**MOLECULAR BIOLOGY
INTELLIGENCE
UNIT**

Muscle Development in *Drosophila*

Helen Sink

Skirball Institute of Biomolecular Medicine
Molecular Neurobiology Program
and Department of Pharmacology
New York University School of Medicine
New York, New York, U.S.A.

LANDES BIOSCIENCE / EUREKAH.COM
GEORGETOWN, TEXAS
U.S.A.

SPRINGER SCIENCE+BUSINESS MEDIA
NEW YORK, NEW YORK
U.S.A.

MUSCLE DEVELOPMENT IN DROSOPHILA

Molecular Biology Intelligence Unit

Landes Bioscience / Eurekah.com
Springer Science+Business Media, Inc.

ISBN: 0-387-30053-8

Printed on acid-free paper.

Copyright ©2006 Eurekah.com and Springer Science+Business Media, Inc.

All rights reserved. This work may not be translated or copied in whole or in part without the written permission of the publisher, except for brief excerpts in connection with reviews or scholarly analysis. Use in connection with any form of information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed is forbidden.

The use in the publication of trade names, trademarks, service marks and similar terms even if they are not identified as such, is not to be taken as an expression of opinion as to whether or not they are subject to proprietary rights.

While the authors, editors and publisher believe that drug selection and dosage and the specifications and usage of equipment and devices, as set forth in this book, are in accord with current recommendations and practice at the time of publication, they make no warranty, expressed or implied, with respect to material described in this book. In view of the ongoing research, equipment development, changes in governmental regulations and the rapid accumulation of information relating to the biomedical sciences, the reader is urged to carefully review and evaluate the information provided herein.

Springer Science+Business Media, Inc., 233 Spring Street, New York, New York 10013, U.S.A.
<http://www.springer.com>

Please address all inquiries to the Publishers:

Landes Bioscience / Eurekah.com, 810 South Church Street, Georgetown, Texas 78626, U.S.A.

Phone: 512/ 863 7762; FAX: 512/ 863 0081

<http://www.eurekah.com>

<http://www.landesbioscience.com>

Printed in the United States of America.

9 8 7 6 5 4 3 2 1

Library of Congress Cataloging-in-Publication Data

Muscle development in drosophila / [edited by] Helen Sink.

p. ; cm. -- (Molecular biology intelligence unit)

Includes bibliographical references and index.

ISBN 0-387-30053-8 (alk. paper)

1. Drosophila--Physiology. 2. Muscles--Differentiation. I. Sink, Helen. II. Series: Molecular biology intelligence unit (Unnumbered)

[DNLM: 1. Drosophila melanogaster--genetics. 2. Drosophila melanogaster--growth & development. 3. Muscle Cells--physiology. 4. Muscle Development--physiology. QX 505 M985 2006]

QL537.D76M87 2006

573.7'515774--dc22

2005030264

CONTENTS

1. An Introduction to Muscle Development in <i>Drosophila</i>	1
<i>Helen Sink</i>	
The Muscle Pattern of <i>Drosophila</i>	1
Mesoderm Formation in the <i>Drosophila</i> Embryo	3
Development of the Cardiac Musculature, Visceral Musculature, Somatic Gonad and Fat Bodies	3
Development of the Somatic Musculature	4
Metamorphosis and the Adult Musculature	6
Approaches to Studying <i>Drosophila</i> Muscle Development	7
2. The Muscle Pattern of <i>Drosophila</i>	8
<i>Volker Hartenstein</i>	
Somatic Musculature	8
The Somatic Musculature of the <i>Drosophila</i> Larva	10
Pattern of Thoracic and Abdominal Larval Muscles	10
Pattern of Muscles in the Larval Head and Tail	12
The Somatic Musculature of the Adult Fly	13
Pattern of Abdominal Muscles of the Adult Fly	13
Characteristics of the Thoracic Body Wall Muscles	15
Articulation of Legs and Wings with the Body Wall	16
General Bauplan of the Thoracic Musculature	16
Musculature of the <i>Drosophila</i> Legs and Wings	17
Musculature of the Thorax Other Than Wing and Leg Muscles	17
Musculature of the Head	19
Visceral Musculature	21
Visceral Musculature of the Foregut	21
Visceral Musculature of the Mid- and Hindgut	22
Circulatory System	22
Structure of the <i>Drosophila</i> Circulatory System	25
3. Mesoderm Formation in the <i>Drosophila</i> Embryo	28
<i>Noriko Wakabayashi-Ito and Y. Tony Ip</i>	
Establishment of Dorsal-Ventral Polarity during Oogenesis	29
The Toll Pathway in the Oocyte and Embryo	30
Zygotic Gene Activation and Mesoderm Specification	32
Mesoderm Invagination	33
4. Development of the Cardiac Musculature	38
<i>Rolf Bodmer</i>	
From Mesoderm to Heart Progenitors	40
Cardiac Lineages	40
Specification and Positioning of the Cardiac Mesoderm	42
Specification of Cardiac Cell Types	43
Hox Gene Function in the Heart	45

