**Arabidopsis thaliana**, a plant model organism for the neuronal microtubule cytoskeleton?

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Received 5 July 2010; Revised 24 July 2010; Accepted 17 August 2010

**Abstract**

The microtubule cytoskeleton is an important component of both neuronal cells and plant cells. While there are large differences in the function of microtubules between the two groups of organisms, for example plants coordinate the ordered deposition of cellulose through the microtubule cytoskeleton, there are also some notable similarities. It is suggested that *Arabidopsis thaliana*, with its superior availability of knockout lines, may be a suitable model organism for some aspects of the neuronal microtubule cytoskeleton. Some cellular processes that involve the neuronal microtubule cytoskeleton including neurotransmitter signalling and neurotrophic support may have homologous processes in plant cells. A number of microtubule-associated proteins (MAPs) are conserved, including katanin, EB1, CLASP, spastin, gephyrin, CRIP, Atlastin/RHD3, and ELP3. As a demonstration of the usefulness of a plant model system for neuronal biology, an analysis of plant tubulin-binding proteins was used to show that Charcot–Marie–Tooth disease type 2D and spinal muscular atrophy may be due to microtubule dysfunction and suggest that indeed the plant microtubule cytoskeleton may be particularly similar to that of motor neurons as both are heavily reliant upon motor proteins.

**Key words:** *Arabidopsis thaliana*, microtubule, motor neuron, neuroscience.

**Introduction**

Microtubules in both plants and animals are composed of heterodimers of α- and β-tubulin which bind a molecule of GTP. GTP bound to α-tubulin is stable while GTP bound to β-tubulin may be hydrolysed to GDP. A microtubule with GDP-tubulin is prone to depolymerization, and there is generally a cap of GTP-tubulin protecting the microtubule from disassembly. Many proteins interact with microtubules (microtubule-associated proteins or MAPs) and are involved in critical functions such as microtubule growth, stabilization, destabilization, and interaction with other cellular organelles (Wade, 2009). While some MAPs are specific to either plants or animals, some are found in both groups of organisms. The neuronal microtubule cytoskeleton plays a key role in many cellular processes including protein transport, neurite extension, and cell division (Jaglin and Chelly, 2009), whereas in plants it coordinates the deposition of cellulose microfibrils in the cell wall and thus regulates plant growth and development, and plays a key role in responses to hormones, pathogens, and environmental stress (Buschmann and Lloyd, 2008).

The conservation of actin-interacting proteins between plants and neurons has been discussed, including the possibility that they form ‘plant synapses’ between cells (Baluška et al., 2005). Here the similarities between the plant microtubule cytoskeleton and the neuronal microtubule cytoskeleton are discussed. Although the two are only distantly related in evolutionary terms, they share many features, thus suggesting that *Arabidopsis thaliana* L. may indeed be a useful model organism for neurons. Although it may seem that *Arabidopsis*, an organism made up of many cells, might not
reflect the function of individual neurons which are highly specialized cells, neural tissues made up of many neurons function as an entity possibly in much the same way as a plant. It is also possible that within each plant cell there are microtubule-based domains which are each analogous to a single neuron (see discussion of EB1 below).

Similarities between Arabidopsis and neurons are emphasized at the levels of both sequence similarity and functionality. Many MAPs are conserved and it is to be expected that, as a result of this, functionality will also be conserved. Arabidopsis has several advantages over animal cells as a model organism, including short generation time and particularly the availability of knockout lines for virtually every gene. Indeed it is suggested that an analysis of plant tubulin-binding proteins offers a novel insight into Charcot–Marie Tooth (CMT) disease and spinal muscular atrophy. In addition, knowledge of the microtubule cytoskeleton from neuroscience studies will continue to prove useful in plant biology.

Here the functional similarities of the microtubule cytoskeleton between plants and neurons are first examined, in particular neurotransmitter function and neurotrophic support. Conserved MAPs and their function as cytoplasmic MAPs and scaffolding MAPs are then discussed. Next comes an examination of the similarities between motor neurons and plants, focusing again on the MAPs involved, before insights into motor neuron diseases revealed through analysis of plant tubulin-binding proteins are discussed.

