The Genetics and Biology of DROSOPHILA

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10. Non-Sexual Behavior of *Drosophila*

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I. Introduction

A. Historical

The first publication to report use of *Drosophila* as an experimental organism dealt with the characterization of its behavioral responses (Carpenter, 1905). This is the first general survey of the non-sexual behavior of *Drosophila* since that time. For this reason, a number of older references have been included to indicate the antecedents of many current questions as well as to show the kinds of approaches that have been explored in the past. Additionally, these older reports do form the basis for much that is common knowledge in *Drosophila* laboratories. In the 70 years since Carpenter's work, the behavior of *Drosophila* has attracted the attention of workers in nearly every discipline of biology. The varied interests have incorporated a diversity of approaches and techniques including population sampling, the construction of ethograms and the development of instrumentation to record the electrical activity of single cells. The earliest work on non-sexual behaviour involved descriptions of reactions to a variety of stimuli. The effect of simultaneously presenting inputs of different sensory modalities was noted and found to be complex. Much of the work after that period used *Drosophila* as a test organism for analysing sensory input, especially visual input. The burgeoning of *Drosophila* genetics and systematics led to fragmentary reports, often incorporated in work of a different nature, concerning aspects of behavior. The past 20 years has witnessed use of *Drosophila* by workers interested in behavior *per se* and this period incorporated analysis of behavioral responses of a variety of activities. The relative ease with which various responses, such as phototaxis, can be quantified produced a literature on the measurement of the responses. More recent years have yielded analyses of the behavior of *Drosophila* species in the field and detailed analyses of sensory capabilities. Some of this latter work was a more sophisticated approach to responses used by earlier workers, but much of it represented a new approach based on the development of models to quantify input–output relationships of sensory mechanisms and motor activity. While mutants had been used over the years to explore aspects of behavior, or to quantify sensory input, the past few years have witnessed the use of mutations specifically induced in particular physiological systems subserving behavior. Underlying much of the work have been attempts to relate genetics and behavior, first at the level of how genetic lesions affect behavior and, more recently, the mode by which genes specify the neuronal interconnections responsible for motor output. Some studies have been couched in behavioral terms, others have not. The problems posed by earlier workers with respect to synergistic

effects and heteromodal summation of stimuli are now receiving new attention, with the use of behavioral mutants and more sophisticated modes of analysis.

B. Behavioral Analysis

A "simple" condition of behavioral analysis, the identification and quantification of the requisite stimuli and their processing to produce a motor response, has not been met for many aspects of *Drosophila* behavior. Analysis of visual input has used an experimental system wherein the turning tendency or torque produced by a tethered fly can be related to the width and number of alternate light and dark stripes, their movement across the visual field and the light intensity of the stripes. In this case the carefully defined visual input can be related to motor output to predict how the fly will move in a particular environment. Other behavioral measurements have not incorporated detailed stimulus specifications. Yet for many behaviors information is available on the limiting factors or boundary conditions for the expression of particular stimulus–response relations. The level of behavioral analysis varies from noting that particular wavelengths of light are not perceived, and consequently play no role in behavioral responses, to characterization of increased sensitivity to particular wavelengths as a result of central nervous system processing. The general problem of integrative mechanisms involves a range of phenomena which have not been quantified. How does the CNS process information concerning a partially full crop, high light intensity and the smell of food into movement of legs and wings? Are all factors equally weighted or is there a subtle nonlinear algebra which produces locomotion. At a simpler level, how does a foot dipped in sugar cause proboscis extension. At yet a simpler level, how did the tarsus know it was sugar?

Many terms have been used in the literature to characterize particular modes of response. Various kineses, or increases in activity, have been described, with orthokinesis referring to a general increase in activity with increasing stimulation and klinokinesis indicating an increased rate of random turning (which may have the effect of decreasing stimulation). The taxes, or directed reactions, include klinotaxis and tropotaxis referring to, respectively, comparison of stimuli on two sides successively or simultaneous comparison of stimuli by symmetrically placed receptors. Teletaxis implies fixation and orientation towards one source of stimulation while photo- and geotaxis imply orientation with respect to the appropriate source of stimulation. Menotaxis implies the maintenance of a constant visual input by appropriate orientation. The prefixes hygro- and chemohave been used to denote random or directed movement with respect to

water or chemicals and thigmotaxis has been used to refer to the effect of contact with an object *per se*. These terms are used here to a limited extent since their use does permit quick reference to a more or less defined component. These terms, however, do not suggest a mechanism or an approach to analysis of a mechanism.

Analysis of some responses has involved use of appropriate instrumentation or modes of analysis which will be noted at the appropriate point. In spite of the range of analyses, there are aspects of *Drosophila* behaviour that are relatively untouched by physiological probing of the sensory basis of the behaviour or by a descriptive analysis of the response patterns.

C. Scope of Discussion

The literature survey is fairly inclusive and was completed in June, 1976. Many items that were of a preliminary nature and were subsequently presented in detail have not been noted. This is less true of some of the older literature. Where possible, the sensory input and central nervous system processing of information have been discussed together and in conjunction with available information on the genetic contribution to a particular facet of behavior. Where information on *Drosophila* is lacking for specific aspects of behavior, information gained from other higher Diptera has been used to assist in a more coherent presentation of non-sexual behavior. Unless otherwise stated all discussion pertains to *D. melanogaster*.

Data gained from one species has been used, in the literature, to interpret information derived from another species. There are many species of *Drosophila*. While species may share a physiological similarity, the expressed behavior in a particular environment may not be the same, even for closely related species An attempt has been made to indicate the species involved in any particular analysis. In some cases this has meant stipulating generic or subgeneric classifications. It is sufficient to note here that the genus *Drosophila* as well as several closely related genera each contains several subgenera.

Many aspects of non-sexual behavior are clearly related to sexual behavior, in terms of both sensory capabilities and integrative mechanisms. These have been discussed in the chapter on sexual behavior (see Chapter 11). An example is audition, which is more appropriately discussed under courtship behavior.

The link between physiological mechanisms and behavior is quite close and discussion of physiological analyses is included in the chapters dealing with *Drosophila* physiology. Included there are discussions of visual system mutations as well as the detailed presentation of electro-

physiological analysis for those systems where information is available.

The ubiquity of circadian rhythms has been noted in laboratory and field studies of many species of *Drosophila*. The literature on field studies alone reflects the importance of this factor in the observed activity patterns. This topic is discussed in a separate chapter. The central position occupied by *Drosophila* in genetics for many years has not diminished. Both population biology and neurobiology can claim *Drosophila* as its own and each can benefit from the others claim. The study of habitat selection or dispersal cannot be done in a vacuum of knowledge concerning the capabilities of the organism which is dispersing. By the same token, a knowledge of the environment and evolutionary history of an organism can produce a clearer understanding of the mechanism undergoing analysis. Since they both converge on *Drosophila*, both areas of biology can benefit from the breadth of one approach and the focus of the other.

II. Sensory Input

A. Vision

Drosophila has a visual system capable of detecting light intensity, discriminating among wavelengths of light, and discerning patterns. Many aspects of *Drosophila* behavior are closely mediated by its visual system. In this it is quite similar to other higher Diptera which have contributed to an understanding of visual function and information processing in the compound eye. An overview of visual physiology and its consequences for neural model building with respect to information flow and motor control is presented elsewhere (Pak and Grabowski, Ch. 9). Much of this information has been acquired through quantification of behavioral responses to well-defined visual stimuli in either tethered or freely moving flies. These data differ from those produced by phototactic assays in the degree to which the stimulus is defined with respect to spatial organization and movement in the visual environment. Phototaxis permits a fly to distinguish relative intensity and wavelength variables but not those variables requiring perception of pattern. Behavioral measurement of contrast or pattern perception, since it relies on properties of the visual system itself, is relatively free of the problems associated with the several biological variables attendant in phototaxis assays. In some cases the measurement can be made with the responding fly immobilized in position.

The visual behavior of *Drosophila* has been characterized by phototaxis, optomotor response, fixation and pattern contrast measurements. Heisenberg (1972) has used different assays of visual function to discriminate between mutants that appear similar in their abnormal electroretinograms.

Fast phototaxis implies relatively rapid movement and choice among alternate light intensities (see Phototaxis). The slow phototaxis used by Heisenberg allows flies 24 h to choose among stimulus intensities (Heisenberg and Gotz, 1975). Use of 24 h intensity preference tests could discriminate among mutant strains, whereas these strains behaved similarly in "fast phototaxis". Other assays measure the capability of the system to respond even with movement of the fly, and may consequently be useful in characterizing species or strains with greater precision than phototaxis. Hengstenberg and Gotz (1967) were able to elicit mutant eye responses from wild type eyes with appropriate stimulus conditions, illustrating the level of understanding that exists with respect to certain stimulus parameters and their visual processing. In a sense, the closer the behavioural assay is to the physiological system underlying the behavior, the closer the approach to comprehension of the mechanism involved. On this basis, Gotz (1968) has presented a minimum model for the neural control of the responses subserving movement control by vision.

1. Characteristics of the Drosophila *visual system*

In the case of the compound eye the visual surface consists of a number of elements, or ommatidia, each one of which consists of eight receptor cells. These receptor cells are organized into two central (R 7/8) and six peripheral (R 1–6) cells with each group of cells having different spectral sensitivities and neuronal connections. The visual unit that looks at a point in the visual field is at the level of the optic cartridge in the first optic ganglion where receptor cell (R 1–6) information converges. Phototaxis has been used as an assay procedure to determine that *D. melanogaster* can see and react to ultraviolet light (but less well to the red end of the spectrum; Lutz and Richtmeyer, 1922; Lutz and Friesewood, 1934; Bertholf, 1933; Brown and Hall, 1936; Medioni 1959a) as well as being able to detect and react to plane polarized light by aligning the body axis parallel to the plane of the light (Stephens *et al.*, 1953). This latter effect was not noted at low light intensities and may suggest that retinula cells R7 and R8, the high acuity visual input system (Heisenberg, 1972), serves to process polarized light. A number of other workers have used the relative strength of phototactic response to determine the action spectrum of *D. melanogaster* (Fingerman, 1952; Fingerman and Brown, 1953; Wolken *et al.*, 1957; Wehner and Schumperli, 1969; Schumperli, 1973).

