BioOne COMPLETE

Impaired Flagellar Regeneration Due to Uncoordinated Expression of Two Divergent Actin Genes in Chlamydomonas

Author: Kato-Minoura, Takako

Source: Zoological Science, 22(5) : 571-577

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.22.571

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Zoological-Science on 02 Aug 2024
Terms of Use: https://bioone.org/terms-of-use

ZOOLOGICAL SCIENCE **22**: 571–577 (2005) © 2005 Zoological Society of Japan

Impaired Flagellar Regeneration Due to Uncoordinated Expression of Two Divergent Actin Genes in *Chlamydomonas*

Takako Kato-Minoura[1*†]

[1]*Department of Cell Biology, National Institute for Basic Biology, Okazaki 444-8585, Japan*

ABSTRACT—*Chlamydomonas* has two actin genes: one encoding a conventional actin (90% amino acid identity with mammalian actin) and the other a highly divergent actin (NAP; 64% identity). The expression of the two genes is regulated in a mutually exclusive manner. Thus, *ida5*, a mutant that lacks the conventional actin (CrA) gene, expresses NAP abundantly, whereas wild-type cells express NAP only negligibly under normal conditions. To explore the physiological significance of the two actins, chimeric genes with the 5' upstream region of one gene replaced by that of the other were constructed and used to transform *ida5*. The transformant (*TF5*) with a chimeric clone comprising the 5'-untranslated region from the NAP gene and the CrA-encoding sequence recovered the dyneins missing in *ida5* and showed almost normal motility. After deflagellation of this transformant, however, only about 30% of cells grew flagella, unlike wild-type cells, >80% of which displayed reflagellation. Transformant *TF10*, which contains the CrA upstream region and NAP coding region, underwent reflagellation normally, as did the parent strain, *ida5*. In *TF5*, the mRNA level of both CrA and NAP was increased greatly during reflagellation. In light of the recent finding that NAP mRNA is expressed transiently upon reflagellation in wild-type cells, the described results suggest that 1) the expression of NAP mRNA is indispensable for flagellation and 2) robust expression of CrA may inhibit proper flagellation by interfering with the function of NAP in the early stages of reflagellation.

Key words: 5'-UTR, transformation, flagella, IFT

INTRODUCTION

Chlamydomonas has two actin genes, one encoding a conventional actin (CrA) with ~90% amino-acid identity with mammalian actin, and the other a highly divergent actin (NAP, novel actin-like protein) having ~64% identity with mammalian actin (Kato *et al*., 1993; Sugase *et al*., 1996; Kato-Minoura *et al*., 1997; Lee *et al*., 1997; Kato-Minoura *et al*., 1998). Phylogenetic analysis has shown that NAP has evolved independently from the conventional actin lineage since algal actins first diversified (Kato-Minoura *et al*., 2003). The presence of these divergent actins in a single cell suggests that they each have specific functions, but their functional difference is not understood. In *Chlamydomonas* and many other organisms, actin is a subunit of axonemal inner-arm dyneins, i.e., the protein complexes that produce force for ciliary and flagellar movements (Piperno and Luck, 1979; Muto *et al*., 1994). The actin subunit may be involved in the docking of inner arm dyneins to the correct loci on the outer doublet microtubules (Yanagisawa and Kamiya, 2001). The mutant *ida5*, which lacks the gene for CrA (Kato *et al*., 1993; Kato-Minoura *et al*., 1997), lacks four of the six species of actin-containing inner-arm dyneins and cannot form fertilization tubules but grows at the same rate as the wild type. The inner-arm dyneins present in *ida5* contain NAP instead of CrA. Hence NAP can substitute for CrA in most, but not all, actin-based functions.

Intriguingly, NAP is expressed only negligibly in wild-type cells, although it is expressed abundantly in *ida5*. In *ida5* cells transformed with the genomic CrA gene, the level of NAP message is inversely related to the level of expressed actin protein (Ohara *et al*., 1998). These observations led to the hypothesis that the expression of NAP is negatively regulated by actin. Recently, Hirono *et al*. (2003) found that a considerable level of NAP is expressed in wild-type cells during the reflagellation process after flagellar amputation. NAP expression ceases with flagellar growth. This observation suggests that NAP may function in flagellation, and the controlled expression of the two genes may be important in this process.

* Corresponding author. Phone: +81-3-5454-6657;
Fax : +81-3-5454-6657;
E-mail: mtakako@bio.c.u-tokyo.ac.jp

† Present address: Division of Biology, Department of Life Sciences, Graduate School of Arts and Sciences, University of Tokyo, Tokyo 153-8902, Japan

Downloaded From: https://bioone.org/journals/Zoological-Science on 02 Aug 2024
Terms of Use: https://bioone.org/terms-of-use

To determine whether balanced expression of the two actins is important for flagellar regeneration, I transformed cells with chimeric genes in which the 5'-untranslated regions (5'-UTRs) were swapped between the NAP and CrA genes. The ability of cells to re-grow flagella was impaired greatly when *ida5* was transformed with a chimeric actin gene consisting of the 5'-UTR sequence from the NAP gene and coding sequence from the CrA gene. This result supports the view that NAP plays an important role in the early stage of flagellar regeneration.

