Neurospora kinesin (Nkin) is a distant relative of the family of conventional kinesins, members of which have been identified in various animal species. As in its animal counterparts, Nkin most likely is an organellar motor. Because it is a functional homologue of the kinesin heavy chain of higher eukaryotes, its biophysical and motility properties were compared with those of other conventional kinesins. Purified Nkin behaves as a homodimeric complex composed of two subunits of a 105-kDa polypeptide. Based on its hydrodynamic properties (Stokes radius and sedimentation coefficient), Nkin is an elongated molecule, although it is more compact than its animal counterparts. A detailed comparison of the motility properties of Nkin with those of animal conventional kinesins reveals similarities and some intriguing differences. Nkin is less effective than other kinesins in the use of natural nucleoside triphosphates but responds to a selection of ATP analogues in a similar fashion as mammalian kinesins. Even in the presence of saturating concentrations of ATP, Nkin is significantly more sensitive to ADP or tripolyphosphate than other kinesins. Both the ATP-driven microtubule gliding activity and the microtubule-stimulated ATPase activity of Nkin obey Michaelis-Menten kinetics. Surprisingly, however, the $K_m$ values for both these activities are approximately an order of magnitude higher than those of other kinesins. Whether the low affinity for ATP suggested by these high $K_m$ values is related to the high rate of motility remains to be determined.

Kinesin and kinesin-like proteins comprise a superfamily of microtubule-dependent molecular motors important for various functions in intracellular organelle movements, mitosis, and karyogamy (for reviews see Goldstein (1993), Walker and Sheets (1993), and Bloom and Endow (1994)). Among the at least seven families and several (as yet) single representatives, the family of "conventional" kinesins identified in animals. Nkin exhibits several unusual structural and functional properties, such as a high rate of microtubule transport, a lack of copurifying polypeptides, a second $\alpha$-helical peptide motif, and the presence of a highly conserved peptide motif in the C terminus. The first organellar motor related to conventional kinesins identified in fungi, Nkin represents an intriguing "outsider" of this otherwise homogenous protein family. To link the biochemical and biophysical properties of these motors to their biological function, we have analyzed the enzymatic, biophysical, and motility properties of Nkin and compared them, where possible, with those of animal kinesins.

**EXPERIMENTAL PROCEDURES**

Cell Cultures—*N. crassa* wild type 74A was grown in Vogel’s minimal medium at 25 °C under continuous aeration and illumination with white light for 14–16 h as described by Sebold et al. (1979).

Preparation of Tubulin—Microtubule protein from pork brain was prepared using three cycles of polymerization and depolymerization according to the method of Shelanski et al. (1973) with modifications according to Mandelkow et al. (1985). Tubulin was further purified by dynamic light scattering.

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1 The abbreviations used are: Nkin, Neurospora kinesin; PIPES, 1,4-piperazine diethanesulfonic acid; AMPPNP, 5'-adenyl-γ-phosphoribosylphosphate; ATPγS, adenosine 5'-O-(thiotriphosphate); 8-azido-ATP, 8-azidoadenosine 5'-triphosphate; GMPCPP, guanosine 5′-(α,β-methylene)triphosphate.

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phosphocellulose column chromatography according to the method of Weingarten et al. (1975) and stored at -80 °C.

Purification of Kinesin from N. crassa—N. crassa was grown for 16 h, harvested, and ground with quartz sand (Merck) in the presence of AP100 buffer (10 mM PIPES, pH 6.9, 2 mM MgCl2, 1 mM EDTA, 1 mM EGTA, 1 mM dithiothreitol, 1 mM phenylmethylsulfonyl fluoride, 10 μg/ml aprotinin, 10 μg/ml soybean trypsin inhibitor, 1 μg/ml aprotinin, 1 μg/ml pepstatin, 1 μg/ml leupeptin). After a low speed centrifugation at 10,000 x g for 20 min to remove the sand and cell debris, a high speed supernatant (S2) depleted of organelles was prepared (120,000 x g for 1 h). Tubulin was polymerized with 1 mM GTP and 10% Me2SO (v/v), stabilized with taxol (0.7 μM), and added to the polymerization buffer at concentration of 0.7 mM GTP. Additional taxol (7 μM) as well as appyrase (5 units/ml; Grade VIII, Sigma) were added, and the mixture was incubated on ice for 1 h. In other experiments 2-4 mM AMPNP alone or 0.2 mM AMPPPN in combination with 5 units/ml apyrase were used instead. The microtubules were sedimented (100,000 x g for 30 min), carefully resuspended in AP100/50 mM KCl, and centrifuged through a 10% sucrose cushion in AP100 (90,000 x g for 30 min). The resulting microtubule pellet (P4) was resuspended in AP100 with 5-10 mM ATP and placed on ice for 10 min. After centrifugation (100,000 x g for 30 min), the resulting supernatant (S5) was tested in a gliding assay (see below). The S5 was stored on ice and normally stayed active for several days. For additional purification the motor activity was fractionated on a linear 5-20% sucrose gradient (5 ml) in AP100 and centrifuged at 100,000 x g for 12 h. In a Beckman SW 50.1 rotor. Fractions of 100–300 μl were collected from the bottom and checked for motor activity in gliding assays. For gel filtration a superose-6 column was used in fast protein liquid chromatography (Pharmacia Biotech Inc.). The column was equilibrated with 3 volumes of AP100, 150 mM NaCl, 1 mM dithiothreitol, 0.05 mM ATP. 400–500 μl of the sample were concentrated for further use (microcon tubes, Amicon).