Flies presented with a choice of phototaxis to white and monochromatic light of varying intensities were unable to discriminate colors at low light intensity. The choice of a particular wavelength at higher intensities, when given a choice of monochromatic lights of the same energy content reveals

which wavelength is perceived most readily since that wavelength will elicit a response at lower intensity. Schumperli (1973), using such an equal energy spectrum (where the problem of spurious effects of differential energy, e.g. heat from infra red wavelengths, are removed), suggested that *D. melanogaster* had color vision. In his single fly phototaxis system, one peak was in the UV (350 nm) and another in the green (500 nm). These peaks reside in the peripheral retinula cells (R1–6), or high sensitivity system of the ommatidium, while a blue–green peak (475 nm) resides in the central (R7 and R8) retinula cells (high acuity system) of the ommatidium (Heisenberg, 1972; Alawi *et al.*, 1972). A shift of the spectral sensitivity of the green peak to a shorter wavelength was observed with increasing intensity (Schumperli, 1973) which suggested the presence of different visual pigments at different intensities. A shift in spectral sensitivity had been noted by earlier workers (Fingerman and Brown, 1952) who noted its similarity to the change from cone to rod vision in vertebrates at low light intensity. Current understanding of the photopigments in the eight cells of each ommatidium in the fly eye suggests that there are three different receptor types in the eye (see Stark *et al.*, 1976). It may be stressed here that the photopigments are not the screening pigments (the ommochromes and pteridines that impart the characteristic color to the *Drosophila* eye). The photopigments are in the rhabdomere portion of each of the eight receptor cells in each ommatidium. Peripheral receptor cells 1–6 (R1–6) contain a pigment whose spectral sensitivity peaks at 470 nm while central cell 7 (R7) has a pigment that peaks at 370 nm and is a UV receptor. Short wavelength and ultraviolet adaptation converts these nonbleaching visual pigments into a stable metarhodopsin, which is the termination of the light initiated reaction. The rhodopsin of R1–6 is converted to a metarhodopsin that peaks at 570 nm and R7 rhodopsin is converted to a metarhodopsin that peaks at 470 nm. If rhodopsin (*R*) and metarhodopsin (*M*) absorption spectra differ, then high intensity stimulation with an appropriate wavelength will convert *R* to *M* or *M* to *R* (see Minke *et al.*, 1975; Stark *et al.*, 1976). The third type of receptor cell, R8, possesses yet a different pigment which either interconverts *R* and *M* very rapidly or has no separate states for its photopigment. Different genera of flies do have different adaptation responses for their photopigments. These results are in good agreement with electrophysiological measurements (Minke *et al.*, 1975; Meffert and Smola, 1976) in showing three different receptor types in flies eyes. Of these two complementary visual input systems, the central cells, specialized for optimal contrast transfer, are 20–45 times less sensitive to light than the peripheral retinula cells. The early work suggesting color vision with perhaps two color receptors, one in the UV and one at about 500 nm (Fingerman and Brown, 1953; Bertholf,

1933; Wolken *et al.*, 1957), has thus received substantial confirmation with more sensitive measurement of some of the same behavioral responses. However, three receptor types are present. Flies thus have the capability for trichromatic color vision. This system may be mediated through adaptational control of the separate inputs of the three receptor types. It is not clear whether flies make use of color information or over what range of light intensity color vision may play a role in behavior. Schumperli (1973) states that the absolute threshold of choice behavior is 3×10^{-3} ergs sec^{-1} cm^{-2} in the ultraviolet region of the spectrum.

In a light-adapted eye, tiny pigment granules, the screening pigments, move in the cytoplasm of R1–6 and cluster along the wall of the rhabdomeres (Franceschini and Kirschfeld, 1976). They attenuate light impinging on the photopigment and the attenuation spectrum matches that of the ommochrome pigment. These granules thus act as a scotopic pupil at low light levels. Similarly, there is an effective photopic pupil in R7 which attenuates light for R7 and R8. The threshold for the photopic pupil is 2 decades higher than the scotopic pupil at a light intensity where the scotopic pupil is saturated. This photopic pupil saturates at a light intensity 1–2 decades above threshold. The threshold of the scotopic pupil appears to be 3–5 decades higher than the absolute threshold for movement perception. The *D. melanogaster* mutant w^a has only a scotopic pupil while ommochrome deficient mutants, e.g. *v*, *cn*, lack both types of pupil. After 1 h of darkness, high light intensity can close the scotopic pupil within 10 sec and the photopic pupil in no less than 30–60 sec. Pigment migration of the granules in the peripheral retinula cells occurs with a time constant of 1·75 sec at a light intensity about 10^4 that of threshold (Schumperli, 1973).

Much of the early work used various eye color mutants to characterize responses to different wavelengths and ascertained that the more pigmented the eye the stronger the photoresponse that could be elicited (McEwen, 1918; Brown and Hall, 1936; Scott, 1943; Fingerman, 1952). Mutants used in these experiments are listed in Table I. Few of these experiments controlled either light intensity or adaptation of the eye. It is clear that the properties of the visual system must be taken into account in evaluating the response of flies to visual stimuli. Many cases of fast phototaxis operate in a time frame where adaptational characteristics could alter the photoresponse of flies. It is also clear that some mutations would permit abnormally high light stimulation to occur and thus may disturb the integrative mechanisms involved in establishing a coherent motor output, or behavior of a a fly. There has been little work aimed at establishing the extent to which aberrant sensory input of one modality can perturb heteromodal stimulus summation.

TABLE I[a]. Tabulation of morphological mutants tested for a behavioural trait in *D. melanogaster*.

Gene symbol	Gene name and location	Phenotype	Observed effect	Reference
al	aristaless 2–0·01	aristae reduced	No effect on wing beat frequency.	Williams and Reed, 1944
ant	antennaless 2–?	antennae missing	Poor response to chemical stimuli; Humidity response opposite to Wild Type. Temperature response normal. Respond to repellent.	Begg and Hogben, 1946 Becker, 1970
**Antp*^{LC}	Antennapedia 3–? of Le Calvez	arista and antenna malformed	Flight and wing motion absent.	Williams and Reed, 1944
Antp^{B}	Antennapedia of Bacon 3–48	antenna replaced by leg cuticle	Leg tarsi with normal response to sugar stimulation; antennal leg not responsive.	Deak, 1976
b	black 2–48·5	body, tarsi and wings darker	Optomotor response normal. ERG normal Locomotor activity reduced.	Kalmus, 1943 Hotta and Benzer, 1969
B	Bar 1–57·0	eyes narrow	Optomotor response reduced; phototaxis reduced.	Kalmus, 1943; Hecht and Wald, 1934; Medioni, 1959a, b; Durrwachter, 1957; Brown and Hall, 1936.
			Locomotor activity reduced.	Elens, 1965b
			Wing beat frequency normal; larvae feed more slowly than wild type.	Williams and Reed, 1944 Bakker, 1961.
**bc*	buckled 2–?	wings twisted and curled	Cannot fly; can beat wings.	King, 1948
bi	bifid 1–6·9	wing veins fused at base	No hypoplasia of t.-a. ganglion. Flight weak and erratic.	Power, 1950 King, 1948
Bld	Blond 1– or 2–	bristles yellow at tips	ERG normal	Hotta and Benzer, 1969

TABLE I.—(*continued*)

Gene symbol	Gene name and location	Phenotype	Observed effect	Reference
bs^{2}	blistered 2–107·3	wings blistered;	Can beat wings and take off.	King, 1948
bs^{cy}	blistered—curly	vesiculated and curled up	Flight absent, if wing severely affected.	
bw	brown 2–104·5	eye lacks red pigments	Optomotor response normal.	Kalmus, 1943
			Phototaxis normal.	Fingerman, 1952
			Preference for green oviposition substrate.	Volpe *et al.*, 1967
			Phototaxis superior to *w*.	Scott, 1943
bx	bithorax 3–58·8	metathorax mesothoracic; halteres enlarged	Flight ability lost in severe expression; halteres motionless.	Williams and Reed, 1944
bx^{34e}			Will not fly; no hypoplasia of t.–a. ganglion.	Power, 1950
			*Hyper*plasia of t.–a. ganglion.	Chiarodo *et al.*, 1971
c	curved 2–75·5	wings curved downward	Can beat wings erratically; stroke amplitude reduced.	Williams and Reed, 1944
			Cannot fly.	King, 1948
			Flight absent; no hypoplasia of t.–a. ganglion.	Power, 1950
ci	cubitus interruptus 4–0	wing vein L4 has gaps	Flight restricted; reduced wing beat frequency in combination with *ey*.	Williams and Reed, 1944
cl	clot 2–16·5	eye color dark maroon	Significant preference for clumped oviposition.	Gress and Nickla, 1973
cn	cinnabar 2–57·5	eye color bright red	Wing beat frequency increased.	Williams and Reed, 1944
			Optomotor response normal.	Kalmus, 1943
ct	cut 1–20·0	wings cut to points; edges scalloped.	Wing beat frequency increased.	Williams and Reed, 1944
			Flight normal.	King, 1948
ct^{6}		lacks pleiotropic effects of *ct*	No hypoplasia of t.–a. ganglion.	Power, 1950; Chiarodo *et al.*, 1971
cu	curled 3–50·0	wings curved upward	Phototaxis reduced.	McEwen, 1918; Durrwacht, 1957
			Flight absent.	King, 1948
			No hypoplasia of t.–a. ganglion.	Power, 1950
cv	crossveinless 1–13·7	wing crossveins absent	Wing beat frequency reduced.	Williams and Reed, 1944
Cy	Curly 2–6·1	wings curled upward	Occasional rapid, inconsistent wing stroke; no sustained flight.	Williams and Reed, 1944 King, 1948
			No hypoplasia of t.–a. ganglion.	Power, 1950; Chiarodo *et al.*, 1971
dp^{ov}	dumpy-oblique vortex 2–13·0	wings reduced; oblique	Can beat wings; do not fly.	King, 1948
dp^{ovdr}	dumpy-oblique vortex drumlins	more pronounced vortex effect	Can beat wings; do not fly.	King, 1948
e	ebony 3–70·7	body color black	Phototaxis reduced.	Durrwachter, 1957
			ERG lacks on and off transients (*e* and *e*^{11}).	Hotta and Benzer, 1969; Grossfield and Pak, 1971
			Optomotor response normal.	Kalmus, 1943
			Locomotor activity reduced.	Elens, 1957, 1965a
			Least active of tested strains using old flies.	Elens 1972a
			Selection for phototaxis more effective using old (30 day) flies.	Elens 1972b
			More active in tube maze.	Spatz *et al.*, 1974
ec	echinus 1–5·5	eyes rough and bulging	No reduction in optomotor response.	Kalmus, 1943
ey	eyeless 4–2·0	eyes reduced	Flight restricted; reduced wing beat frequency in combination with *ci*.	Williams and Reed, 1944
			Reduction of facet number to half shows decreased optomotor response.	Kalmus, 1943

TABLE I.—(*continued*)

Gene symbol	Gene name and location	Phenotype	Observed effect	References
fa	facet 1–3·0	eyes rough	No reduction of optomotor response	Kalmus, 1943
fu	fused 1–59·5	wings extended, veins fused, ocelli reduced	Normal phototaxis	Benzer, 1967
g	garnet 1–44·4	eye color purplish ruby	Response to repellent identical to wild type	Becker, 1970
gl	glass 3–63·1	eyes reduced facets fused	Wing beat frequency increased.	Williams and Reed, 1944
			ERG absent.	Pak *et al.*, 1969
Gl	Glued 3–41·4	eyes rough, facets fused	ERG absent.	Grossfield, unpublished
			Eyes and optic lobes abnormal.	Power, 1950
L	Lobe 2–72·0	eyes smaller, nicked	Wing beat frequency reduced.	Williams and Reed, 1944
lt	light 2–55·0	eye color yellowish pink	Oviposition pattern as in wild tupe	Gress and Nickla, 1973
Ly	Lyra 3–40·5	wings excised	Flight absent; no hypoplasia of t.–a. ganglion.	Williams and Reed, 1944 Power, 1950
lz	lozenge 1–27·7	eyes narrow, rough	ERG normal	unpublished
m	miniature 1–36·1	wing size reduced	Wing beat frequency increased.	Williams and Reed, 1944
			Flight restricted or absent.	King, 1948
Ns	Nasobemia 3–48	antenna replaced by leg	Leg tarsi with normal response to sugar stimulation; antennal leg not responsive.	Deak, 1976
nub	nubbin 2–47·0	wings small	Poor phototactic response	Benzer, 1967
oc	ocelliless 1–23·1	ocelli absent	Normal phototaxis	Benzer, 1967
Rev^{B}	Revolute of Bridges 2–?	wings spread and curled	Wing beat feeble; flight absent.	King, 1948
s	sable 1–43·0	body color dark	ERG normal.	Hotta and Benzer, 1969
Sb	Stubble 3–58·2	bristles short	Can beat wings; flightless in combination with *Gl*.	King, 1948
			No hypoplasia of t.–a. ganglion.	Power, 1950
se	sepia 3–26·0	eye color brown; darkens with age	Wing beat frequency normal.	Williams and Reed, 1944
			Phototaxis increased.	Fingerman, 1952
			Pattern contrast normal.	Hengstenberg and Gotz, 1967
			Visual orientation normal.	Wehner *et al.*, 1969
			Dispersal activity same as wild type.	Wallace, 1970
			Dispersal stimulated by presence of flies of other strains.	Narise, 1974
so	sine oculis 2–57·1	ocelli absent; eye as groups of ommatidia	Optomotor response normal, phototactic response poor.	Gotz, 1970; Benzer, 1967
spa^{pol}	sparkling-poliert 4–	eyes small, smooth	ERG absent.	Grossfield, unpublished
sr	stripe 3–62·0	dark median stripe on thorax	Cannot fly; motor output abnormal.	Levine and Wyman, 1973
ss^{a}	spineless, aristapedia 3–58·5	antennae tarsus-like	Flightless; no hypoplasia of t.-a. ganglion.	Power, 1950
			Olfactory response reduced, humidity response stronger, temperature response poor.	Begg and Hogben, 1946
			Leg and antennal tarsi with similar response to sugar stimulation; both insensitive to salt inhibition of response.	Deak, 1976
stw	straw 2–55·1	hair's yellowish	ERG normal.	Hotta and Benzer, 1969
stw^{5}		wings thin and warped	ERG normal.	Hotta and Benzer, 1969
stw^{D}		body also yellow: wings thin and curled	Can beat wings; flight absent.	King, 1948
svr	silver 1–0·0	color of legs, wings, body pale and silvery	ERG normal.	Hotta and Benzer, 1969