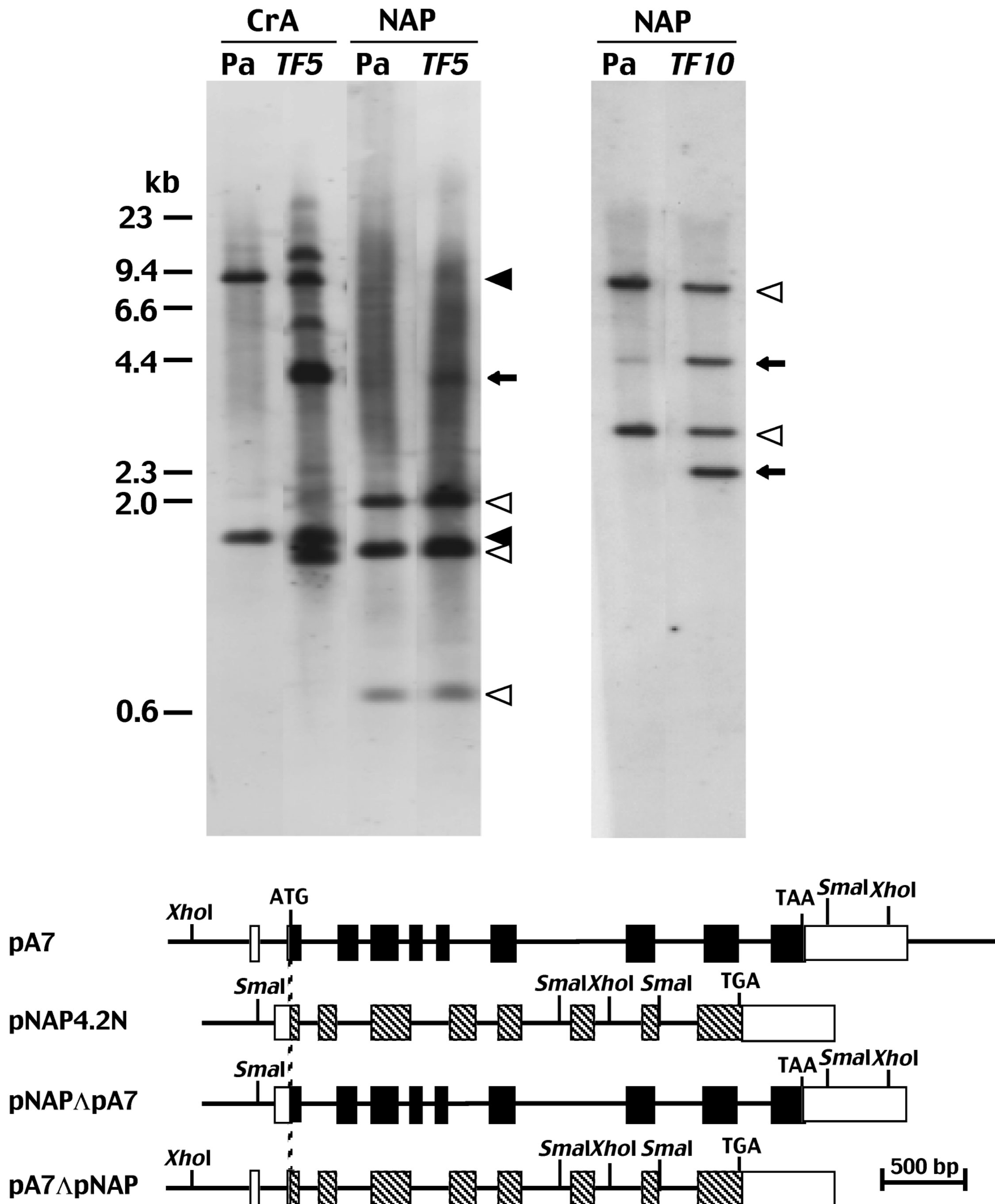

Fig. 1. (Upper) Southern blot analyses showing the chimeric genes used for transformation. Genomic DNA from the transformants (*TF5* and *TF10*) and the parent strain (Pa; *ida5/arg2*) was digested with *Sma*I (left panel) or *Xho*I (right panel) and probed with cDNA fragments of protein-coding regions from CrA or NAP. Arrows indicate the restriction fragments from the chimeric genes. Closed and open arrowheads indicate the fragments of wild-type genes. In *TF5*, several fragments (probably byproducts of the transformation) were seen. (Lower) Structure and restriction map of the two *Chlamydomonas* actin genes and the chimeric genes constructed in the present study. pA7, CrA genomic clone; pNAP4.2N, a NAP genomic clone; pNAPΛpA7 and pA7ΛpNAP, chimeric genes composed of reciprocal portions of the two actin genes. Solid boxes indicate coding exons of pA7, and shaded boxes indicate those of NAP. Open boxes represent 5'- and 3'-UTR, and lines mark introns and flanking DNA. Restriction sites used in the Southern analyses and the translation start (ATG) and stop (TAA or TGA) codons are shown.