Motility Assay—The motor activity of Nkin was measured using an in vitro motility assay (Vale et al., 1985b) and video-enhanced DIC microscopy (Allen et al., 1981) as described in Steinberg and Schliwa (1995). For each data point the velocity of at least 6 microtubules (slow velocities) or 15 microtubules (fast velocities) from at least two different Nkin isolations were determined. All assays were performed in AP100; no differences were observed between sucrose-gradient fractions and gel filtration fractions. Because the motility of the Neurospora kinesin was very sensitive to the absence of nucleotides, the motor was stabilized with 0.05 mM ATP or ATP-S in the sucrose gradients and the column buffer, respectively. This nucleotide "contamination" had no significant effect on the motility as tested in several control experiments. To determine the Km, for microtubule motility, the motor solution was placed in a flow-through chamber. After adsorption of Nkin the column buffer was replaced by fresh AP100, followed by microtubules and AP100 with the desired nucleotide concentration. To determine the Km, for microtubule motility, the velocities at a range of ATP concentrations were plotted against the nucleotide concentration (three different preparations).

ATPase Assay—the ATPase activity of purified motor (gel filtration fractions) was measured with the Malachite Green method (Itaya and Arisaka, 1974) and stored at –80 °C. The ATPase activity of purified motor (gel filtration fractions) was measured with the Malachite Green method (Itaya and Arisaka, 1974). The ATPase activity of purified motor (gel filtration fractions) was measured with the Malachite Green method (Itaya and Arisaka, 1974).

RESULTS AND DISCUSSION
Native Nkin was isolated from cytoplasmic extracts of hyphae based on its nucleotide-sensitive binding to and release from pig brain microtubules (Steinberg and Schliwa, 1995). A typical experiment yielded 10–20 μg of motor from 30 g of packed hyphae. We routinely used apyrase to deplete ATP from cytoplasmic extracts for microtubule binding, but motor could also be isolated using AMPNP as originally described (Brady, 1985; Vale et al., 1985a). The best purification was achieved by...
Biophysical and Motility Properties of Kinesin from N. crassa

Table I

Biophysical properties of Nkin compared with bovine brain kinesin

| Property                                      | Nkin\(^a\) | Kinesin\(^b\) |
|-----------------------------------------------|-------------|---------------|
| Apparent molecular weight in SDS-polyacrylamide gel electrophoresis (kg mol\(^{-1}\)) | 105/108     | 124/64        |
| Native molecular weight (kg mol\(^{-1}\))      | ~277        | ~379          |
| Sedimentation coefficient (S\(_{w20}\))        | (199–260)   | (294–494)     |
| Stokes radius (nm)                             | 6.27 ± 0.53 | 9.64 ± 0.87   |
| Diffusion coefficient (D\(_{w20}\))           | 3.34 ± 0.20 | 2.24 ± 0.21   |
| Axial ratio                                    | ~12         | ~20          |

\(^a\) All estimations concerning gel filtration were done nine times; the S\(_{w20}\) coefficient was measured four times.
\(^b\) Bloom et al., 1988.
\(^c\) Estimated from Stokes radius or D\(_{w20}\) coefficient for globular proteins summarized in Andrews (1970).
\(^d\) Folded conformation.

Table II

Biophysical properties of Nkin in comparison with other conventional kinesins

| Property                                      | Nkin (n = 3) | Other Conventional Kinesins |
|-----------------------------------------------|--------------|-----------------------------|
| Molecular mass (kDa)                          | 227           | 379                         |
| Axial ratio                                   | ~12           | ~20                         |
| Stokes radius (nm)                            | 6.27 ± 0.53   | 9.64 ± 0.87                 |
| Diffusion coefficient (D\(_{w20}\))           | 3.34 ± 0.20   | 2.24 ± 0.21                 |

The fundamental hydrodynamic and diffusion properties of Nkin reported here are those of an elongated molecule. Its Stokes radius, however, is considerably smaller than that of bovine kinesin, suggesting that Nkin is more compact than other conventional kinesins. This is reflected also in a smaller axial distance ratio of 12:1, as opposed to bovine brain kinesin, whose axial ratio is 20:1 (Bloom et al., 1988) for the "folded" form of kinesin and more like 40:1 for the fully extended molecule (Hackney et al., 1992).

