit (Vector, Burlin-
game, CA). After rinsing three times in PBS, the sections were
immersed in a solution of 0.02% 3-3' diaminobenzidine-4HCl
(DAB; Sigma-Aldrich, St. Louis, MO) and 0.003% hydrogen peroxide.

After staining, the sections were mounted on gelatinized
glass slides, dehydrated in increasing concentrations of eth-
anol, cleared in xylene, and coverslipped with DPX medium.
Several unstained sections were mounted on glass slides for
purposes of comparison with immunocytochemically pro-
cessed sections, in order to compute shrinkage factors due to
immunocytochemical processing.

Image acquisition

Glass-mounted sections were scanned at 20× (0.46 μm/pixel)
in an Aperio ScanScope T3 scanner (Aperio Technolo-
gies, Vista, CA), specially adapted to accommodate 3 ×
2-inch slides, to generate virtual (i.e., digital) slides and sub-
sequently uploaded to the publicly accessible BrainMaps.org
server (Mikula et al., 2007). All image data used in this study
All images for publication were composed in Photoshop CS3
(Adobe Systems, San Jose, CA), and optimized for brightness
and contrast.

3D reconstruction

3D reconstruction involved striosome segmentation (see
Supplementary Fig. S1), image alignment, isosurface extrac-
tion, and surface rendering. The total numbers of sections
used for 3D reconstructions are as follows: 1) case 76R, 92
sections at 30-μm thickness; 2) case 91L, 99 sections at
25-μm thickness; 3) case 91R, 99 sections at 25-μm thick-
ness; and 4) case 111R, 33 sections at 30-μm thickness.
Gradients in the immunostained striatal neuropil validated
striatal and striosomal segmentations relying on global
thresholds, and so semimanual segmentation was employed
by using the tracing or magic wand tools in Photoshop CS3
and validated with manual inspection. RGB images were con-
structed so that the first channel contained the grayscale
image of the entire section, the second channel contained
the segmented striatum, and the third channel contained the
segmented striosomes. Automated rigid body image alignments
of the RGB images was performed in ImageJ (Rasband, 1997)
by using the plug-in, StackReg, that implements a pyramid
approach to subpixel registration based on pixel intensity
(Thevenaz et al., 1998). 3D volumetric reconstructions were
performed by using Imaris, a freeware program that uses
regularized marching tetrahedra for iso-surface extraction
(Teece et al., 1999) and were validated against volumetric
renderings of the original aligned RGB image stack by using
Imlaris, v5 (Bitplane, Zurich, Switzerland). 3D reconstructions,
using the extracted isosurfaces, were rendered in Lightwave
3D, v9.3.1 (Newtek, San Antonio, TX).

Spatial averaging across striosomes

Grayscale (intensity) and binary image stacks of the strios-
omes from cases 76R, 91L, and 91R were rigidly aligned in
ImageJ, and subsequently imported into Matlab (Mathworks,
Natick, MA) for spatial averaging, which consisted of comput-
ing intensity and binary products on a voxel-wise basis. Computation of percentage of striosome overlap utilized the spatially registered binary image stacks. Visualization of results was performed in Imaris, v5 (Bitplane).

**Skeletonization and morphometric analysis**

Striosome image stacks were down-sampled to generate voxel sizes of 110 × 110 × 150 μm for cases 91L and 91R and 110 × 110 × 180 μm for case 76. Skeletonization of the 3D striosome volumes was performed in Imaris (Bitplane) by using the Autopath method for skeletonization, which is a 3D extension of the 2D method described in Meijering et al. (2004). This method uses spot objects; the starting point (large) and end points (small) are defined in the dataset volume. Then a Fast Marching algorithm is used to connect end points to the starting point, along the path of greatest intensity. The resulting skeleton is defined in terms of striosome segments connected by branch points. Skeletonizations were exported from Imaris and imported in Matlab for computation of skeleton branching angles, segment orientations (in spherical coordinates), segment lengths, and segment diameters by using custom-coded scripts. Striosome orientations were binned into $5^\circ$ theta and phi increments, in spherical coordinates, where theta is the angle that the projection of the striosome segment makes in the coronal plane, ranging from 0° to 360°, and where phi is the angle offset of the striosome segment from the coronal plane, ranging from 0° to 90°. These binned striosome segmentations were subsequently mapped onto the sphere for visualization purposes.