Downloaded From: https://bioone.org/journals/Zoological-Science on 02 Aug 2024
Terms of Use: https://bioone.org/terms-of-use

MATERIALS AND METHODS

Strains and cell culture

The *Chlamydomonas reinhardtii* actin-less mutant, *ida5* (Kato *et al*., 1993) and a double mutant, *ida5/arg2* (Ohara *et al*., 1998), were used. The arginine-requiring mutant *arg2* was obtained from Dr. E. Harris of the *Chlamydomonas* Genetic Center (Department of Botany, Duke University, Durham, NC). In motility and reflagellation assays, cells were grown in liquid Tris–acetic acid–phosphate (TAP) medium (Gorman and Levine, 1965).

Construction of chimeric actin genes and transformation

The CrA genomic clone (pA7) is described in Sugase *et al*. (1996). A genomic clone of NAP was obtained by screening a *C. reinhardtii* genomic library (λFIX II, Stratagene, La Jolla, CA) with an NAP 3'-UTR sequence as a probe (Kato-Minoura *et al*., 1998). A 4.2-kb *Not*I fragment derived from a positive phage plaque was subcloned into pBluescript (pNAP4.2N). The chimeric actin genes were constructed as shown in Fig. 1. Primers used for chimeric genes construction were 5'crA1.g (TCGAGGGGGCCACATCCC) and 3'NdcrA738.g (ACACGCAGGATTCAAACATATGCC) to amplify the 5'-UTR of pA7; 5'NdNap97.cL (GGCATATGACTTCCGGCCTTCCA-GACACTGATACT) and 3'KS+30 (AGCTTGATATCGAATTCCTG-CAGCCCGGGG) for the coding region of pNAP4.2N; 5'Nap-93.g (CTGGGAGGCTGGGCTGCG) and 3'NcNap81.c (AACAGCGCA-GACCAAACCCATGGCC) for the 5'-UTR of pNAP4.2N; and 5'NccrA50.c (TTCCATGGCTGACGAGGGCGAGGTCTCTGCTCTG) and 3'crA4534.g (TAAAAATGCTACACACGAAATGGTCCGAGC) for the coding region of pA7. Each amplified fragment was subcloned into pBluescript, and the 5'-UTR and coding regions were linked using either the *Nde*I or *Nco*I site. These chimeric genes were linearized by digestion with *Hin*dIII and then used to transform *ida5/arg2*, as described in Ohara *et al*. (1998).

Transformation assessments

Southern and Northern blotting analyses were performed as in Kato-Minoura *et al*. (1997). The composition of dynein heavy chains was analyzed by SDS-polyacrylamide gel electrophoresis (SDS-PAGE) with an acrylamide gradient of 3 to 5% and a urea gradient of 3 to 8 M (Pfister *et al*., 1982). Western blotting was performed mainly as described in Kato-Minoura *et al*. (1997). For flagellar fractions, signals of immunoreaction were detected using the ECL system (Amersham Pharmacia Biotech). A monoclonal antibody specific for p28, a light chain of the inner-arm dynein, was a generous gift from Dr. G. Piperno (LeDizet and Piperno, 1995).

Motility assays

The swimming velocities and flagellar beat frequencies of the mutant and wild-type cells were measured as described in Kato *et al*. (1993).

Flagella length measurements

Deflagellation was induced by pH shock (Witman, 1986). During the recovery, aliquots of cells were fixed with glutaraldehyde (final concentration, 4%) and evaluated using dark-field microscopy. The flagellar length was measured from the video-recorded image by using the public domain NIH Image program (developed at the U.S. National Institutes of Health). In each analysis, more than 50 flagella were measured.

RESULTS

Two chimeric genes of NAP and CrA were constructed as illustrated in Fig. 1. In both constructs, the 5'-UTR region of one gene was conjugated to the protein-coding region of the other. Because the 5'-UTR most likely contains regulatory elements for gene expression (Brunke *et al*., 1984), I expected that swapping of this region between the two

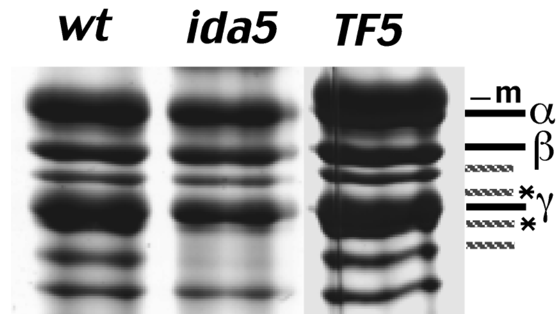

Fig. 2. SDS-PAGE patterns of the axonemes of wild type (wt), *ida5*, and *TF5*. Only a portion of the gel showing dynein heavy chains is presented. m, membrane contamination; α, β, and γ, outer dynein heavy chains; bands indicated by hatched lines, inner dynein heavy chains; hatched lines with asterisks, heavy chains missing in *ida5* (almost overlapping with γ chain).