Neuronal processes involving microtubules that may have homologous processes in plants

Neurotransmitters and the microtubule cytoskeleton

Glutamate is an important neurotransmitter in neurons and modulates the function of the microtubule cytoskeleton. Activation of glutamate receptors 1 and 5 increases MAP2 phosphorylation (Llansola et al., 2005), which would destabilize microtubules, and glutamate also promotes calpain-mediated proteolysis of MAP2 (Minger et al., 1998). Arabidopsis also possesses glutamate as a signalling molecule, and glutamate receptor proteins are encoded in the Arabidopsis genome. In Arabidopsis, glutamate causes microtubule depolymerization and membrane depolarization, and both of these effects are blocked by a specific antagonist of ionotropic glutamate receptors, 2-amino-5-phosphopentanoate. Aluminium toxicity involves damage to the microtubule cytoskeleton, which also appears to be mediated via efflux of a glutamate-like ligand and its binding to a glutamate receptor (Sivaguru et al., 2003). Thus glutamate acts as a microtubule-disrupting agent in both neurons and Arabidopsis cells.

Glycine acts as a signalling molecule in plants. Glutamate and glycine synergistically control ligand-mediated gating of calcium and hypocotyl elongation in plants. Transient increases in cytosolic calcium and hypocotyl elongation were inhibited by 6,7-dinitroquinoxaline-2,3 dione (DNQX), a competitive inhibitor of animal glutamate receptors (GLRs). Interestingly, molecular modelling shows that glycine and not glutamate is likely to be the natural ligand for most plant GLRs (Dubos et al., 2003). Here it appears that glycine may promote transverse orientation of microtubules and increase cell elongation rates in a manner similar to that of serotonin in plants.

Serotonin in neurons is a key neurotransmitter and is a target for drugs used to treat depression and other illnesses. The drugs target serotonin breakdown (monoamine oxidase A inhibitors) or serotonin reuptake from the synapse. In neurons, serotonin is released from axons into the synaptic gap via exocytosis and diffuses to dendritic spines where it binds to various serotonin receptors and activates intracellular second messenger cascades. Serotonin may play a key role in promoting microtubule stability in neurons by increasing levels of the microtubule-stabilizing protein MAP2 (Whitaker-Azmitia et al., 1995). Serotonin has been found in >42 plant species and it appears to play key roles in growth and development. It stimulates root growth, the growth of the hook of oat coleoptiles, and the germination of radish seed and pollen of Hippeastrum hybridum (Kang et al., 2007). Surprisingly there have been no studies on the role of serotonin in A. thaliana. The role of serotonin in stimulating root elongation and coleoptile growth suggests that it could promote ordering of cortical microtubule arrays, perhaps by modulating the level of a MAP as in neurons.

Neurotrophic support and the microtubule cytoskeleton

Neurotrophic support is a key process leading to survival of neurons, and is dependent upon an intact microtubule cytoskeleton. Neurotrophins, or neurotrophic factors, can up-regulate antioxidant proteins and antioxidant processes in neuronal cells (Gardiner et al., 2009). Neurotrophins include brain-derived neurotrophic factor (BDNF), neurotrophin-3 (NT3), neurotrophin-4/5 (NT4/5), and nerve growth factor (NGF). These proteins are generally viewed as target-derived survival factors that guide neuronal axons to the target tissue. The terminals of the axons bear receptor tyrosine kinases (TrkA, TrkB, TrkC, and the p75 neurotrophin receptor p75NTR) that bind the neurotrophins. The neurotrophins are then endocytosed (Kuruvilla et al., 2004; Hibbert et al., 2006) and trafficked by motor proteins along microtubules to the cell body (Gauthier et al., 2004), where they induce gene expression (Roberts et al., 2006). BDNF is also trafficked in the opposite direction (Butowt and von Bartheld, 2007). There is a positive feedback loop in operation, with greater transport of BDNF and other neurotrophic factors along microtubules leading to greater expression of BDNF and other neurotrophic factors, and hence increased neuronal survival. While it appears that neurotrophic support is basically a process found only in neurons, it is worth noting that Arabidopsis eukaryotic initiation factors eIF3 and eIF4 share a motif with BDNF (E-x-L-x-x-D-x-x-V-x-P-x-E-E-N). Both eIF3 and eIF4...
associate with microtubules (Chuong et al., 2004), as does BDNF via motor proteins and in neurons. In addition, BDNF induces translation initiation processes involving eukaryotic initiation factors (Takei et al., 2004). Thus there may be some similarities in function between BDNF and plant eukaryotic initiation factors, possibly involving the microtubule cytoskeleton.