**RESULTS**

KChIP1 is a novel immunocytochemical marker for the striosomes in macaque

KChIP1 is a remarkably clear-cut immunocytochemical marker for the striosomes in the macaque monkey (Fig. 1). Coronal sections at the level of the anterior commissure showing KChIP1 immunoreactivity in the striosomes (Fig. 1a), when compared with adjacent sections stained for calbindin immunoreactivity, reveal (Fig. 1b) a striking complementarity: calbindin exhibits high immunoreactivity in the matrix compartment and KChIP1 in the striosome compartment of the caudate nucleus and putamen. There is no KChIP1 immunostaining of the nucleus accumbens, which is more or less homogeneously immunoreactive for calbindin. In sections cut approximately parallel to the internal capsule (dashed line in Fig. 1a), a lattice-like pattern of KChIP1-immunoreactive striosomes is evident in the head of the caudate nucleus (Fig. 1c), with complementary immunostaining for calbindin seen in an adjacent section (Fig. 1d). Higher magnification reveals KChIP1 immunoreactivity of somata in both matrix and striosomes (Fig. 1c, upper inset), but heavy immunoreactivity of the neuropil only in the striosomes (Fig. 1c, lower inset). This neuropil immunoreactivity is made up of interlacing neuronal processes of large and small diameter on a diffusely immunostained background.

Based on the somal diameter (10–15 μm) and morphology (including an apparent lack of dendritic spines) of the immunoreactive neurons, we believe that the KChIP1-immunoreactive somata may belong to the "aspyne type I" class of DiFiglia et al. (1976). Preliminary results from double immunocytochemical staining for KChIP1 and calbindin (a marker for medium spiny projection neurons), or for KChIP1 and the striatal interneuronal markers choline acetyltransferase (ChAT), neuropeptide-Y, parvalbumin, and calretinin have revealed no co-localization of KChIP1 and any of these markers (data not shown).

**3D reconstructions and the qualitative organization of the striosomes**

In 3D reconstructions (Figs. 2, 3), the striosomes occupy 15.85% of the volume of the striatum (caudate nucleus, putamen, and nucleus accumbens), or 16.64% when the nucleus accumbens, which accounts for about 4.8% of the macaque striatum, is excluded; this agrees with previous estimates of 15% based on counting relative striosome areas in serial sections of enkephalin-immunoreactive material (Johnston et al., 1990).

3D reconstructions demonstrate that the striosomes form a connected reticulum. Many striosomes extend from the putamen into the caudate nucleus through the neuronal bridges in the internal capsule. These "bridge" striosomes have an antero-dorso-medial to postero-ventro-lateral bias, the same as the neuronal bridges. The caudate striosomes are located predominantly in the head of the caudate nucleus and are organized as a series of serpentine, finger-like structures, which we call striosome branches; 3D reconstructions demonstrate that the branches also have a pronounced antero-dorso-medial to postero-ventro-lateral bias, often running through the internal capsule into the putamen through the cell bridges. Striosomes are sparse in the body of the caudate nucleus and are absent from the tail.

In the putamen, there is one striosomal sheet at the anterior pole of the putamen and a second in its lateral aspect, which extends through the anterior half of putamen, running parallel to the claustrum. Although these features of the putamen striosomes were constant across monkeys and cerebral hemispheres of the same monkey, there is considerable variability in their exact shape, as demonstrated in Figures 2c and 3c.

**Spatial averaging across striosomes**

Spatial averaging over all volumetric striosome data reveals markedly little overlap (<5%) due to variability in the shape of the striatum between animals, which results in poor rigid registration results (data not shown). Nevertheless, rigid registration of striata (and corresponding striosomes) from the two hemispheres of the same animal (cases 91L and 91R) produced a very good fit, and resulted in a 14.7% overlap between the striosomes in the two striata of the same animal (Fig. 4), with a large fraction of the overlap attributable to the striosomal sheet in the lateral putamen. Lesser disconnected regions of overlap were observed in the striosome branches.

**Morphometrics and the quantitative organization of the striosomes**

Skeletonization of the striosomes, which preserves the overall morphology of the striosomes, and subsequent morphometric analysis, offers a way to bypass the difficulties encountered in spatial averaging across striosomes. Comparison of striata from hemispheres 76R, 91L, and 91R (Figs. 5, Supplementary S2, Supplementary S3), revealed marked variability in the overall skeletonizations, and of the morphologies of different striosomes. By contrast, morphometric measures (Figs. 5, Supplementary S2, Supplementary S3), including striosome segment orientations, bifurcation angles, striosome diameters, and segment lengths, revealed a striking similarity.
For case 91R, bifurcation angles \((n = 878)\) had a mean of \(87.3 \pm 31.6^\circ\) (Fig. 5d). Striosome diameters \((n = 776)\) had a mean of 348.8 ± 110.2 \(\mu\)m, and lengths \((n = 776)\) a mean of 1,045.8 ± 738.7 \(\mu\)m (Fig. 5e). These values are comparable to the corresponding values for cases 76R (Supplementary Fig. S2) and 91L (Supplementary Fig. S3).