Motility Properties of Nkin—The motility characteristics of Nkin in comparison with other conventional kinesins are summarized in Table II. One of the most dramatic differences between Nkin and other kinesins existed in terms of its rate of...
motility. Among the kinesin motors identified so far, it was
did not work at all with the conventional kinesins, Nkin was less
effective in the use of these analogues, and the rate of microtubule
5% the rate of microtubule movement in standard gliding assays was
2.7–3.0 (30–40% in control). The concentration of MgATP in the
2.1–3.0 (100) 100
0.4–0.6 (10%) 30
1.5–1.7 0.3–0.6
30–40 5
2.6–5.0 (30–90) 150
0–60 0–90
2.6 0–2–5
100 (100) 100
0.0–0.4 (0–10) 0–9
2.5–3.1 (100) 91
1.0–1.5 (50) 78–100
1.0–0.6 (9–19) 0–31
30–40 0–38
0
0
2.4–2.7 (90–110) 130
0.8–1.0
2.7–3.0
2.3–2.5
>0.2–0.4 0.49
>70 >0.2–0.4
>2–5
200–400
110–200
0.01–0.09
0.05–0.2
0.01–0.11
0.06–3.63

TABLE II
Motility characteristics of Nkin compared with kinesin from animal sources

|     | Nkin                  | Kinesin               |
|-----|-----------------------|-----------------------|
| VMT motility [μm s⁻¹] | 2.1–3.8               | 0.4–0.6 [a,c,d,e]     |
| V beads [μm s⁻¹]      | 1.5–1.7               | 0.3–0.6               |
| pH optimum [μg mL⁻¹]  | 6–9                   | 6–9                   |
| [motor]ₜₜₜₜ for motility | 30–40                 | 5                     |
| ATPₜ⁺ [μM; %]         | 2.1–3.0 (100)         | 100                   |
| GTPₜ⁺ [μM; %]         | 1.0–1.5 (50)          | 78–100 [d]            |
| CTPₜ⁺ [μM; %]         | 0.2–0.6 (9–19)        | 0–31 [b,d]            |
| UTPₜ⁺ [μM; %]         | 0.3–0.6 (12–21)       | 0–38 [a,b,d]          |
| ITPₜ⁺ [%]             | 0                     | 27–50 [a,d]           |
| 2'-deoxy-ATPₜ⁺ [%]    | 2.5–3.1 (100)         | 91 [a]                |
| Etheno-ATPₜ⁺ [%]      | 1.8–2.5 (65–85)       | 13                      |
| 8-Azido ATPₜ⁺ [%]     | 0                     | 0 [a]                  |
| ATP-Sₜ⁺ [%]           | 0                     | 0–3 [a,d,f]            |
| ADPₜ⁺ [%]             | 0                     | 0 [a]                  |
| AMP/PNP inhibition     | 2.4–2.7 (90–110)      | 130 [a]               |
| Vanadate inhibition [%]| 70                    | >50–60 [a,b,k]        |
| N-ethylmaleimide inhibition [μM]| >2–5  | >2–5 [e,b,k] |
| Kₐₜₜₜₜ, motility [μM ATP] | 200–400    | 150                   |
| Kₐₜₜₜₜ, ATPase [μM ATP] | 110–200   | ~100 (m,n)            |
| ATPase rate (~MT) [ATP s⁻¹ head⁻¹] | 0.01–0.09 | 0.01–0.11 [c,e,f,p]  |
| ATPase rate (~MT) [ATP s⁻¹ head⁻¹] | 0.05–0.2 | 0.06–3.63 [c,e,f,p] |

[a] Vale et al., 1985.
[b] Porter et al., 1987.
[c] Saxton et al., 1988.
[d] Cohn et al., 1989.
[e] Howard et al., 1989.
[f] Shimizu et al., 1991.
[g] Range of velocities in several experiments (5–20 microtubules each) from at least two different isolations. Percentage relative to ATP in parenthesis. All nucleotides and derivates were added with equimolar Mg²⁺.
[h] Vale et al., 1994.
[i] Values indicate the ratio at an inhibition velocity of ~50%.
[j] Scholey et al., 1989.
[k] Wagner et al., 1989.
[l] Kuznetsov and Gelfand, 1986.
[m] Hadley et al., 1987.
[n] Gilbert and Johnson, 1993.
[o] Cohn et al., 1987.
p Penningroth et al., 1987.

with Nkin and find that three of them (2'-deoxy-ATP, 8-azido-
ATP, and ATP-S) elicited a response similar to mammalian
kinesin. A major difference was found with etheno-ATP, which
was used very effectively by Nkin but not bovine brain kinesin.