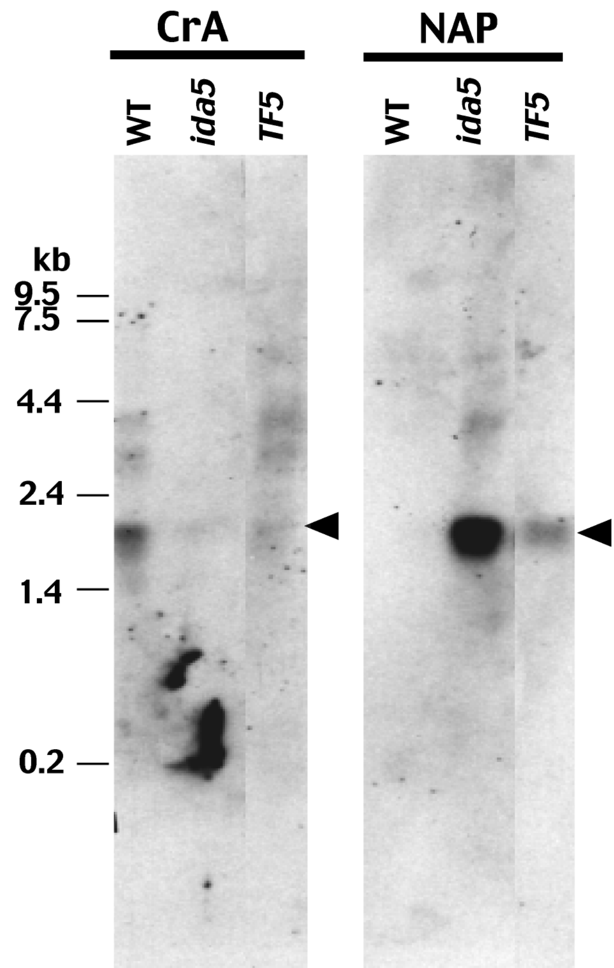

Fig. 3. Northern blot analyses showing CrA and NAP mRNA levels in wild type (WT), *ida5*, and *TF5*. Total RNA was isolated and probed with a portion of the 3'-UTR of either CrA or NAP. Arrowheads indicate positions of CrA and NAP mRNA (almost the same size).

Downloaded From: https://bioone.org/journals/Zoological-Science on 02 Aug 2024
Terms of Use: https://bioone.org/terms-of-use

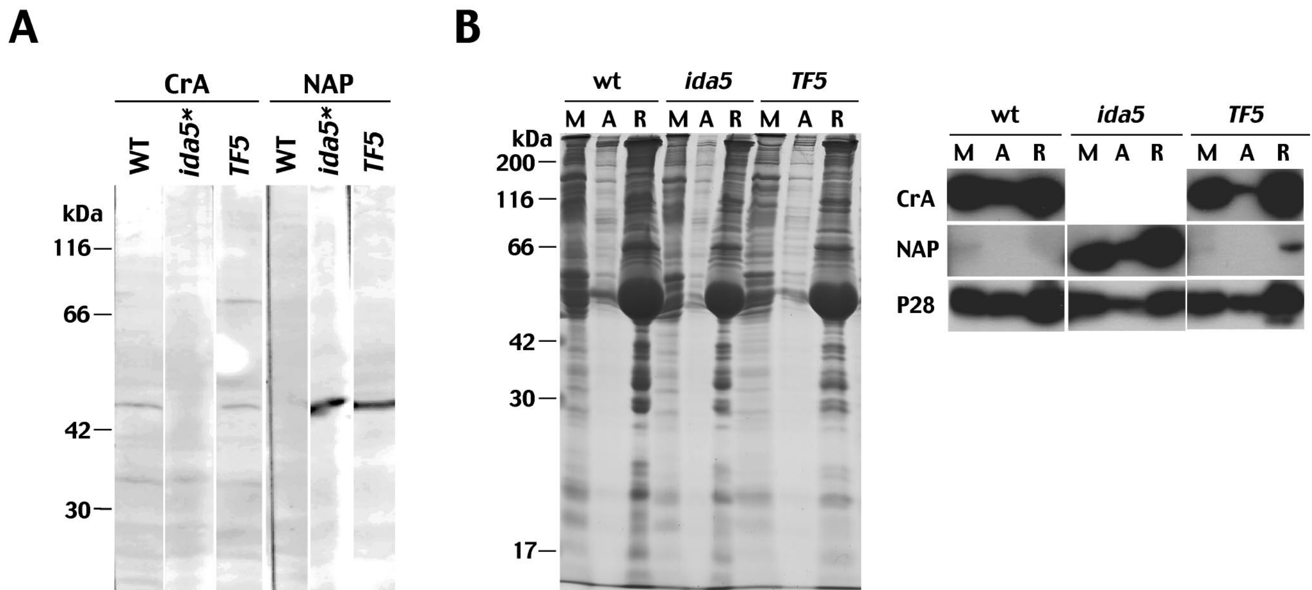

Fig. 4. Western blot analysis. (A) Total cell lysates were electrophoresed, and then probed with anti-CrA or anti-NAP antibody. *ida5**; *ida5/arg2* was used in this experiment. (B) Flagella were isolated and separated into fractions containing 1% NP-40-soluble proteins (M), those released from the axoneme by 10 mM ATP (A), and residual axonemal proteins (R), as described in Pazour *et al.* (1998). Fractions then were electrophoresed and stained with Coumassie Brilliant Blue (left panel) or probed with anti-CrA, anti-NAP, or anti-p28 antibody (right panels).