Figure 6 shows group morphometric analyses of the three coronal cases (cases 76R, 91L, and 91R). Striosome segment...
orientations (Fig. 6a) and polar plots of the projection of the striosome orientations onto the coronal plane (Fig. 6b) revealed three prominent striosome orientation preferences in approximately orthogonal directions: posteromedial-to-anterolateral, anterodorsomedial-to-posteroventrolateral, and anteroventromedial-to-posterodorsolateral. Bifurcation angles (mean 84.6±33.7°, n=2764) are shown in Figure 6c. Striosome diameters (mean 355.3±108.5 μm, n=2,366), fit with a lognormal distribution, are shown in Figure 6d. Striosome lengths (mean 1,013.7±750.9 μm, n=2,366), also fit with a lognormal distribution, are shown in Figure 6e.

**DISCUSSION**

The striosomes in the macaque are organized as a connected reticulum similar to that suggested for cats and rodents (Desban et al., 1989, 1993; Groves et al., 1988; Manley et al., 1994). The 3D reconstructions of the striosomes, made possible by the high-resolution immunostaining for KChIP1, revealed that within the connected reticulum the striosomes form planar sheets that can span several millimeters in the putamen, and long, serpentine, finger-like branches of ~1 mm in length in both the caudate nucleus and putamen. The striosome branches have a consistent anterodorsomedial-to-posteroventrolateral bias, especially in the caudate nucleus. One striosome sheet is consistently observed at the anterior pole of the putamen and a second in the anterior half of the putamen at its lateralmost edge running parallel to the claustrum.

The high variability in the spatial organization of the striosomes precluded useful analysis via spatial averaging across striosomes. Morphometric analyses, utilizing skeletonizations
of the striosomes, however, revealed several quantitatively invariant measures of striosome organization: 1) individual striosome branches are $355 \pm 108.5 \mu m$ in diameter and are $1,013 \pm 751 \mu m$ in length before giving rise to collateral branches, and are both lognormally distributed; 2) the bifurcation angle between striosome branches is $84.6 \pm 33.7^\circ$ and is normally distributed; and 3) striosome branch orientations exhibit pronounced biases in the posteromedial-to-anterolateral, anterodorsomedial-to-posteroventrolateral, and in the anteroventromedial-to-posterodorsolateral directions, approximately orthogonal directions that may have functional significance (see below).

**Comparison with previous studies**

Previous reconstructions of striosomes have depended on their negative visualization in preparations in which the matrix compartment was stained. Full reconstructions of striosomes have been previously performed only in the rat (Desban et al., 1993), although partial reconstructions of those in the caudate nucleus have been done in cats (Desban et al., 1989; Groves et al., 1988; Manley et al., 1994). We did not find a continuous laminar (sheet-like) striosome along the anteroposterior extent of the dorsal caudate nucleus as described by Desban et al. (1989) in the cat. We believe their finding is likely due to incomplete staining of the matrix compartment, which may be brought about by fixative overexposure (Graybiel and Ragsdale, 1978) and thus incomplete visualization of the negatively stained striosomes. Other studies employing positive enkephalin immunostaining of the striosomes also failed to find a sheet-like striosome in the caudate nucleus (Groves et al., 1988). Desban et al (1989) also suggested that striosomes in

![Figure 3.](image-url)

3D reconstructions of the striosomes (green) from cases 91L and 91R viewed in perspective, shown from anterior (a), posterior (b), lateral (c), and medial (d) views as in Figure 2. Rotations of these reconstructions can be seen in the movies provided in the supplementary material.
the cat caudate nucleus resembled a continuous network of channels oriented in parallel arrays in both the rostrocaudal and mediolateral axis. Groves et al. (1988) found instead that the cat striosomes were organized as finger-like structures radiating ventrolaterally from the ventricular edge, connected to each other by smaller cross bridges (their Fig. 6), which is consistent with the present results in the monkey.

**Functional implications**

The observation that a typical striosome segment is 355 \( \mu \text{m} \) in diameter by 1 mm in length suggests that this is a fundamental anatomical and functional entity of the striatum, perhaps analogous to a cortical column (Mountcastle, 1997), although distributed in three dimensions in the striatal volume instead of across the thickness of the cortical sheet. The observation that striosome branches have three strong orthogonal orientation preferences suggests that the striosomes are organized as a lattice. The orthogonal orientation preferences of the striosomes suggests that different types of information could be mapped onto the three different directions, although physiological recordings or other high-resolution neuronal mapping methods, would have to confirm this hypothesis. The mapping of different types of information onto orthogonal directions is a feature of primary visual, auditory, and somatosensory cortices (Linden and Schreiner, 2003), as well as other brain regions, so the three orthogonal orientation preferences of the striosomes is highly suggestive of a similar mapping process. Prelimbic prefrontal cortical areas (areas 25 and 32 in macaque) and midline thalamic