It was reported recently that microtubules polymerized in the
presence of a nonhydrolyzable GTP analogue, GMPCPP,
have a higher flexural rigidity (appear stiffer; Venier et al., 1994) and that they are transported at a 30% higher rate in
gliding assays than GTP microtubules (Vale et al., 1994). When
gliding assays were done with GMPCPP microtubules, such anincrease in the rate of microtubule movement was not ob-
served, suggesting that microtubule stiffness does not alter
microtubule velocity in the case of Nkin.

MgATP-dependent microtubule gliding has been found to be
inhibited by a variety of compounds. In contrast to other con-
ventional kinesins, Nkin appeared to be much more sensitive to
some of these inhibitors. Thus, MgADP, a competitive inhibitor
(Cohn et al., 1989), reduced the rate of microtubule gliding to
about 50% at a ratio of ~1 to MgATP, whereas a 4-fold excess
was needed for sea urchin kinesin (Cohn et al., 1989). Nkin also
was more sensitive toward AMPPNP. Both findings are con-
sistent with a lower affinity of Nkin for ATP, reflected also in the
Kₐₜₜₜₜ values of both ATPase activity and microtubule motility
(see below).

Microtubule gliding activity of Nkin was relatively insensi-
tive to sodium orthovanadate and N-ethylmaleimide. The mode
of inhibition is unexpected. With increasing concentrations of

2 G. Steinberg and M. Schliwa, unpublished results.
both reagents, there was a progressive release of microtubules from the coverslip surface, whereas the rate of movement of microtubules seemed virtually unaffected. At concentrations of orthovanadate of \(0.70 \text{mM}\) and concentrations of N-ethylmaleimide of \(3–5 \text{mM}\), virtually no microtubules were left attached to the coverslip. However, a microtubule occasionally contacting the surface may be transported for several micrometers at normal rates before detaching again.

ATP produced microtubule gliding in a saturable manner. The velocity obeyed a generalized Michaelis-Menten-like law (Leibler and Huse, 1993), as demonstrated by linearity in double-reciprocal plots of motility rates versus ATP concentration (Lineweaver-Burk plot; Fig. 4). In independent experiments with three different preparations of Nkin, linear regression analysis yielded apparent \(K_m\) values of 187, 340, and 393 \(\text{mM}\) ATP.

Native Nkin possessed an ATPase activity that was stimulated approximately 6-fold by microtubules (Steinberg and Schliwa, 1995). As already discussed by Huang and Hackney (1994) and Steinberg and Schliwa (1995), the ATPase rates determined in these assays are inconsistent with the rates of motility observed, suggesting that the ATPase properties of kinesin isolated by conventional procedures do not reflect the properties of the molecule in vivo. Like microtubule motility, the ATPase activity obeyed Michaelis-Menten kinetics (Fig. 5), yielding \(K_m\) values of 112, 145, and 194 \(\text{mM}\) ATP in three independent experiments. The ratio of the \(K_m\) for motility (average 150 \(\text{mM}\)) and the \(K_m\) for ATPase activity (average 306 \(\text{mM}\)) was \(2\times\) (Leibler and Huse, 1993). Studies with sea urchin, Drosophila, and bovine brain kinesin have yielded \(K_m\) values for microtubule gliding ranging from 10 to 60 \(\text{mM}\) (Porter et al., 1987; Saxton et al., 1988; Cohn et al., 1989; Howard et al., 1989); \(K_m\) values of ATPase activity have been determined to be 10–20 \(\text{mM}\) for bovine brain kinesin (Kuznetsov et al., 1986, 1989) and 31 \(\text{mM}\) for recombinant Drosophila kinesin (Gilbert and Johnson, 1993). Thus for both \(K_m\) values, the values of Nkin are approximately an order of magnitude higher. Whether the high rate of microtubule movement is related to the low affinity for ATP remains to be determined. In a theoretical analysis, Leibler and Huse (1993) compared the motors myosin and kinesin and predicted the ratio of the \(K_m\) for motility and the \(K_m\) for ATPase activity to be approximately 2, as in the case of other conventional kinesins. Thus the basic features of the cross-bridge cycle of Nkin probably are similar to those of other kinesins. Nkin therefore seems to be a molecular motor of the "porter" type (Leibler and Huse, 1993), in contrast to myosin and probably also dynein,
which belong to the "rower" class of molecular motors with a ratio of the Km values of >10. The distinction between these two classes of motors on the basis of their Km values for motility and ATPase activity is in agreement with recent studies that directly demonstrate that the chemomechanical cycles of kinesin and myosin are indeed fundamentally different (Romberg and Vale, 1993; Gilbert et al., 1995). It will be interesting to determine whether the high rate of motility of Nkin is based on a larger step size, a shorter cycle time, or both.

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