TABLE I.—(*continued*)

Gene symbol	Gene name and location	Phenotype	Observed effect	References
t	tan 1–27·5	body color tan	Not positively phototactic.	McEwen, 1918
			More photopositive than wild type.	Hadler, 1964a
			ERG lacks "on" and "off" transients.	Pak *et al.*, 1969; Hotta Benzer, 1969
			Light response poor.	Benzer, 1967
tx	taxi 3–91	wings held out; narrow	No wing motion; flight absent.	Williams and Reed, 1944
			No hypoplasia of t.–a. ganglion	Power, 1950; Chiarodo *et al.*, 1971
v	vermilion 1–33·0	eye color scarlet; no brown pigment	Phototaxis reduced.	Fingerman, 1952
			Optomotor response equal to wild type.	Kalmus, 1943
			Preference for blue oviposition substrate.	Volpe *et al.*, 1967
vg	vestigial 2–67·0	wings reduced to vestiges	Optomotor response good; phototaxis reduced.	Kalmus, 1943; Durrwachter 1957; McEwen, 1918,
			Locomotor activity reduced.	McEwen, 1925.
			Cannot fly.	Power, 1950; Williams and Reed, 1944
			Certain alleles reared at high temperatures can fly.	Harnly, 1941
			No hypoplasia in t.–a. ganglion.	Power, 1950
			*Hyper*plasia of this ganglion.	Chiarodo *et al.*, 1971
			Preening identical to wild type.	Szebenyi, 1969
			Dispersal activity stimulated by presence of wild type.	Narise, 1966
w	white 1–1·5	eye pure white	Some alleles increase wing beat frequency; locomotor activity reduced.	Williams and Reed, 1944 Elens, 1965b
			Phototaxis reduced.	Brown and Hall, 1936; Scott 1943; Fingerman, 1952
			Optomotor response reduced; poor contrast perception, longer orientation time.	Kalmus, 1943; Wehner *et al.*, 1969
			Less responsive to pattern contrast.	Hengstenberg and Gotz, 1967
			Certain elements of cleaning activity reduced or enhanced.	Bennett and Hughes, 1971 Bennett and Walke, 1970
			Oviposition pattern as in wild type.	Gress and Nickla, 1973
			Doesn't show normal increase in preening in groups.	Connolly, 1968
w^a	white-apricot	eye yellowish-orange	Less response to pattern contrast but better than *w*.	Hengstenberg and Gotz, 1967
				Wehner *et al.*, 1969
				Kalmus, 1943
			Phototaxis reduced.	Fingerman, 1952
			Dispersal activity influenced by presence of other strains.	Narise, 1974
y	yellow 1–0·0	body color yellow	Locomotor activity reduced.	Burnet and Connolly, 1974
			Optomotor response normal.	Kalmus, 1943
			ERG normal (*y* and y^2).	Hotta and Benzer, 1969
			Phototaxis to UV and white light better than wild type	Medioni, 1959a, b
			Oviposition rate as in wild type.	Parsons, 1968

TABLE I.—(*continued*)

Gene symbol	Gene name and location	Phenotype	Observed effect	References
v;bw		eyes white	Optomotor response reduced.	Kalmus, 1943; Burnet *et al.*, 1968
			Phototaxis reduced	Kikkawa, 1948
			Restoration of visual acuity by feeding kynurenine.	Kikkawa, 1948; Burnet *et al.*, 1968; Connolly *et al.*, 1969
cn bw		eyes white	Optomotor response reduced.	Kalmus, 1943
			Reduced dispersal except when with w^+ flies.	Narise, 1974

[a] Arranged alphabetically by gene symbol. A question mark indicates that the mutation is inseparable from a rearrangement or has not been mapped. Mutants unavailable as an existing strain are marked with an asterisk. Abnormalities are presented relative to wild type. Studies of the degree of hypo- or hyperplasia of the thoracico-abdominal (t.-a.) ganglion have involved multiply mutant stocks.

2. Optomotor response

Hecht and Wald (1934) exploited the reflex of many insects to follow angular motion of objects in their visual field to measure the threshold and visual acuity of *Drosophila*. Determinations were made by moving a vertically striped pattern past a fly in a horizontal cell and noting the combination of intensity and pattern that elicited a response. The number of stripes could be varied to yield narrow striped patterns to find the minimum angle subtending the eye to which a fly would respond. The frequency of the stripes determines the wavelength of the pattern and the proportion of 360° subtended. The interommatidial angle was determined as roughly 4·3°. The finding that the maximum acuity occurred at ~9·3°, indicated that at least two ommatidia, or the neural representation of them in higher order cells, must be involved in motion detection. The entire visual field is covered by a network of movement detectors each consisting of at least two visual elements which can be sequentially exposed to a change of light intensity. Movement detection requires non-linear interactions among these elements. The reactions of the fly in terms of thrust or torque responses depend on the angular velocity (ω) and distance (λ) of a repeated event, e.g. stripe pattern. Maximum response occurs when the frequency of the event $\omega/\lambda \sim 1\ \text{sec}^{-1}$ (Heisenberg and Gotz, 1975)

This opotomotor response is part of a motion control system which relies on visual input. The minimum light required to elicit response is the threshold intensity and the visual acuity is a measure of the resolving power of the visual surface.

The tendency of a fly to follow movement can be determined by placing the fly in a chamber at the center of a rotating striped cylinder (Kalmus, 1943, 1946, 1948). If a fly perceives the movement of the stripes it responds by turning in the direction of their movement. Kalmus determined the effect of a number of mutations on the ability of three species of *Drosophila* to follow movement (see Tables I and II). He noted poor response at 15°C or below and found that reduction of the number of ommatidia or irregularity of the facets decreased optomotor response, as did deficiencies in the amount of screening pigments, e.g. in the mutants *w* or *v;bw*. Restoration of visual acuity in *v;bw* flies can be accomplished by feeding kynurenine to larvae and bypassing the metabolic block imposed by the failure of *v;bw* flies to synthesize the brown (ommochrome) pigments (Kikkawa, 1948; Burnet *et al.*, 1968).

In-flight measurement of the optomotor responses of pigment deficient mutants, using tethered flies, has demonstrated the extent to which equally illuminated eyes actually receive light with and without facet-separating pigments (Hengstenberg and Gotz, 1967). The photoreceptors

TABLE II. Mutations used for behavioral studies in other species of *Drosophila*.

Species	Mutant	Observed effect or usage	Reference
D. pseudoobscura	*or* (orange eye)	Measurement of dispersal rate	Dobzhansky and Wright, 1943, 1947
	w^5 (white eye)	No optomotor response	Kalmus, 1943
	gl (glass eye)	Measurement of activity in a maze	Levine and Kessler, 1965
D. persimilis	*or* (orange eye)	Measurement of activity in a maze	Levine and Kessler, 1965
D. subobscura	*bg* (bulging eye facets)	Optomotor response normal	Kalmus, 1943
	ch (cherry eye color)	Decrement in pattern contrast	Wehner *et al.*, 1969
	ey (eyeless, decreased facets)	No optomotor response if less than a dozen facets	Kalmus, 1943
	lrd (light red eye)	Decrement in pattern contrast	Wehner *et al.*, 1969
	ma (maroon eye)	Pattern contrast normal	Wehner *et al.*, 1969
		Optomotor response normal	Kalmus, 1943
	pl (plum eye)	Pattern contrast normal	Wehner *et al.*, 1969
	pn (prune, diffuse eye pigment)	Reduced optomotor response	Kalmus, 1943
	pr (poppy-red eye)	Pattern contrast normal	Wehner *et al.*, 1969
		Optomotor response normal	Kalmus, 1943
	r (rough eye)	Optomotor response normal	Kalmus, 1943
	s (scarlet eye)	Optomotor response normal	Kalmus, 1943
D. willistoni	Hairless	Measurement of dispersal rate	Burla *et al.*, 1950
D. funebris	*st* (eye) and *ri* (wing)	Measurement of dispersal rate	Timofeeff-Ressovsky and Timofeeff-Ressovsky 1940
D. virilis	veinlet	Measurement of dispersal rate	Gershenson, 1941

wild type, *se*, w^a, and *w* receive light in the ratio 1:1:7:19. Thus the *w* utant receives 19 times more light than the wild type or *se* eye. Additionally, pigment deficient mutants are less sensitive to pattern contrast when ht adapted than either wild type or *se*. When dark-adapted, *w* and w^a more sensitive than pigmented eyes to flash intensity. The sensitivity the receptors and the half-peak width of their visual fields are not ected by the degree of pigmentation.

The degree to which *Drosophila* uses vision in flight control was demon- ted using an elegant experimental system (Gotz, 1968). A fly is mounted a transducer capable of measuring the torque or force generated by its empts to turn and follow movement. Mounted on either side of the fly projection screen capable of presenting moving stripes at any angle. side can be simulating back to front movement (regressive) and the er side front to back (progressive). With this stimulus environment the will attempt to turn and follow the angular movement of the stripes. es react to both vertical and horizontal movement by trying to reduce the tive velocity of the stimulus pattern. Vertical displacement of the mulus produces alteration of the force of flight while horizontal displace- nt is modulated by changing flight torque. These reactions allow tude and course control during free flight. If both screens are presenting nt to back movement the forward thrust of the fly can be measured using ifferent meter. Both eyes are equally sensitive to pattern motion in any ection and the motion detecting units can discriminate between pro- ssive and regressive motion. Each eye is capable of independently trolling the wing beat amplitudes of the ipsilateral and contralateral ng. These two kinds of stimuli elicit opposite reactions from the flight tem. Progressive movement is generally a stronger stimulus. Further tails pertaining to visual control of flight and walking are discussed under ocomotion" (Section IV, F).

3. *Visual fixation and pattern discrimination*

ptomotor response mechanisms suggest that the detection of movement not a property of specific zones of the visual field (see Reichardt, 1969), t rather movement stimuli everywhere in the visual surround can elicit em. A tethered fly orienting preferentially towards a black stripe on a hite background shows visual fixation, where the fixation is a function specific areas of the visual field. Pattern recognition or form perception o depends on specific parts of the visual field. A fly can detect small jects (equal to fly size) in front of a randomly contrasting background the object moves slightly (Heimburger *et al.*, 1976). This case of figure- round discrimination is interpreted as requiring nonlinear inhibitory

interactions among neural elements. A dark target on a bright background is fixated and tracked by a flying fly (Wehrhahn and Poggio, 1976). The delay time in behavioral response to a displacement of the target is of the order of ~20 milliseconds. Artificial perturbation of the delay time may allow insight into how control system information is processed.