**Tubulin isoforms**

*Arabidopsis*, despite its small genome, possesses more tubulin isoforms that in mammalian systems. In the mouse, five α-tubulin genes and six β-tubulin genes are functional (Villasante et al., 1986; Wang et al., 1986), while in *Arabidopsis* at least six α-tubulin genes (Kopczak et al., 1992) and nine β-tubulin genes are expressed (Snustad et al., 1992). In both systems different tubulin isoforms are expressed in different tissues (Villasante et al., 1986; Ludwig et al., 1988), apparently reflecting a fine-tuning of tubulin function during development.

**Cytoplasmic microtubule-associated proteins conserved between plants and neurons**

**Katanin**

Katanin is a microtubule-severing ATPase. In neurons the formation of interstitial axonal branches involves the severing of microtubules at sites where new branches form. Katanin plays a key role in enhancing branch formation through the severing of microtubules (Qiang et al., 2010). Katanin in both neuronal and plant cells acts to cut long stationary microtubules into mobile short pieces which can be reorganized by means of treadmilling (Baas et al., 2005). Indeed it has been proposed that the main activity of *Arabidopsis* katanin is to free cortical microtubules, generating motile microtubules that are incorporated into bundles (Stoppin-Mellet et al., 2006), thus playing a key role in the organization of the plant microtubule cytoskeleton and cell wall deposition (Burk et al., 2001).

**CLASP**

CLIP-associated (CLASP) proteins are found in neurons where they act as microtubule plus end-binding proteins (+TIPs) (Lee et al., 2004). CLASP is also found in *Arabidopsis* where it modulates microtubule–cortex interactions. In CLASP mutants, deviations from normal linear polymerization trajectories lead to increased bundling of microtubules and hyperparallel cortical microtubules in clasp-1 leaf epidermis (Ambrose and Wasteneys, 2008). In neurons, CLASP proteins also interact with actin filaments (Tsvetkov et al., 2007), but this has yet to be shown in plant cells. That CLASP may act as a microtubule–actin cross-linker is exciting since there is known to be interaction between microtubules and actin filaments in plants including *Arabidopsis* (Collings et al., 2006), but the proteins responsible have been elusive.

**EB1**

EB1 +TIPs were first identified in animals. In neurons they play important roles in targeting the F-actin-binding protein drebrin in a process required for neuritogenesis (Geraldo et al., 2008), targeting Kv1 voltage-gated K⁺ channels (Gu et al., 2006), complementing MAP1B during axonogenesis (Jiménez-Mateos et al., 2005), and labelling distal ends of microtubules in neurons (Stepanova et al., 2003). *Arabidopsis* possesses three EB1-like proteins. *Arabidopsis* EB1α–green fluorescent protein (GFP) fusion protein labels microtubule plus ends as a comet but also marks minus ends at sites from which microtubules can grow and shrink. The minus-end nucleation sites are mobile, supporting the idea of a flexible centrosome in plants (Chan et al., 2003). *Arabidopsis* EB1 localizes to microtubule plus ends but also to motile tubulovesicular membrane networks surrounding organelles, similarly to +TIPs such as CLIP-170 (Mathur et al., 2003). Using EB1–GFP-labelled cells revealed that the majority of plant cortical microtubules in ordered arrays face the same direction, with selective stabilization of dynamic cortical microtubules playing a predominant role in their self-organization. Microtubule arrays appear to be organized into smaller domains at the plasma membrane, with microtubules in each domain all facing the same way (Dixit et al., 2006). This suggests that plant microtubule arrays are more similar to axonal microtubules, where polymerization takes place almost exclusively in an anterograde direction, rather than dendrites where both anterograde and retrograde polymerization takes place (Kollins et al., 2009). This idea is strengthened by the observation that EB1 protein levels are increased during axon but not dendrite formation in neuroblastoma cells (Morrison et al., 2002) and by the high constitutive expression of EB1 proteins during plant cell development (Bisgrove et al., 2008).

**Tubulin–tyrosine ligase like**

The *Arabidopsis* genome possesses one homologue of tubulin–tyrosine ligase (Gardiner and Marc, 2003). This tubulin–tyrosine ligase like (TTLL) protein may either catalyse the addition of tyrosine to tubulin (Smertenko et al., 1997) or catalyse the polyglutamylation of tubulin, as do other TTLL proteins (Janke et al., 2008). In neurons, tubulin tyrosination navigates kinesin-1 away from dendritic microtubules to detyrosinated axonal microtubules (Konishi and Setou, 2009), and tubulin post-translational modifications may play a similar role in plants.