genes would disturb their expression. The chimeric genes were transformed into *ida5/arg2*, and strains *TF5* and *TF10* are the transformants of pNAPΛpA7 and pA7ΛNAP, respectively. Success of transformation was confirmed by Southern blotting; in both transformants, restriction fragments from the chimeric genes were detected in addition to the fragments from the intrinsic genomic fragments (Fig. 1).

Transformant *TF5* had regained the inner-arm dynein heavy chains missing in *ida5* (Fig. 2). As shown previously (Ohara *et al.*, 1998), dynein recovery is due to the expression of CrA from the chimeric genes. However, only a small amount of CrA mRNA was transcribed in the *TF5* cells, and, unlike in wild-type cells, NAP mRNA also was expressed (Fig. 3). Despite their low mRNA levels, the CrA and NAP proteins were expressed in considerable amounts, as detected with their specific antibodies (Kato-Minoura *et al.*, 1998) (Fig. 4A). To examine the sublocalization of CrA and NAP within the flagella, wild type, *ida5*, and *TF5* flagella were isolated and fractionated (Fig. 4B). In *TF5* flagella, CrA was abundant, and only a small quantity of NAP was detected, mainly in the fraction of proteins that remained in the axoneme after ATP extraction.

Table 1 summarizes the motility properties of the transformants. *TF5* recovered swimming velocity to 83% of the wild-type level (about 210% of the *ida5* level). In contrast, *TF10* exhibited an even slower swimming velocity than *ida5*.

Closer observation, however, revealed a small population of *TF5* that lacked flagella. Because this finding suggested that the transformant might have defects in flagellar growth, I next examined the flagellar regeneration process in the transformants after deflagellation by pH shock (Fig. 5). When wild-type cells are deflagellated, flagella start to grow within several minutes, and almost all cells resume swimming within 40 min; flagella typically recover their original length (~10 μm) within 2 h (Rosenbaum *et al.*, 1969). In *TF5*, 32% of cells lacked flagella, and the rest of the cells had flagella of various lengths before flagellar amputation (Fig. 5, upper column). After flagellar amputation, only a small population of cells regenerated flagella, and 73% of cells remained non-flagellated even after 60 min. This scenario is in striking contrast with those of wild-type and *ida5* cells, >90% of which regained flagella. In contrast, the number of *TF10* cells that recovered flagella was comparable to that in *ida5*, although the transformant also showed some abnormality in the distribution of flagellar lengths.

To see whether the reduced flagellation activity of *TF5* is due to irregular protein expression as a result of the chimeric gene transformation, the CrA mRNA level was quantified (Fig. 6). When wild-type cells were deflagellated, there was relatively slow upregulation of CrA compared with that of NAP, as previously reported by Hirono *et al.* (2003). In contrast, in *TF5*, rapid and robust expression of CrA was observed. As in *ida5* and wild-type cells (Hirono *et al.*, 2003), the expression of NAP was conspicuously upregu-

Table 1. Motility of *C. reinhardtii* clones used in this study.

	Swimming velocity [μm /sec] *	Beat frequency [Hz]
wild type	118.0 ± 33.6	58
ida5	46.3 ± 17.3	18 to 60‡
TF5	98.4 ± 24.0	55
TF10	36.3 ± 11.2	30 to 60‡

* Data are given as mean ± SD in more than 50 measurements.
‡ *ida5* has a broad range of beat frequency (Kato *et al.*, 1993).

Downloaded From: https://bioone.org/journals/Zoological-Science on 02 Aug 2024
Terms of Use: https://bioone.org/terms-of-use