A different assay of contrast perception has used a cylindrical drum (180° black, 180° white) in which flies were allowed to run spontaneously from the center towards the black and white areas (Wehner *et al.*, 1969). The path of each fly was determined, within 10°, at four distances from the center as it ran to the periphery. A number of mutants of *D. melanogaster* and *D. subobscura* were tested (see Tables I and II). A preference for the black area and the contrast line was correlated with the amount of screening pigment in the compound eye. The stimulus efficiency of this portion of the drum was 1:1·4:2·8:3·5 for *w*, w^a, wild type and *se* respectively, in *D. melanogaster*. The mean orientation times were, in the same order, 17:5:1:1. In contrast to wild type and the other mutants, the over-pigmented mutants (e.g. *se*) of both species showed the maximum of the distribution curve shifted 10° to the black area rather than coinciding with the contrast line at the interface of black and white areas.

Freely moving flies thus show the same decrease in contrast perception, when light intensity at the receptors increases due to loss of screening pigments, as the immobilized flies tested with moving patterns. Any behavior requiring intensity discrimination and form or contrast perception in moving or stationary flies can be expected to be affected by extreme loss of the screening pigments, which serve to visually separate ommatidia within the compound eye.

Flies were allowed to spontaneously run inside a cylindrical white drum towards a black area of varying width and subtending different angles by virtue of varying height (Wehner, 1972). The maximum reaction shifted from the center of the black area to the contrast line as a black stripe stimulus was incrementally increased in height. Black areas more than 30° high elicited maximum response when more than 180° wide. To maintain a constant response of the flies, the vertical contrast lines had to be increased in length as the width of the black area decreased. Wehner suggests that this indicates a topological representation of the visual field within the visual system, and that different parts of the visual field are of unequal importance for form perception. Wehner and Wehner-von Seqesser (1972), using a similar apparatus for presenting vertical and horizontal black stripes to freely moving flies, found a preference for vertical stripes. By using different pattern wavelengths these workers were able to calculate a receptor spacing of 4·8° and suggested the vertical stripe preference to be a mechanism of locomotor movement control. Flies showed only phototaxis,

with no pattern preference, if the stimuli were presented on a ground glass screen which served to diffuse the light. Thus it was also suggested that pattern recognition requires a minimum ratio of overall light intensity to the light intensity of a perceivable pattern. Work with *Calliphora* (Jander and Schweder, 1971) has suggested the same characteristics as requisite for target orientation, namely: dark contrasting area, vertical contrast edge and disruption of shape. The difference between the stimulation of any area of the eye by movement, and the processing of fixation and form contrast stimuli depending on their position in the visual field, has been found for other higher Diptera as well.

Fixed flying *Musca* in an apparatus where the lift force of flight of the fly was able to move a vertical panorama, demonstrated that the two eyes of the fly are perceptually additive in a dynamic system (Wehrhahn and Reichardt, 1975). Wehrhahn (1976), working with *Musca*, suggests that the central cells R7/8 are necessary for height orientation and probably for pattern-induced flight orientation.

4. *Perturbations of visual behavior*

A number of agents are capable of interfering with normal visual function at the cellular level. These include various drugs and gases. Many effects produced in this fashion are understandable on the basis of visual physiology. Also in this category are the effects of light adaptation. Flies that are physiologically dark adapted will show a higher sensitivity to light and the intensity of the light may determine which types (high acuity or high sensitivity) of cells in the visual system are detecting the light at any point in an experimental system. Dim light may only excite the high sensitivity cells which have a different spectral sensitivity than the high acuity cells. Sensitivity to heat or infra-red radiation, not detected via the visual system, may give spurious effects.

Other effects on the visual system clearly need more work before they can be ascribed to visual input. The jumping response of certain strains to a light-off stimulus (Nakashima-Tanaka and Ogaki, 1970), involving interaction of genes on the same chromosomes carrying markers rendering the eye white, may be a result of pigment deficiency accentuating a normal escape response to bright light. Since this behavior involves gene interaction, the analogy made with it and the stn^{ts} single gene mutants may not hold. The stn^{ts} mutants jump with a similar stimulus. The neural circuitry tying visual imput to movement is complex, and inundation with bright light may produce a variety of effects in strains with varying thresholds at relevant control points.

At the population level, Koch (1967) has demonstrated that orientation

of flies in the field involves the same stimuli elucidated in studies of form perception in laboratory measurements. Chabora (1969) has noted that the emigration behavior of *Phaenica* yellow eye mutants is apparently dependent on their response to an exit opening, and Connolly (1968) has noted that pigment-deficient flies are insensitive to the presence of other individuals with respect to preening.

It may be anticipated that assays more directly related to visual function will become part of the armamentary of those investigating behavioral differences between populations, as well as of those investigating the capability for locomotion and dispersal of different species.

In summary, differences in photoresponse may represent the variation seen in measurements of threshold illumination or in sensitivity of central and peripheral retinula cells. Changes in sensitivity can also be mediated at the level of the central nervous system, where integrative processes can alter responses as well. Measurements of tethered flies have indicated that a fraction of a population does not respond to progressive movement of a striped pattern, which suggests the reality of photoresponse variation at integrative levels in a wild type population.

Differential characterization of visual system mutations, using a variety of visual assays (Heisenberg, 1971a, b, 1972; Heisenberg and Gotz, 1975), demonstrates that perturbations of visual function at integrative levels can be detected and quantified. The response of flies to pattern contrast stimuli, both moving and stationary, provides a basis for visual preference assays and underscores the differential processing of information by different parts of the CNS. Edge perception, while a variable in a maze assay, is nonetheless a measure of photoresponse. The problem lies in the unification of the stimulus with the response. Preference tests for intensity demonstrate the existence of a comparison network or reference point in CNS processing. It may well be that the comparator is set at different points (= different light intensities) in different members of a population, providing a basis for differential choice behavior by mutants of *D. melanogaster* where circuitry or processing may be impaired. Wild type individuals of other species may thus possess natural variation in the cumulated subsystems which is subject to selection. Mutations may cause a partial block in information flow while variation may exist in gate points for response. Alteration of information flow can result from stress perturbations of CNS sensitivity as illustrated by differences in "at rest" and "disturbed" photoresponses as is discussed in section IV, A on "Phototaxis". The sensitivity setting of the CNS to stimuli that is noted for chemoreception and the central excitatory state (see "Feeding Behavior", Section IV, I) that exists for proboscis extension may be analogous to this kind of differential setting.

The link between visual input and motor control with respect to both walking and flying is quite strong in *Drosophila*. Bright light produces negative kinesis, then inhibits movement and finally produces an escape response. High intensity stressful stimulation of several mutants results in a jumping response. The disturbed condition thus respresents an accentuation of a normal response or a change in the processing tie-in to the effector system. The threshold for the effector control may involve processing through a network which is bypassed in a stress response.

The existence of a less drastic kinetogenic response to light off stimuli as part of the normal behavior in other species and some strains of *D. melanogaster* suggests that the response be viewed as part of a continuum rather than as an isolated phenomenon. The mutations (see "Mutations Affecting Behavior", Section IV, M) may alter the sensitivity or processing of the normal network. The general point emerges that stress may elicit a component of the repertoire not usually observed. Mutations provide discrete alterations of a continuous process involving several subsystems. The types of analyses performed for characterization of the visual control of flight and of pattern perception were performed on individuals. The information gained provides baseline knowledge which contributes significantly.

The discussion of phototaxis involves tests generally performed with populations. Interpretations of population phenomena would appear more puissant when based on parameters linked to specific stimuli.

B. Chemoreception

Dethier *et al.* (1960) have suggested that, in addition to the designations attractant and repellant for substances causing oriented movement, three other terms would be useful in denoting the responses of insects: arrestant, stimulant, and deterrent. The first class of substances involves progression towards and aggregation at a source, the second class elicits a variety of activities while the third class inhibits activity. Clearly the same source can produce more than one class of behavior and any distinction must perforce be made on the basis of the behavior prior to and after a fly encounters the sources. Another such distinction is present with respect to contact in contrast to distance stimuli for chemoreception and olfaction.

Barrows (1907) demonstrated that odor is detected by the third segment of the antennae. If one antenna was removed, *D. melanogaster* individuals circled in the direction of the intact side, to orient towards an odor source. Without both antennae flies could come within a centimeter of the source and not detect it. On this basis it was suggested that olfactory orientation occurs by unequal stimulation of the two receptors and adjustment of

movement accordingly. The same guidance system appears to operate in flight (Kellogg *et al.*, 1962). Flies were observed to move into the wind and, up to a certain windspeed, follow odor carrying air back to the source.

Begg and Hogben (1943, 1946) reported that antennaless flies lacking both antennae failed to respond to odor. Flies with one antenna responded weakly to odor in both 2-way choice chambers and in differential trapping assays. The olfactory response of aristapedia was less intense than wild type. Since this mutant lacks the pit organ on the antennae, it was suggested that this organ is involved in olfaction and that the sensillae (peg organs or cones) on the segment also serve as chemoreceptors. However, Becker (1970) reported that antennaless flies were sensitive to the odor of a repellent. He selected wild type strains, using a Y maze, that were insensitive to a repellent and found that they were also insensitive to a second repellent. While a response to selection was obtained, no mutants were detected. Gerreshiem (1973) pointed out that the failure to detect mutants with this regime probably resulted from use of a stimulus odor that was not specific for a particular receptor type. It could well be that antennaless differs from normal flies in the number and kind of receptor sites.

Dethier (1972) demonstrated that contact chemoreceptors on mouthparts and legs of *Phormia* that normally respond to aqueous solutions can also respond to certain compounds in the gaseous phase. A variety of organic and inorganic acids and unrelated polar compounds could stimulate salt receptors. Some nonpolar substances could inhibit or stimulate salt receptors. Several substances irritating to man had no effect. Flies with all known olfactory receptors removed would still show aversive behavior by withdrawing the proboscis or retracting their legs. Dethier suggested that, since flies can thus use the information about odors detected by contact chemoreceptors, there may be a general chemical sense akin to that in vertebrates. Others have suggested that molecules producing a specific olfactory response form a common sequence, intimating a common sensory mechanism shared by invertebrates and vertebrates (Burgess and Wright, 1974). Dethier recorded from individual sensory hairs using a side wall technique, wherein the electrode tip contacts the hair perpendicularly to the long axis of the hair. Using either this technique or recording from the tip of sensory hairs on tarsi or mouthparts, Shiraishi and Tanabe (1974) determined the electrophysiological threshold, in impulses/0·1 sec, for several sugars. They also proposed a reclassification of the tarsal and labellar chemosensory hairs of *Phormia*. Six functional types of tarsal hairs were characterized on the basis of sensitivity to sugar, salt or water and whether the salt receptor or an unspecified receptor produced spontaneous impulses. Five types of labellar hairs were recognized. Each of the tarsal and labellar chemosensory hairs contains five neurons, one of which

terminates at the proximal portion of the sensillum and is a mechanoceptor. The other neurons terminate at the distal end of the sensillum and respond to sugar, water, or salt. The function of the remaining neuron is not known.