**MAP kinase**

MAP kinase (MAPK) associates with microtubules in the brain where it integrates signal transduction cascades (Morishima-Kawasima and Kosik, 1996). Similarly, MAPK4 of *Arabidopsis* is necessary for overall microtubule
organization, with a homozygous mutant demonstrating abnormal cell growth such as branching of root hairs and swelling of epidermal cells (Beck et al., 2010).

**Scaffolding MAPs conserved between neurons and plants**

**Gephyrin**

Gephyrin is a postsynaptic density protein that plays a key role in maintaining a high concentration of inhibitory glycine receptors juxtaposed to presynaptic releasing sites (Zita et al., 2007) through its association with the microtubule cytoskeleton (Prior et al., 1992). Arabidopsis possesses a gephyrin homologue which is crucial for the formation of the molybdenum cofactor (MoCo) and which also associates with the actin cytoskeleton, as does its mammalian homologue (Schwarz et al., 2000). Indeed due to the ability of gephyrin to rescue a universal MoCo-deficient mutation in plants, gephyrin was identified as the gene affected in a patient with symptoms typical of MoCo deficiency (Reiss et al., 2001). It is not known as yet whether the Arabidopsis gephyrin homologue plays a role in microtubule organization and receptor clustering.

**CRIPT**

CRIPT is a postsynaptic protein that binds selectively to the third PDZ domain of PSD-95. In neurons, CRIPT binds directly to microtubules, thus linking PSD-95 to the microtubule cytoskeleton. Disruption of the CRIPT–PSD-95 interaction with a PDZ3-specific peptide prevents the association of PSD-95 with microtubules and inhibited the synaptic clustering of PSD-95, chapsyn-110/PSD-93, and GSKAP (a PSD-95-binding protein), but the number of synapses and synaptic clustering of N-methyl-D-aspartic acid (NMDA) receptors was unaffected (Passafaro et al., 1999). The Arabidopsis homologue of CRIPT (At1g61780), which is 66% identical to CRIPT, may also localize to microtubules. Arabidopsis CRIPT possesses the consensus PDZ-binding C-terminal sequence (x-S/T-x-V-COOH). PDZ domain proteins play key roles as scaffolds for a variety of receptor proteins in neurons (Neff et al., 2009). There appears to be only one PDZ protein in the Arabidopsis genome, GAN or At1g55480, which is involved in drought and salinity tolerance. Thus there may be an interesting link between the microtubule cytoskeleton, receptor-based signalling, and environmental stress.

**MAPs crucial for motor neuron function which are conserved in plants**

**Kinesins**

A number of MAPs which are crucial for motor neuron development and function are also crucial for plant growth and development. This suggests a certain similarity between plant cells and motor neurons. Motor neurons are particularly sensitive to disruption of microtubule-based protein trafficking, although axonal transport also plays a part in other neurological diseases such as Alzheimer’s disease and Huntington’s disease (Holzbaur, 2004). Plant cells are also highly dependent upon motor proteins (particularly kinesins) and indeed Arabidopsis possesses a grand total of 61 kinesins (Lee and Liu, 2004). It is not clear why plants have so many kinesins, but this does indicate that any perturbation of the microtubule cytoskeleton and kinesin function is likely to have severe consequences for plant growth and development, as with motor neurons. The large number of kinesins in Arabidopsis has perhaps enabled the divergence of highly specialized proteins with unusual functions. For example, two kinesin-like proteins KAC1 and KAC2 appear not to bind microtubules but rather actin during chloroplast movement (Suetsugu et al., 2010). In comparison, neuronal kinesins appear to be more constrained in their function, generally transporting cargo along microtubules (Goldstein et al., 2008).