5. Development of the Somatic Gonad and Fat Bodies	51
<i>Mark Van Doren</i>	
Specification of the Fat Body and Somatic Gonad	51
Morphogenesis and Function of the Fat Body	54
Morphogenesis of the Gonad	55
6. Development of the Larval Visceral Musculature	62
<i>Hsiu-Hsiang Lee, Stephane Zaffran and Manfred Frasch</i>	
Morphogenesis and Functions of Trunk Visceral Mesoderm and Circular Midgut Muscles	65
Morphogenesis of Longitudinal Midgut, Foregut and Hindgut Muscles	65
Genetic and Molecular Mechanisms Controlling Visceral Mesoderm Development	67
7. Development of the Larval Somatic Musculature	79
<i>Ana Carmena and Mary Baylies</i>	
Allocation of Somatic Mesoderm-Mesodermal Subdivision	81
Birth of a Muscle Founder Cell	83
Integration of Signal Transduction Pathways during Muscle Progenitor Specification	86
Muscle Identity Is Regulated by Muscle Founder Identity Genes	86
A Molecular Definition of Muscle Founder Cell and Fusion-Competent Myoblasts	89
8. Muscle Morphogenesis: The Process of Embryonic Myoblast Fusion	92
<i>Susan M. Abmayr and Kiranmai S. Kocherlakota</i>	
Ultrastructure of the Adherent Myoblast Interface	93
Myoblast Recognition and Adhesion	94
Intracellular Events Associated with Myoblast Fusion	98
Other Genes with Roles in Myoblast Fusion	100
9. Muscle Attachment Sites: Where Migrating Muscles Meet Their Match	104
<i>Talila Volk</i>	
Determination of Epidermal Muscle-Attachment Precursors	104
The Guidance of the Muscle Towards Its Tendon Attachment Site	107
The Essential Role of Muscle Signaling in Tendon Cell Maturation ...	108
The Requirement for Muscle-Tendon Junctions for Proper Muscle Function	108
The Cytoplasmic Composition of the Muscle and Tendon Junctional Complexes	109
10. Neuromuscular Development: Connectivity and Plasticity	113
<i>Louise Nicholson and Haig Keshishian</i>	
Motoneuron Organization	113
Axonal Outgrowth	115

Target Selection	117
Establishing the Synapse	119
Neuromuscular Activity and Connectivity	120
11. Metamorphosis and the Formation of the Adult Musculature	125
<i>Devkanya Dutta and K. VijayRaghavan</i>	
Architecture of Adult Flight Muscles and Abdominal Muscles	125
Developmental Profile of Adult Muscles	127
Templates, Nerves, the Epidermis and Muscle Pattern	130
Vestigial, Cut and Apterous Impart Diversity within Thoracic Myoblasts and Canalize Them into Different Muscle Forming Pathways	131
Adult Founder Cells, Identified by <i>Dumbfounded</i> , Regulate Muscle Fiber-Number and Muscle Position	133
Antagonistic Activities of Notch and D-Mef2 Regulate Myoblast Proliferation versus Differentiation	133
Homeotic Identity Control Muscle Organization in Adult Thoracic Segments	135
<i>Stripe</i> -Expressing Muscle Attachment Sites—Their Specification and Differentiation	138
12. Molecular Basis of Muscle Structure	143
<i>Jim O. Vigoreaux</i>	
Structure and Composition of the Myofibril	143
Ultrastructure of Developing Myofibrils	145
Genetics of Myofibrillar Proteins	146
Thin Filament and Z Band Proteins	149
Myofibril Assembly	152
13. Whole Genome Approaches to Studying <i>Drosophila</i> Muscle Development	157
<i>Eileen E.M. Furlong</i>	
Transcriptome Analysis	158
Phenome Mapping	165
Localizome Mapping	165
Interactome Mapping	166
14. Comparison of Muscle Development in <i>Drosophila</i> and Vertebrates	169
<i>Michael V. Taylor</i>	
Overview of <i>Drosophila</i> Muscle Development	170
Overview of Vertebrate Muscle Development	171
Somatic/Skeletal Muscle Development	172
Heart Development in <i>Drosophila</i> and Vertebrates	187
Visceral Muscle Development	190
Index	205