Behavioral thresholds were determined by touching the tarsi or labellum with a sugar solution (Shiraishi and Tanabe, 1974). The minimum concentration of sugar that would elicit the proboscis extension was designated the acceptance threshold. Receptors in individual hairs showed unique concentration threshold curves. Sugar or salt receptors in certain types of tarsal hairs did not respond unless the temperature was above 21°C. Concentration response curves were compared for electrophysiological and behavioral measurements. Labellar thresholds agreed well but the fit of tarsal thresholds was not as good and the difference was ascribed to the fact that impulses from tarsal receptors must be summed before producing an effective output for proboscis response. Differences in the sensitivity of central nervous system integrative mechanisms were also implicated.

Thus the specificity of behavioral responses to contact stimuli reside in discrete receptor sites which are sensitive to physical factors. Additionally, summation of the response of certain receptors is necessary before information is transmitted to the central nervous system. The effect of a particular input is dependent on the level of sensitivity obtaining in the integrative circuitry at that point in time. Discussion of factors influencing sensitivity are included under "Feeding Behavior" (Section, IV, I).

Isono and Kikuchi (1974a) have used both a behavioral assay and electrophysiological recording from a type of labellar hair to characterize the preference of *D. melanogaster* for a number of sugars. Flies aged 0–3 days were fed 0·1 M sucrose, starved for 20 h at 20°C, and transferred to a petri dish with four rings containing, alternately, 2 % agar or 2 % agar plus sugar solution. The distribution of the hundred or so flies in each dish was recorded photographically every 15 min of a 2 h test period. The response was evaluated as a graph of the ratio of flies on sugar rings to the total versus time. The response value was estimated for each concentration as the Y-intercept at 15 min of the regression line for the eight values of a test period. At high concentrations of certain sugars there was a decrease with time in the number of flies on the sugar rings. This was interpreted as a change in threshold due to ingestion of the sugar. The behavioral responses to eight sugars demonstrated a diminution of response at high concentrations of sucrose, maltose, glucose and fructose. The response to ribose, xylose, galactose and mannose did not diminish, illustrating that flies were less sensitive to these sugars. Recordings from labellar hairs demonstrated sensitivity to the sugars maltose, sucrose, glucose and fructose in that order of decreasing sensitivity. No impulses were elicited

with the other sugars, suggesting the existence of different types of receptor sites.

The preference–aversion test, using rings containing fructose, glucose, sucrose and water in each petri dish, was used to detect an imbalance in the distribution of mutagenized flies among those choices (Isono and Kikuchi, 1974b). Concentrations of sugars and water in the rings was adjusted to give a distribution of normal flies of 1:1:1:0·2. An autosomal recessive mutation simultaneously affecting response to glucose, sucrose and maltose was recovered. The mutation showed normal response to fructose demonstrating the existence of at least two different receptor sites in labellar chemosensory hairs.

Assay of choice response in the two arms of an olfactometer resulted in the isolation of another mutant strain which was attracted by chemicals that were repellent to normal flies (Kikuchi, 1973a, b). The olfactory mutant (*HPB–1*) appears to be dominant on the second chromosome. Kikuchi suggests that the attractiveness of those odors to which the mutant responded is due to the presence in the molecule of a "bifunctional unit" consisting of a proton acceptor and a proton donor with an average separation of about 3Å. The location of the receptor site has yet to be determined but the mutation demonstrates that excitation at this site leads to oriented movement towards an odor source. The response of the mutant strain *HPB–1* is sensitive to the effects of larval medium before testing, the length of the starvation period prior to testing and the concentration of odor used (Kikuchi, 1973a). High concentrations of odorant will repel both normal and mutant flies. West (1961) noted the effect of starvation in increasing the attractiveness of tested substances. Hay (1972a) has suggested that the responsiveness of adult flies may be influenced by recognition of a "colony odor" of flies held in the same bottle since eclosion.

The isolation of mutations affecting both contact chemoreception and olfaction as well as the characterization of attractiveness at the molecular level implies that an understanding of at least some of the mechanisms of chemoreception may be forthcoming.

The existence of different receptor sites may aid in explaining the greater attractiveness of mixtures of substances for normal flies (Begg and Hogben, 1943, 1946; Mason *et al.*, 1963; West, 1961). Such mixtures might represent attractiveness summed over different receptors or accentuated by increased volatility. Hutner *et al.* (1937) tested 150 chemicals and oils by counting the relative number of flies in funnel traps, and found that those which acted as attractants were similar to oviposition stimuli. Some mixtures approached natural substrates in efficacy. The "yeast odor" was an important constituent of these mixtures. Acetaldehyde, acetals, cyclohexane and diphenylmethane were found to be attractive. Ethyl alcohol

and acetic acid were found to be attractants by Reed (1938). Concentrations above 25 % ethanol or 5 % acetic acid acted as repellants.

The convulsive reflexes produced by certain mixtures (Carpenter, 1908) might represent inundation of central nervous system processing stations, similar to the effect of high intensity light. Such integrative centers might be capable of processing a finite amount or sequence of information. Too high an input may perturb the system to an extent that results in loss of coordinated motor output.

Differences between species in their response to the same mixture (West, 1961) may reflect different kinds of receptor sites, different thresholds for individual chemosensory cells or differences in central nervous system integration. *Drosophila pseudoobscura* was more responsive to more compounds than either *D. melanogaster* or *D. virilis* in tests of a number of bait mixtures (see West, 1961). The failure of *D. virilis* to respond to odors in the absence of light suggests that the sensitivity of central nervous system processing of chemoreception is subject to mediation by other modalities of sensory input. Differences among even closely related species of *Drosophila* in host plant discrimination (see Habitat Selection, Section 7, H) are illustrative of the changes in receptor and CNS threshold functions that have occurred in the evolution of this group.

Olfaction involves antennal receptors and may utilize some contact chemoreceptors responding to certain compounds in the gas phase. The general problem has been approached by analysis of behavioral tests of preference for or aversion to one or another mixture or compound. An alternate approach has been the isolation and analysis of mutations affecting the behavior. One approach which may serve to integrate these two would be a detailed exploration of species differences in the relative attractiveness of substances. Species may differ in their receptor sites or central nervous system responsiveness to various substances. Comparative species studies may aid in defining both the extent and mechanisms of such differences.

C. Humidity

Relative humidity (RH) is one of the factors which serves as a boundary condition for *Drosophila* activity. Field studies of a number of species have indicated the relevance of this parameter (Dobzhansky and Wright, 1947; Koch, 1967; Grossfield, 1968; Carson *et al.*, 1970). Differences between closely related species in their reaction to humidity differences have been observed (Greuter, 1963; Koch, 1967). This factor interacts with temperature and light to control voluntary movement of flies in the field. To date, only *D. melanogaster* has been used to analyse the mechanism of response to humidity.

Flies given a choice of two humidities avoided both high (100, 97, 87 % RH) and low (0, 20, 34 % RH) humidities if the difference between the two choices was not large (Perttunen and Erkkila, 1952). Both males and females chose 77 % RH when presented with an alternate of 34, 67 or 87 % RH. Desiccation over silica gel at 26°C produced a strong reaction to the more moist side of the apparatus, illustrating that the intensity of the reaction is dependent on the degree of water loss. Undesiccated females chose the drier side of a 100 or 34 % RH condition. When desiccated for 3 h they showed a moderate reaction to the moist side, which was increased strongly by 5 h of desiccation. Males were more sensitive to desiccation and showed a strong response after only 3 h. At the moist end of the scale, flies can perceive and react to a 3 % RH difference.

The movement of flies in any particular condition clearly depended on the choice available and in most cases they would react to a difference of 10 % RH (Perttunen and Salmi, 1956). The preference of normal flies for the more moist side of a 77 %–20 % choice can be intensified by desiccation just as the normal preference for the drier side of a 100 %–87 % choice can be reversed by desiccation. The reversal occurs when a 12–26 % water loss is reached (Syrjamaki, 1962). The intensity and direction of response is dependent on age (Perttunen and Ahonen, 1956). Test of flies aged 0–4 h to 56 days with a choice of 100 % or 77 % RH showed that younger flies preferred the drier side, especially on the first day. The response declines to indifference at 2 weeks of age. After this time, males showed a slight preference for the moist side. This may reflect the greater susceptibility of older flies to desiccation. Removal of antennae, palps, and proboscis showed that all three are involved in humidity perception with the funiculus segment of the antennae mediating the dry response in a choice of 100 or 77 % RH (Perttunen and Syrjamaki, 1958; Syrjamaki, 1962). Flies with only a proboscis or proboscis and palps cannot perceive a difference of 23 %, while flies with both of these subsidiary humidity receptor sites can perceive a 66 % RH difference. Removal of all three organs results in failure to respond even to this difference. Amputation of fore, mid, or hind tarsi had no effect on humidity perception. Begg and Hogben (1946) reported that antennaless flies showed no humidity response. Their assay system involved only flies desiccated at 30°C. Since the palps and proboscis as well as the antennae participate in a humidity response and the antennaless mutant does not show such a response, this may suggest that the mutation affects other structures of the fly besides the antennae. Alternatively, the different conditions in the two test systems could explain the failure of antennaless flies, with normal proboscis and palps, to respond to humidity.

Responses of normal adult flies then, are similar to those of larvae in that

the intensity of response is relative to the choices available. The dry response toward the lower relative humidity of a choice between 100 or 77 % RH suggests, as for larvae, that an aridity receptor may act as the controlling sensory input. It may be that the differences found for closely related species in their humidity responses reflect different set points for this control element. This might suggest peripheral rather than CNS mediation of the response.

The effect of humidity on behavior could involve second order phenomena such as altered hormone levels. In contrast to males, females must deposit eggs at some point in their existence. Not enough is yet known of *Drosophila* reproductive physiology to state the effect that humidity might have on egg production, hormonal changes, and consequent behavior. Detailed comparison of the humidity response of sibling species might be instructive with respect to habitat selection and niche separation in the ecology of *Drosophila* species.

D. Temperature

The effects of temperature are of interest from two superficially disjunct aspects of *Drosophila* behavior: ecological studies and temperature sensitive neurological mutations. Field studies involve temperature limitations on *Drosophila* activity while temperature sensitivity involves behavioral alterations which are expressed only at or above a critical temperature. Temperature is also a factor in evaluating humidity, desiccation and activity studies (Kalmus, 1945). Each value of temperature has associated with it a particular relative humidity unless care is taken to adjust the two factors separately. Different species show different optimum temperatures and it is thoughtless to compare reactions of two species when one of them is near its maximum survival temperature. Some species cannot be grown above a certain temperature, which may be 16–30°C depending on the species. Many species will be rendered sterile by prolonged exposure to temperatures above their optimum. Adults and larvae of some species will survive 17 h periods of freezing.

Carpenter (1908) noted that *D. melanogaster* exposed to 45°C became violently active, vibrated their wings and showed spasmodic muscle contractions. This convulsive reflex produces a spinning motion which moves flies rapidly from one place to another. A similar convulsive reflex, with spinning and rigid extension of the wings, was seen when flies were exposed to very low temperatures. Flies become motionless but will recover if placed at room temperature. Carpenter interpreted the rapid spinning as a reflex mechanism which would serve to remove a fly from a region of stress. The first convulsive reflex appears between 36 and 38°C

and general convulsions become evident between 38 and 40°C. Carpenter noted that high intensity light produced convulsive reflexes at a temperature of 30°C. This synergistic effect drops the threshold for convulsions by about 10°C, and suggests heteromodal summation of sensory inputs affecting motor activity. Evidence for this kind of interaction of stimulus inundation of CNS centers to produce disinhibition, emerges from studies of white eyed *Hk*^{1} *para*^{ts} double mutants (Williamson *et al.*, 1974). These flies can be made to jump at high levels of sensory input at a temperature where they are normally paralysed.