**Atlastin/ROOT HAIR DEFECTIVE 3 and spastin**

Hereditary spastic paraplegia (HSP) is an inherited neurological disorder characterized by progressive spasticity and weakness of the lower extremities. The most common form of early-onset HSP is caused by mutation in the human gene encoding the dynamin family GTPase Atlastin. Atlastin is required for normal growth of muscles and synapses at the neuromuscular junction and correct endoplasmic reticulum and Golgi morphogenesis. It appears to act with the microtubule-severing protein spastin to disassemble microtubules in muscles, with the microtubule-stabilizing drug vinblastine alleviating synapse and muscle defects in mutant Drosophila (Lee et al., 2009). In Arabidopsis, the homologue of Atlastin is ROOT HAIR DEFECTIVE 3 (RHD3). Loss of function of RHD3 in an Arabidopsis mutant results in an almost complete loss of the normal epidermal cell file rotation, root skewing, and waving on hard agar surfaces. The mutant does not respond to low doses of the microtubule-depolymerizing drug propyzamide (Yuen et al., 2005), indicating that RHD3 also destabilizes microtubules in Arabidopsis and that its loss of function will in fact stabilize microtubules. Indeed the microtubule-stabilizing drug taxol causes wavy root hairs (Carol and Dolan, 2002), as seen in the RHD3 mutant (Schiefelbein and Somerville, 1990). RHD3 loss of function also alters vacuole enlargement (Galway et al., 1997) and is required for cell wall biosynthesis and actin organization (Hu et al., 2003). There are two Arabidopsis proteins with a high degree of homology to spastin, indicating that RHD3 may interact with these proteins, as in animals. Interestingly a mutation in spastin can cause amyotrophic lateral sclerosis (Münch et al., 2008), and mutations cause HSP (Errico et al., 2002), again linking a MAP conserved between plants and humans to motor neuron function.
Elongator protein 3

Acetylated tubulin may be important in both plant cells and motor neurons. In *Nicotiana tabacum*, acetylated tubulin was detected in the generative cell of pollen tubes and in kinetochore fibres, in polar spindle regions, and in the cell plate of the phragmoplast during generative cell division (Aström, 1992). Acetylated tubulin was also found in leaves of *Zea mays* L. but not in roots (Wang et al., 2004). The tubulin acetylase ELP3, a component of the Elongator complex, is present in both plant cells. In *A. thaliana* the elongata mutants elo1, elo2, and elo3 have decreased leaf and primary root growth due to reduced cell proliferation (Nelissen et al., 2010). To date no studies on tubulin acetylation have been performed in *Arabidopsis* so it is unknown whether these growth defects are associated with a reduction in acetylated tubulin. However, it is likely that ELP3 acts as a tubulin acetylase in plants since ELP3 binds to α/β-tubulin heterodimers (Chuong et al., 2004; Gardiner et al., 2007).

In mammalian systems, ELP3 plays various roles. It is important for zygotic paternal genome demethylation through its radical S-adenosylmethionine (SAM) domain (Okada et al., 2010). It is important for the migration and branching of projection neurons, probably due to its α-tubulin acetylase activity (Creppe et al., 2009). α-Tubulin acetylation is of key importance in neurons as it regulates the binding of kinesin motor proteins to microtubules, and hence controls the transport of proteins and organelles within the cell (Reed et al., 2006). It may also play a role in the regulation of the actin cytoskeleton and mitochondria in human cells (Johansen et al., 2008; Barton et al., 2009). ELP3 variants are associated with motor neuron degeneration in amyotrophic lateral sclerosis, with risk-associated ELP3 genotypes correlated with reduced brain ELP3 expression (Simpson et al., 2009). Thus, here, *Arabidopsis* may serve as a model system for studies of the aetiology of motor neuron disease. The function of the Elongator complex appears to be conserved between plants and animals in at least some respects, for example in its role as an α-tubulin acetylase. It seems likely that the presence of acetylated tubulin in the mitotic spindle of plant cells may act to promote the binding of motor proteins during cell division and that this may prove to be a useful model system for understanding the role of ELP3 in neuronal cells.

Tubulin folding cofactor E

Tubulin folding cofactor E (TBCE) is highly conserved between animals and plants. In animals it binds microtubules and proteasomes and protects against misfolded protein stress (Voloshin et al., 2010). There is an antagonistic interaction between TBCE and the microtubule-severing protein spastin and indeed TBCE appears to be a tubulin-polymerizing protein. A mouse *Tbce* mutation causes progressive motor neuropathy (Jin et al., 2009). In *Arabidopsis*, the TBCE homologue (a PILZ group protein) is embryo lethal when deleted, with plants lacking microtubules entirely (Steinborn et al., 2002). Thus here again a MAP necessary for motor neuron function is also required for proper development of *Arabidopsis*.