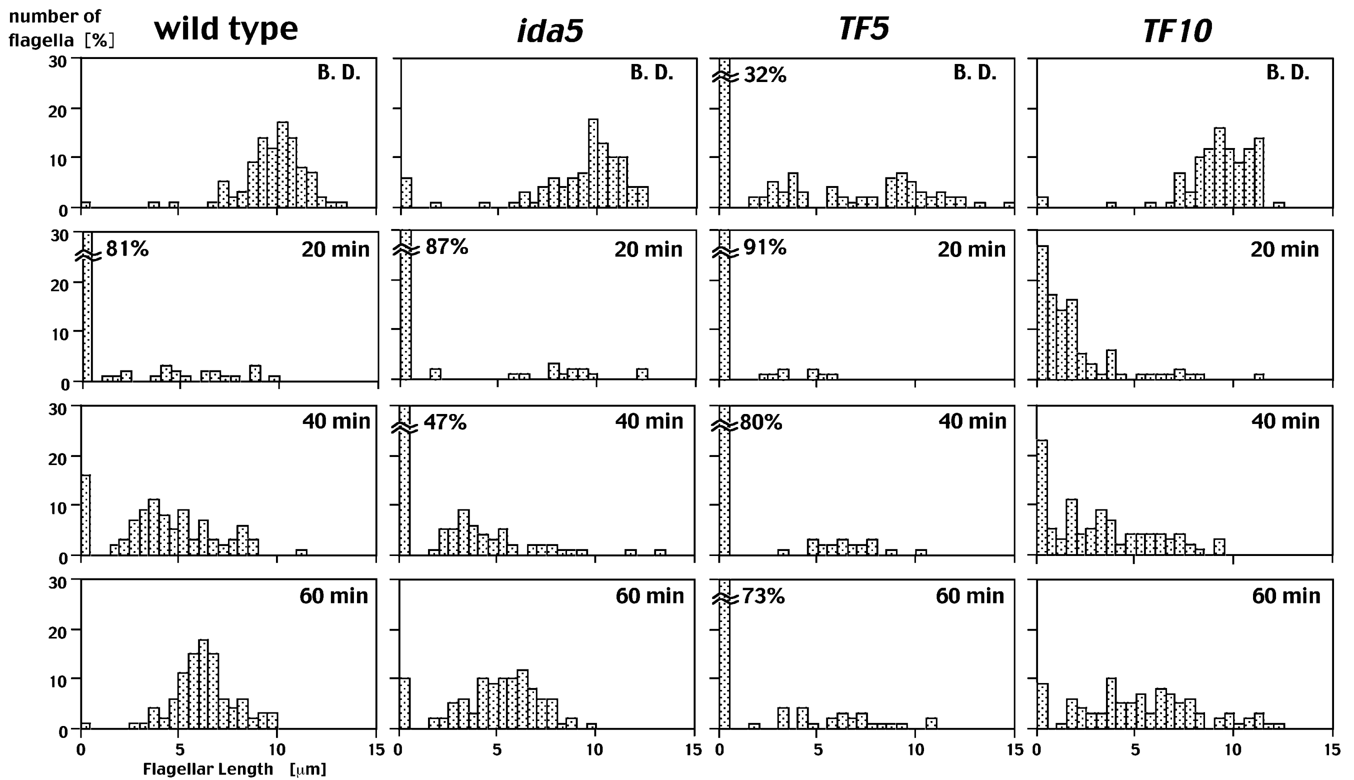

Fig. 5. Histograms showing flagellar length recovery during reflagellation. For bars representing >30% of flagellar number, the net values are also indicated. B. D., before deflagellation. Time after deflagellation is noted.

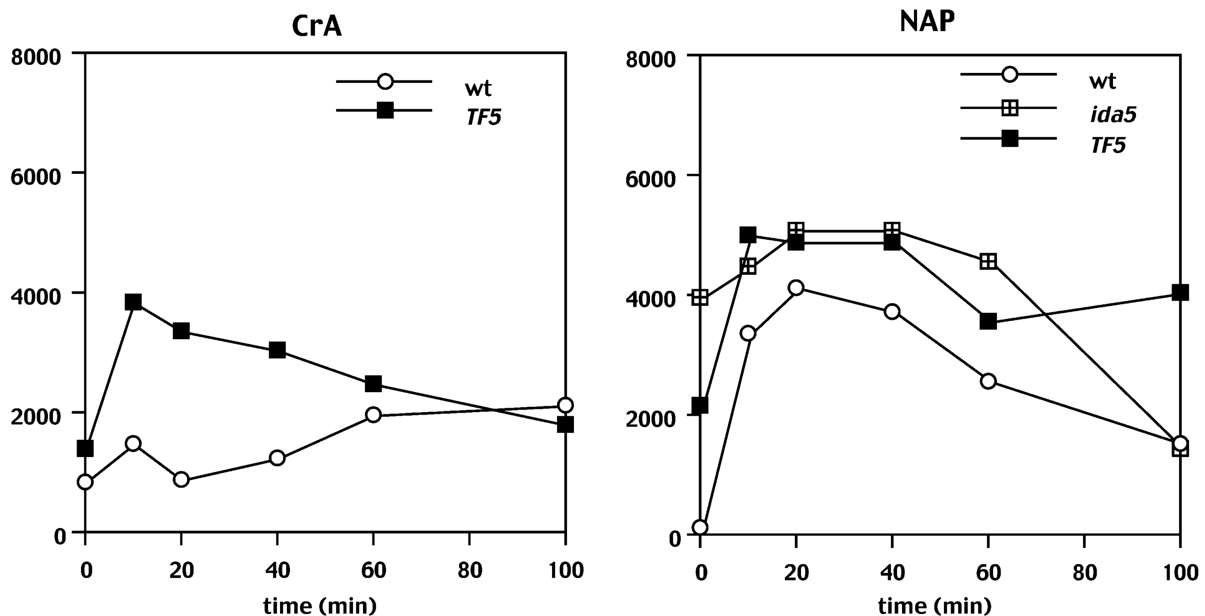

Fig. 6. Expression of CrA and NAP after deflagellation. mRNA level was quantified by Northern blotting, and the signal densities of corresponding bands were estimated using NIH image software. Horizontal axes indicate time after deflagellation; vertical axes indicate signal density (arbitrary units).