Carpenter also noted that flies given a temperature gradient chose room temperature in preference to either hot or cold extremes. Begg and Hogben (1946) demonstrated temperature choice behavior using a thermal gradient tube, a dumb-bell shaped two way chamber and a T-junction tube with the arms of the T at different temperatures. Flies moved to the cooler end of a 22·5 to 34·5°C gradient. In the two way choice tests they did not respond well unless the high temperature was over 31°C and showed a strong response when it was 41°C. Flies homozygous for antennaless showed a strong reaction to this temperature but flies homozygous for aristapedia showed no reaction. There is no data on the temperature preferences of these mutants at less extreme temperatures, nor has the effect of *ss*^{a} on thermoreception been confirmed.

Both high and low temperatures during development have been shown to affect adult behavior. Flies reared at 13°C showed reduced activity after being held at 25°C for four days (Cohet, 1974). Maze running speed and movement through a tube were lower, with 70% of flies reared at 25°C completing the maze in 10 min compared to less than 1% of flies reared at 10°C. Survival of D. *subobscura* at high temperatures involves a developmental acclimatization to higher temperature during pre-adult life and a physiological acclimatization in adults kept at a higher temperature (Maynard Smith, 1957). Death at 33·5°C occurs as a result of cumulative water loss and part of physiological acclimatization involves a behavioral response. When first shifted to 33·5°C, flies are extremely active. After 50 min they become sluggish and remain so even when transferred to 20°C, where they perform the minimum movements necessary to drink and feed. When shifted to 33·5°C again after 3 h they are very inactive compared to control flies. Whether this is a physiological stress reaction or involves the effect of experience *per se* is not known.

Field studies suggest that activity of *D. melanogaster* and other species of *Drosophila* occurs within certain limits of temperature. Little activity was seen below 13°C (Michelbacher and Middlekauf, 1954; Koch, 1967) and it has been suggested that 12°C might be the minimum for the genus (Grossfield and Parsons, 1975). Lewis and Taylor (1964) have suggested

that a temperature threshold operates for morning activity and a light threshold for evening activity. They note that dark body color in a small insect may be sufficient to give a 1–2°C rise in body temperature in daylight, and permit activity near a threshold temperature. *Drosophila* in Hawaii have been taken in overnight light traps, set after dusk and sampled before dawn, where the minimum temperature was 8–12·5°C (Grossfield, 1968). The overwintering of some species in ground beneath snow may involve microenvironment temperatures above the threshold. The same would be true of *D. busckii* active on pumpkin at 10°C.

Koch (1967) has found that *D. subobscura* and *D. obscura* have lower activity below 10°C, with the latter species more sensitive to temperature changes than the former. Yerington and Warner (1961) report no flight activity for *D. melanogaster* at temperatures over 26·5°C. Bidirectional selection for temperature preference has been reported (Richmond and Finkel, 1973).

Temperature sets upper and lower limits for activity and interacts with light levels to determine responses in both laboratory and field. The receptor location and mechanism are unknown but mutations affecting the presence and/or distribution of various sensilla might be useful in approaching the problem. In the case of two species of the *obscura* group there is a difference between species with respect to the effect of temperature. Whether other species or mutations will show different temperature effects is unknown. It might be noted that the effect of light, unless heat filters are used, could result from an increase in temperature.

E. Light

Lewis and Taylor (1964) and Michelbacher and Middlekauf (1954) state that light intensity is a major factor in determining flight activity. Bright light has been reported to inhibit activity (Carpenter, 1905; Kekic and Marinkovic, 1974; Dobzhansky *et al.*, 1974) and prevent flight (Johnson, 1969). Avoidance of bright light in the field has been noted for many species (Spencer, 1940; McCoy, 1962; Carson *et al.*, 1970). Part of this avoidance may be a temperature effect and part may involve saturation of the visual system and attendent motor responses. Species can be characterized in the field by their light level preference (Grossfield, 1968). Additionally, activity in the field is often greatest at the interface of light and dark areas, as where discrete shafts of sunlight strike the ground, creating adjacent patches of different intensity.

Koch (1967) observed *D. subobscura* and *D. obscura* in transparent arenas at forest edges. The former species is found mainly in open fields or forest edges while the latter is usually found inside forests. In daylight

D. subobscura oriented toward the forest and at night, towards open field. *Drosophila obscura* oriented toward the forest day and night. With this species, bright light, high temperature, and low relative humidity cause a decrease in orientation to dark and an increase in activity. *Drosophila subobscura* reacts oppositely to these conditions and, of the two species, is more sensitive to light and has a lower intensity threshold for activity. Quick decrements of light intensity induce locomotor activity in both species.

Other Diptera also show an effect of light intensity on their activity. Tsetse flies (Huyton and Brady, 1975) are inhibited in their movement at high light intensity. At 26°C these flies tend to go toward the light. As the temperature is raised, they move toward darkness. Each log unit increase in light intensity results in a 2·2°C decrease in the temperature at which flight is initiated. These results are in accordance with field data for this species.

Light intensity is thus a factor involved in the partitioning of resources as well as the activity and separation of species in the field. It is a factor which has received relatively little attention (see Habitat Selection, Section IV, H).

F. Wind

Several reports have noted that *Drosophila* is most active in calm conditions (Michelbacher and Middlekauf, 1954; McCoy, 1962; Yerington and Warner, 1961; Carson *et al.*, 1970; Dobzhansky, 1974). Yerington and Warner (1961) note that flies will tend to fly against a wind up to about 16 km/h. After exposure to strong wind, a fly may often retreat into crevices (Grossfield, 1968).

Kalmus (1942) tested a number of species for their response to air currents without odor. A number of species (*D. virilis*, *D. americana*, *D. subobscura*, *D. funebris*) turned sharply towards the tube from which air was flowing and walked against the flow. Removal of wings, antennae, or both, did not abolish the reaction. *Drosophila melanogaster* and *D. busckii* showed no reaction and *D. pseudoobscura* showed a slight response. Quantification of these results would be interesting in view of their value in evaluating the effect of winds in studies of dispersal.

There are reports that *D. melanogaster* can detect electrical changes preceding storms (Maw, in Johnson, 1969). Since aversive conditioning paradigms using shock have been applied to *Drosophila*, confirmation of the ability to change activity pattern with respect to voltage gradients might be useful (see Spontaneous Locomotor Activity, Section IV, E).

Richardson and Johnston (1975a) have determined that *D. mimica* will move into wind currents below 3·3 km/h and will be blown involuntarily by current above 8 km/h (see Dispersal Activity for greater detail). In view

of the ability of *D. melanogaster*, noted above, to fly against a wind of 16 km/h, the obvious implication is that wind level can have strikingly different effects on different species. To date, no detailed study has been made of the responses of a number of species to wind, nor has there been investigation of the point at which wind level becomes sufficient for passive dispersal of various species of *Drosophila*. The force necessary to dislodge a fly from a resting place may well differ among species. The receptor mechanisms involved in perceiving wind current may be proprioceptors at joints and bristle sockets that detect displacement of body parts or bristles.

III. Larval Behavior

A normal *D. melanogaster* culture will have newly hatched larvae on the surface of the medium, in a blob of yeast or a scarification of the food. After 24 h larvae begin to burrow and by 52–72 h most have disappeared into the medium. At 96 h the culture will have a tunnelled appearance. The maximum depth a larva will burrow has been reported as 20 mm (Sameoto and Miller, 1966). Larvae tend to use mainly the upper half of the available medium but *D. simulans* larvae have been reported to use the lower half to a significantly greater extent than *D. melanogaster* (Barker, 1971).

Other species differ from these two in their spatial distribution in the medium and some species will extend full length to reach undisturbed medium and remain in that position with only their posterior spiracles near the surface. Other species will burrow deep into their natural substrate and slowly feed. Larvae of leaf mining species e.g. *D. inornata*, when brought into the laboratory, will preferentially burrow into rolls of dental plug rather than non-fibrous material. In field observations (Grossfield, 1968) larvae of *D. melanoloma* were seen to leave a fungus substrate and then crawl back to it several minutes later. Hawaiian *Drosophila* species have larvae that may crawl in the ground for several days before pupating (Carson *et al.*, 1970).

1. Skipping behavior

Larvae of some species of the related genus *Zaprionus* and those of the *Drosophila* subgenus *Scaptodrosophila* have a "skipping" behavior. A larva will bring its anterior end near its posterior, forming a circle, and rapidly extend its body full length, propelling the larva up to 20 cm in some of the Australian *Scaptodrosophila* species. Some species in the *D. saltans* subgroup and *D. cardini* group also have this behavior. It is generally associated with a tendency to pupate in the plug of a container and may possibly

represent a dispersal mechanism. de Souza *et al.* (1970) have reported a gene in *D. willistoni* which leads larvae to pupate outside of food cups. They mention that some *cardini* group species usually pupate in the same location, while larvae of species in the *saltans* and *melanogaster* groups behave in this fashion under conditions of high humidity. No account was given of how the larvae moved from the food cups. In some of the *Drosophila*, species skipping may, in fact, be a vestigial behavior which is no longer functional for that species, but which can be elicited by stress.

2. *Humidity dependent behavior*

Drosophila melanogaster larvae can perceive small differences in humidity at high relative humidity (RH), while detectable differences are large in dry air (Benz, 1956). The sensory capability resides in the tufted organs on the ventral side of the thoracic segments. The threshold for sensation is high in dry air and Benz concluded that the absence of humidity irritates these sense organs and that they are therefore aridity receptors. The behavioral assay used was the introduction of larvae into the middle of a tube with different humidities at the two ends. Hafez (1950), using a circular arena with steep humidity gradients, reached similar conclusions for the housefly larva. These larvae could detect a 5 % RH difference between 95 % and 100 % RH. They avoid the drier choice above 5 % RH; below this point they are least sensitive. Adaptation to humidity was evident. In contrast to this preference for moisture in young larvae, older larvae, ready to pupate, show a preference for the drier choice. At some point then, a switch in programmed preference occurs.

3. *Odor and Light Dependent Behavior*

Young housefly larvae do not react to odor or light (Bolwig, 1946). At the second and third instars they can react precisely and will avoid light. The sense organs are two groups of cells on each side just above the anterior end of the cephalopharyngeal sclerites. Their anterior end will move from side to side to seek the minimum amount of light. They may be able to detect wavelength differences. These measurements were made by placing the larvae in a drop of methylene blue and allowing them to record their track. Dürrwächter (1957), using several strains of *D. melanogaster* and *D. funebris*, noted similar searching movements of larvae tested for phototaxis. No differences between strains were found. His test procedure consisted of placing 50 larvae on damp filter paper for 5 min test periods and allowing them to crawl while two lamps at opposite ends of the experimental field went on and off alternately. The angle of movement

towards the light constituted the measurement. Negative phototaxis was the rule and no effect of differential rearing in light or dark was noted.

The olfactory sense of housefly larvae resides in the dorsal papillae of the cephalic lobes (Bolwig, 1946). These larvae show avoidance of high and low temperatures. Decapitated larvae avoid high temperatures and low humidity as well as do normal larvae (Hafez, 1950). Hafez suggests that overall larval behavior is dominated by temperature and RH while larvae will quickly adapt to odor and light stimuli.

4. *Feeding behavior*

The feeding behavior of *Drosophila* larvae consists of a series of extensions and retractions of the cephalopharyngeal sclerites together with pumping movements of the pharynx. The movement of larvae in a substrate involves an extension of the head and a thrust of the mouth hooks into the medium. An anterior–posterior wave of compression and relaxation of each body segment in sequence progresses to reach the posterior end, when the cycle is repeated. There is some evidence, based on Bakker's (1961) conclusion that rate of feeding determines rate of development, that light and noise might increase larval movement (Oshima and Choo, 1973).