EDITOR

Helen Sink

**Skirball Institute of Biomolecular Medicine
Molecular Neurobiology Program
and Department of Pharmacology
New York University School of Medicine
New York, New York, U.S.A.
Email: sink@saturn.med.nyu.edu**

Chapter 1

CONTRIBUTORS

Susan M. Abmayr
The Stowers Institute
for Medical Research
Kansas City, Missouri, U.S.A.
Email: sma@stowers-institute.org
Chapter 8

Mary Baylies
Program in Developmental Biology
Sloan Kettering Institute
Memorial Sloan Kettering Cancer Center
New York, New York, U.S.A.
Email: m-baylies@ski.mskcc.org
Chapter 7

Rolf Bodmer
The Burnham Institute
La Jolla, California, U.S.A.
Email: rolf@burnham.org
Chapter 4

Ana Carmena
Program in Developmental Biology
Sloan Kettering Institute
Memorial Sloan Kettering Cancer Center
New York, New York, U.S.A.
Chapter 7

Devkanya Dutta
National Centre for Biological Sciences
Tata Institute of Fundamental Research
Bangalore, India
Chapter 11

Manfred Frasch
Brookdale Department of Molecular,
Cell and Developmental Biology
Mount Sinai School of Medicine
New York, New York, U.S.A.
Email: Manfred.Frasch@mssm.edu
Chapter 6

Eileen E.M. Furlong
Developmental Biology
and Gene Expression Programmes
EMBL
Heidelberg, Germany
Email: Eileen.Furlong@embl.de
Chapter 13

Volker Hartenstein
Department of Molecular Cell
and Developmental Biology
University of California Los Angeles
Los Angeles, California, U.S.A.
Email: volkerh@mcdb.ucla.edu
Chapter 2

Y. Tony Ip
Program in Molecular Medicine
University of Massachusetts
Medical School
Worcester, Massachusetts, U.S.A.
Email: Tony.Ip@umassmed.edu
Chapter 3

Haig Keshishian
Molecular, Cellular and Developmental
Biology Department
Yale University
New Haven, Connecticut, U.S.A.
Email: haig.keshishian@yale.edu
Chapter 10

Kiranmai S. Kocherlakota
Integrative Biosciences
Graduate Program
The Huck Institutes of Life Sciences
The Pennsylvania State University
University Park, Pennsylvania, U.S.A.
Chapter 8

Hsiu-Hsiang Lee
Brookdale Center for Developmental
and Molecular Biology
Mount Sinai School of Medicine
New York, New York, U.S.A.
Chapter 6

Louise Nicholson
Molecular, Cellular and Developmental
Biology Department
Yale University
New Haven, Connecticut, U.S.A.
Chapter 10

Michael V. Taylor
Cardiff School of Biosciences
Cardiff University
Park Place, Cardiff, U.K.
Email: TaylorMV@cf.ac.uk
Chapter 14

Mark Van Doren
Department of Biology
Johns Hopkins University
Baltimore, Maryland, U.S.A.
Email: vandoren@jhu.edu
Chapter 5

Jim O. Vigoreaux
Department of Biology
University of Vermont
Burlington, Vermont, U.S.A.
Email: jvigorea@uvm.edu
Chapter 12

K. VijayRaghavan
National Centre for Biological Sciences
Tata Institute of Fundamental Research
Bangalore, India
Email: vijay@ncbs.res.in
Chapter 11

Talila Volk
Department of Molecular Genetics
Weizmann Institute of Science
Rehovot, Israel
Email: lgvolk@wicc.weizmann.ac.il
Chapter 9

Noriko Wakabayashi-Ito
Program in Molecular Medicine
University of Massachusetts Medical
School
Worcester, Massachusetts, U.S.A.
Chapter 3

Stephane Zaffran
Department of Developmental Biology
Institut Pasteur
URA 2578 CNRS
Paris, France
Email: zaffrans@pasteur.fr
Chapter 6