Downloaded From: https://bioone.org/journals/Zoological-Science on 02 Aug 2024
Terms of Use: https://bioone.org/terms-of-use

lated in *TF5* upon deflagellation.

DISCUSSION

NAP was first discovered in the *Chlamydomonas* mutant *ida5*, which lacks the gene for conventional actin. This discovery has caused us to wonder why the NAP gene is preserved in wild-type cells, which express only negligible amounts of NAP under normal conditions. Recently, however, Hirono *et al.* (2003) found that NAP is expressed shortly after flagellar amputation in wild-type cells. From this observation, these investigators suggested that NAP might somehow be involved in the flagellation process. The findings presented in the current paper support their suggestion.

The most important finding of the current study is that a transformant (*TF5*) with a chimeric gene combining the 5'-UTR region of NAP with the coding region of CrA, exhibited a notable deficiency in flagellation activity (Fig. 5). The flagellar deficiency seems to be confined to the flagellation process, as flagellated cells recovered dynein composition and motility to the same degree as transformants with wild-type *CrA* (Fig. 2 and Table 1; Ohara *et al.*, 1998). In contrast, *TF10*, in which the transforming construct comprises the CrA 5'-UTR region plus the NAP coding region, has normal flagellation activity (Fig. 5), suggesting that the process of transformation with a chimeric gene itself has no influence on flagellation. Rather, the 5'-UTR of NAP that was included in pNAPΛpA7 must have caused a change in the re-flagellation activity of *TF5*. When wild-type cells are deflagellated, the expression of NAP message precedes that of the CrA message; the NAP message is expressed maximally <20 min after flagellar amputation, whereas actin expression reaches a peak 40 min after amputation. In addition, the increase in message expression is much larger for NAP than CrA (Hirono *et al.*, 2003). In the present study, CrA mRNA expression in *TF5* occurred very rapidly and robustly after flagellar amputation, as did NAP mRNA from the native gene. Abnormal expression of CrA immediately after flagellar amputation may inhibit proper flagellation, possibly by interfering with the function of NAP, which plays a crucial role during an early phase of flagellar regeneration.

What specific role does NAP play? NAP is present in growing flagella of wild-type cells, but it is gradually lost as flagellar growth is completed (Hirono *et al.*, 2003). During flagellation, several axonemal proteins are transported to the site of assembly by means of intraflagellar transport (IFT), in which moving particles termed “rafts” are observed in the space between the axoneme and membrane (Kozminski *et al.*, 1993; Cole *et al.*, 1998; Scholey, 2003). When flagella are extracted with detergent, rafts and other soluble proteins are released in the “membrane-plus-matrix” fraction. Extraction of the remaining axoneme with ATP releases IFT motors and associated compounds that are bound to the axoneme in an ATP-sensitive manner. In wild-type and *TF5* cells, faint bands of NAP were detected in the membrane-plus-matrix fraction (Fig. 4B). This observation suggests that NAP may function in IFT as a minor component of rafts.

Various protein assemblies are transported first as precursors and then converted into mature forms in the axoneme. For example, the radial spoke complex enters growing flagella as a 12S precursor and is converted into a 20S form (Qin *et al.*, 2004). Such conversion occurs also in inner-arm dyneins (Piperno and Mead, 1997). Therefore, actin may well replace NAP in the inner-arm complex during the process of maturation. In *TF5*, however, the axoneme contained a considerable amount of NAP despite the cells' recovery of dynein composition and motility (Fig. 4B). In this case, abnormal expression of CrA may have interfered with the NAP–actin exchange that would have readily taken place under normal conditions. Alternatively, NAP may participate in the transport or localization of inner arms to specific loci on the outer doublet. Chemical crosslinking experiments have shown that actin is associated indirectly with inner arm heavy chains, through light chains that are bound to the N-terminal half of the heavy chain (Yanagisawa and Kamiya, 2001). Because ATP-independent dynein–microtubule association likely occurs at the N-terminal portion of the heavy chain, it seems possible that NAP and actin are somehow involved in the correct localization of inner-arm dyneins. The exact functions of NAP and actin await studies using strains in which the expression of NAP is reduced.

ACKNOWLEDGMENTS

I thank Prof. Ritsu Kamiya and Dr. Masafumi Hirono (University of Tokyo) for critically reading the manuscript and Prof. Osamu Numata (Tsukuba University) for support. This work was supported by Grants-in-Aid for Encouragement of Young Scientists from Japan Society for the Promotion of Science.