A study of larval feeding demonstrated that larvae feed continuously during development, the rate changes with the physiological age of the larvae, and is constant over a yeast concentration of 0·25–25 % (Sewell *et al.*, 1975). Breaks in feeding occur at ecdysis and when larvae contact each other. Feeding rate was measured as the number of cephalopharyngeal retractions in a 1 min test period. A similar period was used to count the number of forward or reverse movements as an index of locomotor activity. Locomotion is constant across development at about 34 events/min. Feeding rate increases from 100/min at the end of the first instar to 140–150/min through the second and third instars. It decreases prior to pupariation.

Feeding rate responds to bidirectional selection, with the fast lines reaching a plateau at 50–60 retractions/min above control and the slow lines at 45–65 below control lines (Sewell *et al.*, 1975). The heritability of feeding rate ranged from 11 to 21 % and the selected lines performed at their respective levels on different media. Dominance for fast feeding was shown. The slow feeding lines showed a correlated reduction in locomotion but the fast feeding lines did not. No correlation with adult activity was observed. It would appear then that larval feeding rate and locomotor activity are controlled independently from each other and from adult behavior.

These selection lines were analysed for the levels of three biogenic

amines (Sewell *et al.*, 1975) in order to assess whether a balance among those compounds control larval activity, as had been proposed for adult activity (see Spontaneous Locomotor Activity, Section IV, E). Serotonin levels were the same in control, fast, and slow larval feeding lines. Noradrenaline levels were lower than control levels in one fast feeding line but not the other. Dopamine levels were depressed in one of the two fast feeding lines and were elevated in one of the slow feeding lines. Thus no correlation exists, in larvae, that is comparable to the balance suggested for levels of dopamine and noradrenaline in influencing adult locomotor activity.

Tests of *D. pseudoobscura* and *D. persimilis* larval food preference among four species of yeast on replica yeast plates showed differential choice behavior (Lindsay, 1958). Larvae were placed at the center of a petri dish and counted after 3 h. A similar test among 10 species of yeast, where larval position was scored after 1 h, revealed preference for the yeast on which they grew best (Cooper, 1960). Larvae and adults of the same species may differ in their preference for specific yeasts. Differential yeast preferences were also shown by larvae of *D. melanogaster* and *D. simulans* (Ali and El-Helw, 1974). This assay sampled the yeasts ingested by the larvae and thus may not be a purely behavioral effect.

The manifold capabilities of larvae in sampling and reacting to their environment have just begun to be utilized as a research tool. Feeding rate studies, selection lines and comparative species studies have yet to be molded into a coherent picture of how larvae decide what to do at any moment in time. It is likely that species comparisons with respect to environment sampling and biochemistry will prove profitable for ecological studies. The larva itself will certainly be useful as an experimental tool in electrophysiological probing of sensory input and motor coordination.

A. Puparіation

At the end of the larval phase of life, mature third instar larvae form a puparium which incorporates the larval skin. The site chosen for pupariation by a larva is a component of behavior influenced by the environment and demonstrating variation between strains and species. High humidity or high moisture content of the medium in shell vials tends to increase the proportion of *D. melanogaster* larvae that choose peripheral as opposed to central pupariation sites (Sokal *et al.*, 1960). While earlier pupariating larvae tend to be peripheral and later larvae tend to pupariate in the center, the age of the medium itself does not seem to have any effect. At densities of over about 50 eggs/vial a greater number of prepupae are formed on the food surface than on the wall of the vial. In a medium that liquifies as

larvae develop, they tend to pupariate at a fixed height above the food slurry (Wallace, 1968a). In some strains 80% of the prepupae may be 2–3 cm above the food, while in others this proportion may be within the first 2 cm above the food. The activity of subsequent larvae may dislodge some of the early prepupae and they may fall into the medium and drown. Similarly, prepupae on a food surface may be submerged by the activity of larvae. Schlager (1960) has shown that fluctuations in pupariation site can be reduced or eliminated by growing flies on a dry sugar medium since the fluctuations are due to chemical changes in karo and molasses used in the usual food medium. Control of micro-flora was not necessary to reduce fluctuations in pupariation site. Increasing temperature (13–25°C) raises the average height of pupariation sites on vial walls but high temperature (29°C) drastically reduces it (Mensua, 1967). The average prepupal height above the medium increases with poor aeration and, for the same flies, tends to increase in bottles as opposed to vials.

A high moisture content of food medium has been found to increase pupariation on the sides of the vessel in *D. simulans* as well as *D. melanogaster* (Sameoto and Miller, 1968). *Drosophila simulans* tends to pupariate on the surface of the food medium while *D. melanogaster* prefers the sides of the food container (Sameoto and Miller, 1966; Barker, 1971). As larval density increased the original proportion of 69% of *D. simulans* prepupae on the surface decreased (Barker, 1971). *Drosophila melanogaster* larvae, however, did not respond to density and 8–12% of all prepupae were on the medium at all densities. The remaining prepupae tended to occur higher on the walls as density increased. The same kind of differences between these species, in the response of *D. simulans* and the lack of response of *D. melanogaster* to changes in density, was found with other strains of these species as well (Sameoto and Miller, 1968).

The sibling species *D. melanogaster* and *D. simulans* show alternate preferences for which choice is made with respect to pupariation site. Another pair of such species show similar behavioral differentiation. *Drosophila virilis* pupariates on the wall of its container while *D. americana* prefers to pupariate in or on the food (Stalker, 1942). In the *tripunctata* group *D. mediopunctata* pupariates on the surface of the food while *D. unipunctata* pupariates within masses of food that the larvae carry up on the surface of the container (Patterson, 1957).

There are thus behavioral responses to changes in conditions in the medium that are reflected in the proportion of larvae pupariating on the surface or on the wall of a vial and in the distribution of puparia on the wall. Larvae of *D. melanogaster* tend to pupariate away from light while those of *D. willistoni* prefer relatively brighter pupariation sites (Rizki and Davis, 1953). The respective behavioral responses are accentuated when the two

species are reared together. Another effect of light may be noted for pupariation site preference in *D. palustris* and *D. subpalustris*. In light, the former pupariates just above the surface and the latter on the walls of the container. In darkness the choice of sites is reversed (Grossfield, unpublished observations).

In field studies (McCoy, 1962), *D. melanogaster* and several other species have been found to pupariate on the dry skin of fruits, on the soil surface, or actually ½ inch below the soil surface. Many of the Hawaiian *Drosophila* routinely pupariate several inches deep in the ground (Carson *et al.*, 1970) and the adults must work their way back up through the soil.

Selection for changes in pupariation site has been successful for both central vs peripheral pupariation and for the distance above the medium that larvae will choose. A strain of *D. melanogaster* selected (Sokal, 1966) for a peripheral site showed a strong response to selection with a plateau at generation 18, while a line selected for central pupariation had a weaker response which flattened out at generation 23. The difference between the two selected populations declined with relaxation of selection. Flies in the peripheral line had a longer larval period and took longer to burrow into the medium. Mensua (1967) showed that disruptive selection for average prepupal height above the medium was successful only for pupariation away from the medium. He reported an increase of about 10mm to the parental strain mean of about 14 mm. de Souza *et al.* (1968, 1970) found that a single major gene was responsible for larval choice of pupariation site in *D. willistoni*. Pupariation outside a food cup in a population cage was dominant to inside pupariation and the gene apparently led to increased adult activity as well. If provided with dental rolls projecting upwards from the medium, larvae of many species will pupariate on the roll. *Drosophila virilis* larvae, however, will still pupariate on the wall of the container. Larvae which skip or wander from the medium also tend not to pupariate on the rolls.

Pupariation represents the end of larval life and as such is a convenient assay for the point at which a larva ceases to move. The differences in pupariation site simply reflect the last behavioral component of larval reactions to prevailing conditions. The fact that variations are so marked underscores the sensitivity of larvae to their surroundings and the relevance of genetic factors that are evident as larvae of different species or genotypes make different choices when confronted with identical environments.

B. Pre-imaginal Conditioning

One phenomenon involving an effect of the larval environment on adult

behavior has been designated "pre-imaginal conditioning". *Drosophila melanogaster* reared on normal medium are repulsed by the odor of peppermint, but flies reared on a medium containing 0·5 % peppermint oil show greatly reduced aversion (Thorpe, 1939). The control line showed 34·9 % of adult flies going to peppermint; 66·5 % of flies exposed to it during larval life were attracted to the odor. This was subsequently interpreted by Thorpe as habituation persisting through the pupal stage.

A different demonstration of this effect showed that *D. guttifera* adults preferred to deposit their eggs in the kind of medium the adults were exposed to as larvae (Cushing, 1941). Clutterbuck and Beardmore (1961) used both the response of adult *D. melanogaster* and the number of eggs deposited to demonstrate attractiveness of peppermint and juniper oils when these were adulterants of larval food. The effect increased with the number of generations flies were reared on adulterated food. This effect was not found with lavender oil as the adulterant. Larval exposure to this substance increased rather than decreased the normal repulsion.

Adults given a choice of normal or peppermint adulterated food in a different apparatus and selected for preference for the adulterant showed a strong inclination to choose peppermint when reared on it (Moray and Connolly, 1963; Arnold and Moray, 1964). Flies selected for aversion to peppermint but reared on it showed a similar response. These aversive flies continued to show a preference for peppermint even after 8 generations on normal medium. These results were interpreted as a genetic assimilation of behavior.

Hershberger and Smith (1967) used a Y tube olfactometer to repeat Thorpe's experiments. They confined peppermint reared adults in scented but foodless containers and demonstrated extinction of the peppermint preference response. These results were interpreted as illustrating conditioning since the peppermint had been associated with food. Manning (1967) suggested that a distinction between habituation and conditioning could be made on the basis of testing flies in the olfactometer a second time. With habituation, the choice of the adulterated arm of the olfactometer should be random on both the first and second trials. Conditioning would suggest that, since the smell was associated with food, an increased proportion of flies should choose the adulterant odor on the second trial. Manning used geranoil rather than peppermint and demonstrated that both first and second trials were the same. Flies chose the geranoil arm of the olfactometer simply because rearing on geranoil medium reduced their aversiveness to it and it became an equally probable choice. Rewarding flies with sucrose for choosing geranoil did not affect their subsequent choice. Counter conditioning adults by associating scent with absence of food reduced aversiveness to the odor for both normal and geranoil

reared flies. If conditioning were involved, the geranoil reared flies should show greater aversion. This result suggests that adults can show habituation as well. This effect may be implicated in the recognition of adults of the same strain by a "colony odor" (Hay, 1972a). Evans (1961) has demonstrated that taste thresholds of *Phormia* for certain sugars are elevated when these sugars are present during development. A detailed repetition of Evans' studies failed to confirm his findings (Dethier and Goldrich, 1971). This subsequent study used sterile medium to assure the presence of the supplementary sugar during development. To avoid exposing flies to more than one test solution, random testing of adults was employed rather than an ascending concentration test regime. Finally, an absolute rather than relative measure of threshold was determined. The addition of certain sugars to larval food did increase taste sensitivity of adults to some sugars, decreased sensitivity to others, and was without effect on still others. There was no correlation between the supplementary sugar and the sensitivity of adults to that sugar. No relationship with metabolic pathways was observed. Thus, although there is an effect, it is far from simple.

The effect of pre-imaginal conditioning may involve an elevation of threshold to the adulterant scent. It is possible that the sensitivity of a central nervous system set point may be altered (see Chemoreception, Section II, B) by the presence of some compounds during development. Manning (1967) reported that a small proportion of flies are unaffected by exposure to an adulterant and remain aversive. This proportion could be increased by selection. Analysis of these lines may help to reveal the source of the response. Addition of compounds which are known to react with specific types of receptor sites might be an approach to the general question of pre-imaginal conditioning as well as the specific question of how compounds present during development can affect adult taste thresholds. This would be of particular relevance to ecological cases where sibling species have diverged in host plant preference, as is the case for some Hawaiian *Drosophila* (cf. Richardson and Johnston, 1975b).