Figure 4.
a,b: Volumetric visualization of results from spatial averaging of striosomes for cases 91L and 91R (Fig. 3). Individual striosomes from the left hemisphere (91L, green) and right hemisphere (91R, yellow), and their voxel-wise product of intensity values (91L x 91R, red). Overlap between the striosomes in the two hemispheres is 14.7% of the total individual striosomes, underscoring the spatial variability of the striosomes.
Figure 5.
a–c: Skeletonization and morphometric analysis of case 91R from anterior (a) and lateral (b) views, with striosome segment orientations (c). d: Bifurcation angles (mean = 87.3 ± 31.6°, n = 878). e: Striosome diameters (mean = 348.8 ± 110.2 μm, n = 776) versus lengths (mean = 1,045.8 ± 738.7 μm, n = 776). Skeletonizations of other cases are shown in Supplementary Figures S2 and S3.
Figure 6.
Group morphometric analyses of all three cases. a: Striosome segment orientations. b: Polar plot of the projection of the striosome orientations onto the coronal plane, showing strong medial, ventrolateral, and dorsolateral biases. c: Bifurcation angles (mean = 84.6° ± 33.7°, n = 2,764). d: Striosome diameters (mean = 355.3 ± 108.5 µm, n = 2,366), fit with a lognormal distribution. e: Striosome lengths (mean = 1,013.7 ± 750.9 µm, n = 2,366), also fit with a lognormal distribution.
nuclei, structures associated with self-monitoring and homeostasis, innervate the striosomes, whereas associational and sensorimotor-related prefrontal areas, and intralaminar thalamic nuclei, innervate the matrix (Gerfen, 1984; Donoghue and Herkenham, 1986; Ragsdale and Graybiel, 1991; Graybiel, 1995; Jones, 2007).

Given the lack of direct connections of midline thalamic nuclei and prelimbus prefrontal areas with other sensorimotor-associational regions of cortex, the striosomes may play a major role in integrating information from these two sources by way of intrinsic striatal connections (Penny et al., 1988; Tepper et al., 2004). In this manner, prelimbus prefrontal areas and midline thalamic nuclei would be able to modulate sensorimotor-associational activities in other regions of the brain through their projections to the striosomes. By forming a connected reticulum throughout the striatum, the striosomes are in a position to modulate matrix activities throughout the striatum via intrinsic connections.

Certain inferences about physiological differences between the striosome and matrix compartments of the striatum can be drawn from the chemical localization of KChIP1 in the striosomal neuropil. KChIP1 is a member of the family of voltage-gated potassium (Kv) channel-interacting proteins (KChIPs, encoded by the KCNIP genes), which belong to the recoverin branch of the EF-hand superfamily of small calcium-binding proteins (An et al., 2000). Members of the KChIP family have highly conserved core domains that contain EF-hand-like calcium binding motifs, and differ in their unique N-termini (An et al., 2000). KChIPs are component cytoplasmic subunits of native Kv4 channel complexes (Rhodes et al., 2004). Different KChIPs exhibit region and cell-type-specific associations with distinct Kv4 family members (Rhodes et al., 2004; Strassle et al., 2005; Menegola and Trimmer, 2006; Menegola et al., 2008), suggesting that the distinct functional properties of specific Kv4/KChIP channel complexes observed in heterologous cells (Jeng et al., 2004) may have important functions in specific neuronal populations.

In rat, KChIP1 is prominently expressed, along with the Kv4.3 primary subunit, in interneurons throughout the brain, whereas other Kv4 and KChIP subunit combinations predominate in principal cells (Rhodes et al., 2004; Strassle et al., 2005; Menegola and Trimmer, 2006; Menegola et al., 2008). Co-expression of KChIP1 and Kv4.3 includes a subset of interneurons in the hippocampus (Menegola et al., 2008), cerebral cortex, and striatum (Rhodes et al., 2004). The specific pairing of KChIP1 and Kv4.3 in interneurons suggests a specific but as yet uncharacterized role for this particular subunit combination in specific interneuron populations. KChIPs regulate the activity of the Kv4 channel complexes, which underlie the somatodendritic A-type potassium currents that are prominent in determining the interval between consecutive action potentials during repetitive firing, and hence neuronal excitability, in response to changes in intracellular calcium (An et al., 2000). The concentration of KChIP1 to the striosomal neuropil suggests that dendrites of neurons here possess functional properties distinct from those of cells in the surrounding matrix.

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LITERATURE CITED