REFERENCES

Brunke KJ, Anthony JG, Sternberg EJ, Weeks DP (1984) Repeated consensus sequence and pseudopromoters in the four coordinately regulated tubulin genes of *Chlamydomonas reinhardi*. Mol Cell Biol 4: 1115–1124

Cole DG, Diener DR, Himelblau AL, Beech PL, Fuster JC, Rosenbaum JL (1998) *Chlamydomonas* kinesin-II-dependent intraflagellar transport (IFT): IFT particles contain proteins required for ciliary assembly in *Caenorhabditis elegans* sensory neurons. J Cell Biol 141: 993–1008

Gorman DS, Levine RP (1965) Cytochrome f and plastocyanin: their sequence in the photosynthetic electron transport chain of *Chlamydomonas reinhardi*. Proc Natl Acad Sci USA 54: 1665–1669

Hirono M, Uryu S, Ohara A, Kato-Minoura T, Kamiya R (2003) Expression of conventional and unconventional actins in *Chlamydomonas reinhardtii* upon deflagellation and sexual adhesion. Eukaryot Cell 2: 486–493

Kato T, Kagami O, Yagi T, Kamiya R (1993) Isolation of two species of *Chlamydomonas reinhardtii* flagellar mutants, *ida5* and *ida6*, that lack a newly identified heavy chain of the inner dynein arm. Cell Struct Funct 18: 371–377

Kato-Minoura T, Hirono M, Kamiya R (1997) *Chlamydomonas* inner-arm dynein mutant, *ida5*, has a mutation in an actin-encoding

Downloaded From: https://bioone.org/journals/Zoological-Science on 02 Aug 2024
Terms of Use: https://bioone.org/terms-of-use

gene. J Cell Biol 137: 649–656
Kato-Minoura T, Okumura M, Hirono M, Kamiya R (2003) A novel family of unconventional actins in volvocalean algae. J Mol Evol 57: 555–561
Kato-Minoura T, Uryu S, Hirono M, Kamiya R (1998) Highly divergent actin expressed in a *Chlamydomonas* mutant lacking the conventional actin gene. Biochem Biophys Res Commun 251: 71–76
Kozminski KG, Johnson KA, Forscher P, Rosenbaum JL (1993) A motility in the eukaryotic flagellum unrelated to flagellar beating. Proc Natl Acad Sci USA 90: 5519–5523
LeDizet M, Piperno G (1995) The light chain p28 associates with a subset of inner dynein arm heavy chains in *Chlamydomonas* axonemes. Mol Biol Cell 6: 697–711
Lee VD, Finstad SL, Huang B (1997) Cloning and characterization of a gene encoding an actin-related protein in *Chlamydomonas*. Gene 197: 153–159
Muto E, Edamatsu M, Hirono M, Kamiya R (1994) Immunological detection of actin in the 14S ciliary dynein of *Tetrahymena*. FEBS Lett 343: 173–177
Ohara A, Kato-Minoura T, Kamiya R, Hirono M (1998) Recovery of flagellar inner-arm dynein and the fertilization tubule in *Chlamydomonas ida5* mutant by transformation with actin genes. Cell Struct Funct 23: 273–281
Pfister KK, Fay RB, Witman GB (1982) Purification and polypeptide composition of dynein ATPase from *Chlamydomonas* flagella. Cell Motil Cytoskel 2: 525–547
Piperno G, Luck DJL (1979) An actin-like protein is a component of axonemes from *Chlamydomonas* flagella. J Biol Chem 254: 2187–2190
Piperno G, Mead K (1997) Transport of a novel complex in the cytoplasmic matrix of *Chlamydomonas* flagella. Proc Natl Acad Sci USA 94: 4457–4462
Qin H, Diener DR, Geimer S, Cole DG, Rosenbaum JL (2004) Intraflagellar transport (IFT) cargo: IFT transports flagellar precursors to the tip and turnover products to the cell body. J Cell Biol 164: 255–266
Rosenbaum JL, Moulder JE, Ringo DL (1969) Flagellar elongation and shortening in *Chlamydomonas*. The use of cycloheximide and colchicine to study the synthesis and assembly of flagellar proteins. J Cell Biol 41: 600–619
Scholey JM (2003) Intraflagellar transport. Annu Rev Cell Dev Biol 19: 423–443
Sugase Y, Hirono M, Kindle KL, Kamiya R (1996) Cloning and characterization of the actin-encoding gene of *Chlamydomonas reinhardtii*. Gene 168: 117–121
Witman GB (1986) Isolation of *Chlamydomonas* flagella and flagellar axonemes. Methods Enzymol 134: 280–290
Yanagisawa HA, Kamiya R (2001) Association between actin and light chains in *Chlamydomonas* flagellar inner-arm dyneins. Biochem Biophys Res Commun 288: 443–447

(Received February 16, 2005 / Accepted April 1, 2005)

Downloaded From: https://bioone.org/journals/Zoological-Science on 02 Aug 2024
Terms of Use: https://bioone.org/terms-of-use