Charcot–Marie–Tooth disease, aminoacyl-tRNA synthetases, and microtubules

A mutation in the protein dynamin, which is involved in endocytic vesicle formation, leads to CMT disease. It has been recently shown that dynamin also participates in microtubule dynamics, with Dyn2 required for proper dynamic instability of microtubules (Tanabe and Takei, 2009). Cells expressing the 551Delta3 mutant protein show an increase in acetylated tubulin, a marker of microtubule stability, and depletion of dyn2 leads to accumulation of stable microtubules. Microtubule-based organelle transport is impaired in cells expressing the mutant protein, with a decrease in the formation of mature Golgi complexes (Tanabe and Takei, 2009). A mutation in the motor domain of the kinesin KIF1B leads to CMT disease type 2A, again showing that disruption of microtubule-based protein trafficking can cause human motor neuron neuropathy (Zhao et al., 2001). In addition, a model of the X-linked form of CMT disease, which is associated with mutations in the *connexin32* gene, shows a depletion of axonal microtubules (Sahenk and Chen, 1998). Microtubule-based transport in the longitudinal bands of Cajal may permit intermodal Schwann cells to lengthen in response to axonal growth, ensuring rapid nerve impulse transmission (Court et al., 2004).

Mutations in aminoacyl-tRNA synthetases cause motor neuron disease. Mutations in glycyll-tRNA synthetase cause CMT disease type 2D and distal spinal muscular atrophy type V in humans, motor and sensory neuropathy in mice, and defects in terminal arborization of axons and dendrites in the fruit fly. A study of tubulin-binding proteins in *Arabidopsis* found that methionyl-, glycyl-, threonyl-, and multifunctional aminoacyl-synthetase all bind to αβ-tubulin (Chuong et al., 2004). A previous study found that yeast vallyl- and hysyl-tRNA synthetases bind to microtubules and cause stabilization and bundling of microtubules without the intervention of an extraneous bundling protein (Melki et al., 1991). This evidence suggests that aminoacyl-tRNA synthetases may play a key role in microtubule function, possibly acting as MAPs that bundle and stabilize microtubules not only in yeast and plants but also in the animal nervous system. It is suggested that diseases caused by mutations in these aminoacyl-tRNA synthetases may be, at least in part, due to disruption of this microtubule-centric function. This idea is supported by a model of dominant-intermediate CMT disease, which is caused by a mutation in tryrosyl-tRNA synthetase, in *Drosophila* which found that the phenotype is not due to a reduction in aminoacylation activity, but either a gain of function or interference with a function of the wild-type protein (Storkebaum et al., 2009).
Tudor domain proteins and motor neuron disease

Similarly, a tudor domain protein has been found to bind xβ-tubulin in Arabidopsis (Chuong et al., 2004). The motor neuron disease spinal muscular atrophy is caused by a mutation in SMN protein, which also possesses a tudor domain. Thus here, as well, the homologue of an Arabidopsis tubulin-binding protein is implicated in motor neuron disease. Indeed the Xtr (Xenopus tudor repeat) protein plays a key role in microtubule assembly during cleavage in Xenopus laevis (Hiyoshi et al., 2005).

Novel plant MAPs with human homologues

A number of plant MAPs have human homologues that have not as yet been shown to have a function in neurons. However, if plant cells really do have such a strong similarity to neurons, particularly motor neurons, this suggests that it may be worth exploring whether neurons also use these proteins. MOR1 (microtubule organization 1) is a homologue of the human protein Dis1/TOG and plays a key role in organizing plant cortical microtubules (Whittington et al., 2001). It is unknown whether it plays a role in the organization of microtubules in neurons but is expressed in oligodendrocytes and neurons and associates with microtubules (Kosturko et al., 2005). In plants, a phospholipase D has been found to play a role in the attachment of microtubules to the plasma membrane (Gardiner et al., 2001; Dhonukshe et al., 2003) and a phospholipase A2 also plays a key role in microtubule organization (Gardiner et al., 2008). Again it is not known whether phospholipases regulate microtubule attachment to membranes in neurons. Other conserved proteins in the PILZ group of genes—tubulin-folding cofactors C and D as well as associated small G-protein Arl2 (Steinborn et al., 2002)—may participate in the regulation of motor neuron microtubules.

Conclusions

It has been demonstrated here that there are many structural and functional similarities between the neuronal microtubule cytoskeleton and the plant microtubule cytoskeleton. In the past many insights from studies of the animal cytoskeleton have proven useful in plant biology, and doubtless this will continue into the future. Recent developments in plant cell biology including the development of resources such as the SALK T-DNA knockout lines mean that plant biology is increasingly in the position of being able to supply useful insights into animal biology, particularly neuronal biology. It is worth noting that both consciousness, the product of the neuronal microtubule cytoskeleton, and plant growth and development, the product of the plant microtubule cytoskeleton, are at heart anti-entropic processes. However, it appears that motor neurons may be the closest homologue of plant cells in the animal nervous system as both are highly dependent upon motor proteins for correct development and function.

References


Molecular Biology of the Cell 17, 1298–1305.