IV. Behavior of Adults

A. Phototaxis

Phototaxis is a complex response that begins when a light stimulus impinges on photoreceptors of specific sensitivity and physiological capability. The information contained in the stimulus is then processed by arrays of cells at different synaptic levels in the visual system and integrated with other intrinsic and extrinsic stimuli to culminate with locomotion or absence of

locomotion with respect to the direction of the stimulus. Research using phototaxis has included physiological, behavioral and genetic approaches and has been directed towards describing the function of the visual system, developing model behavioral response systems, comparing the capabilities of various mutant or inbred strains, characterizing the response of particular populations or species, determining genetic architecture, and evaluating the ecological relevance of the trait. The relative ease, compared to other sensory inputs, with which visual stimuli can be defined has no doubt contributed to the popularity of the response as a research tool. The measurement of light stimuli used has ranged from threshold determinations at the relevant wavelength to the stipulation of light levels as determined by a photometer whose spectral response and sensitivity is quite different from that of the flies. Practically every aspect of the response is subject to a variety of contingent variables which may or may not be of importance in a particular investigation, depending on the goals of the investigator.

1. Design

There are basically three experimental designs that have been used to study phototaxis in *Drosophila* (Hadler, 1964a; Rockwell and Seiger, 1973b). The first permits measurement of movement towards a directive light source at one end of a tube. This design can yield data on the rate of movement (Carpenter, 1905; Payne, 1911; Lutz, 1914; McEwen, 1918, 1925; Lutz and Richtmeyer, 1922; Lutz and Grisewood, 1934; Scott, 1943; McDonald and Parsons, 1973) or the distribution of flies after a fixed interval of time (Carpenter, 1905; Stephens *et al.*, 1953; Dürrwächter, 1957; Carson, 1958; Medioni, 1959; Lewontin, 1959; Campan, 1964; Benzer, 1967; Pak *et al.*, 1969, 1970; Elens and Wattiaux, 1971). The counter current modification of this design (Benzer, 1967) uses successive trials with agitation between trials, to fractionate a population into a number of varyingly phototactic groups.

The second type of design yields a measurement of the distribution of flies in a field, with no partitions, after a specified time. The field or arena may have light of differing quality or intensity impinging perpendicularly on it, serving to visually partition the field (Carpenter, 1905; Fardon *et al.*, 1937; Barigozzi and Tonissi, 1946; Dürrwächter, 1957; Wolken *et al.*, 1957; Medioni, 1959, 1966; Rockwell and Seiger, 1973a; Kekic and Marinkovic, 1974; Parsons, 1975; Rockwell *et al.*, 1975).

The third major design involves determining the number or distribution of flies which have chosen between two alternative light regimes at a choice point. This may involve a Y-shaped tube (Brown and Hall, 1936; Finger-

man, 1952; Fingerman and Brown, 1953; Lewontin, 1959; Wehner and Schümperli, 1969; Schümperli, 1973) or a collection of T-shaped tubes arranged as a maze with a variable number of choice points interposed between the starting chamber and a number of terminal tubes (Hirsch and Boudreau, 1958; Hadler, 1964; Spassky and Dobzhansky, 1967; Dobzhansky and Spassky, 1967, 1969; Walton, 1970; Markow, 1975a, b).

It is clear from the term phototaxis itself that locomotion and general activity are components of any such measurement. Reactivity to other flies or features of the environment also operates to a varying extent, depending on conditions obtaining in any particular system. The open field design of Dürrwächter (1957), where the orientation paths of individual flies to two alternate and opposite light sources is measured, provides a simultaneous estimate of locomotory ability as well, while Benzer's (1967) counter current modification of design 1, by permitting measurement of coupled "to-light" and "from-light" trials, allows evaluation of positive, negative, and neutral phototaxis as well as evaluation of general locomotory activity. This latter design however, does introduce a degree of agitation between trials which increases general activity and locomotion. Since each design system does measure different aspects of the response, measurements made with different systems are not strictly comparable. The agitation present in the counter current design is present to some extent in several other designs as well (Carpenter, 1905; Carson, 1958; Lewontin, 1959; McEwen, 1918; Pak *et al.*, 1969; Rockwell *et al.*, 1975) and agitation itself may be useful in evaluating photoresponse in disturbed as compared with undisturbed conditions. The fact that measurements may differ in the two conditions may, in some designs, aid in determining more exactly what is actually being measured, as well as possibly permitting co-ordinate measures of the effect of light on an "escape response" which may be part of the effect of agitation.

Some photoresponse assays have light impinging on flies that is perpendicular or parallel to the body axis of a fly. While permitting measurement of a response, the mazes used in the various phototaxis studies are different in a number of ways. Some have one-way cones at choice points (Hirsch–Hadler–Dobzhansky) while some do not (Walton). The number of choice points in a maze is 10 (Hirsch), 11(Oshima), 14 (Walton) or 15 (Hirsch–Hadler–Dobzhansky). The choice point itself is a Y (Hadler–Hirsch) or T (Hirsch) junction with cones leaving it or a hemisphere with flattened cones (Oshima), or a more complex design (Hay). The light intensity (100 foot candle, 300 foot candle bulb, 40 watt bulb, or unspecified) could stem from an incandescent bulb, rich in infrared, or a fluorescent bulb, rich in ultraviolet. The time required for a starting population to traverse a maze varied from 20–30 min for 95 % of the flies, to almost all through in

24 h. The ability to survive a maze and the tendency to repeat choices were noted (Murphey and Hall, 1969), as well as the more rapid response to selection which is achieved by choosing as parents of the next generation not the flies in the end tubes, but those in the penultimate tubes (Walton, 1968). The tendency to hug the wall of the maze while traversing it is a factor. Habituation and fatigue could be selected for in maze environments as well. A recent development is the use of mazes constructed of identical molded unit blocks (Hay, personal communication). It seems reasonable that such units could serve to standardize at least the maze component of phototaxis studies in different laboratories. The fact that closely related species differ in both their activity in mazes and in the behavioral architecture of the taxes measured in the maze points to the relevance of gene–environment interaction of the response being measured.

The behavioral component of phototaxis which is actually a photoresponse may thus vary quite widely. A comparison of populations selected in a phototactic maze with and without light may provide a difference measure which, by allowing determination of the extent to which activity differences alone produce the data, can be useful in evaluating the response.

2. *Experimental variables*

Mechanical stimulation is but one of the variables affecting phototactic response. The effect has been noted for *D. melanogaster* (Carpenter, 1905; McEwen, 1918; Hadler, 1964a, Campan, 1966), *D. pseudoobscura* (Pittendrigh, 1958; Lewontin, 1959; Rockwell *et al.*, 1975), *D. persimilis* (Pittendrigh, 1958; Rockwell *et al.*, 1975) and *D. robusta* (Carson, 1958).

Temperature is another such variable and has been shown to affect the response of *D. melanogaster* (Waddington *et al.*, 1954) and of *D. pseudoobscura* and *D. persimilis* (Pittendrigh, 1958; Rockwell and Seiger, 1973a). A comparison of phototactic scores of strains of *D. pseudoobscura* selected for positive and negative response showed no differences when the lines were tested at different temperatures (Dobzhansky *et al.*, 1974). Humidity has been reported to affect phototaxis of these species as well (Waddington *et al.*, 1954; Pittendrigh, 1958; Hadler, 1964a).

Gravity or a geotactic response may change a phototactic response to affect the overall measurement (Dürrwächter, 1957; Lewontin, 1959; Hadler, 1964a). Nutritional factors and desiccation may also alter the photoresponse (Dürrwächter, 1957; Pittendrigh, 1958; Hadler, 1964a).

Age and sex of the flies has been shown to influence the response of *D. melanogaster* (McEwen, 1918; Dürrwächter, 1957; Hadler, 1964a). There is an optimum response when flies are several days old and neither too young or too old. Differences between sexes may be evident when

young flies are used. Differences between strains may be more marked when older flies are tested (Elens and Wattiaux, 1971; Elens, 1972a).

Different species or strains may also vary in their excitability and reactivity with respect to the number and kind of other individuals present (Lewontin, 1958; Benzer, 1967; Narise, 1974). Density effects may be especially marked in starting tubes of various designs, where the movement of flies to the next portion of the apparatus may be affected. A comparison of phototaxis among 18 different populations of *D. melanogaster* demonstrated that populations from northern latitudes were the more photopositive (Medioni, 1961). Differences among several pairs of sibling species in photoresponse have been noted.

The variables noted above may be of varying degrees of importance in different investigations. There are experimental systems capable of measuring photoresponse which do not involve locomotion at all and consequently obviate all variables affecting measurements attendant on the actual movement of the animal (Gotz, 1968). Electrophysiological measurements can also indicate the capability of the visual system to handle various visual stimuli (Alawi *et al.*, 1972; Pak *et al.*, 1969; Hotta and Benzer, 1969; Pak and Grabowski, Ch. 9). Characterization of the visual response by use of optomotor response can detect differences between mutations which appear similar when tested by phototaxis or by measurement of the electroretinogram (ERG), which is a gross measurement of the electrical activity of all cells between the recording electrodes (Heisenberg, 1972). It is possible to have nonphototactic mutants with a normal electroretinogram (Pak *et al.*, 1969; Hotta and Benzer, 1969). Measurement of the phototactic response of electroretinogram mutations such as tan and ebony has yielded different characterizations by different investigators. Thus, tan has been characterized as nonphototactic (McEwen, 1918; Pak *et al.*, 1969; Hotta and Benzer, 1969) and as having normal photoresponse (Hadler, 1964a). The same has been the case for the ebony mutation when tested by optomotor response, phototaxis and electrophysiological means. The various factors discussed above no doubt contribute to such discrepancies. The same applies to mutants such as vestigial, about which one can find differing reports in the literature. This mutant does perform more poorly than wild type, indicating that the wings do play an important feedback role in phototaxis (McEwen, 1918; Dürrwächter, 1957; Benzer, 1967), however, wings do not appear to be important in geotaxis.

The use of mazes to characterize phototaxis introduces an ancillary set of variables and intensifies the effect of some of those mentioned above. Crowding in the starting tube leading to the first choice point may have a distinct influence on the number of flies surviving and entering the maze as well as their rate of movement. The connection of the starting tube to

a maze may also influence movement much as the connection between any pieces of apparatus may have an effect (Dürrwächter, 1957). The width of the channels and the use of one way cones to minimize retracing of paths by flies in the maze also may alter progression through the maze. The tendency of flies of various strains to follow other individuals or to hug the wall of the maze by repeating their choices are other variables (Hay, 1975). The method of computing phototactic scores may also vary. Some investigators report the percentage of all flies in the starting tube that reach the terminal tubes of the apparatus. Other investigators do not supply this information and evaluation of survival in the maze is difficult. Selection for response in a maze may introduce problems of differential relative survival in the maze environment with the variables of desiccation and food for many hours (Murphey and Hall, 1969). The speed of locomotion through the maze may also be involved. It should be stressed that all of the variables mentioned, with the exception of those pertaining to the stimulus itself, apply with equal force to studies of geotaxis in a similar variety of experimental designs. Particular physical and biological variables may interact to modify geotactic response in a different fashion from their combined effect on phototaxis, but the possibility of the interaction cannot be overlooked.

Carpenter (1905) noted the positive phototactic response of *D. melanogaster*, the accentuation of it by mechanical stimuli, and the kinetic as well as the directive influence of light. Very bright light did not have a directive effect. The odor of acetic acid or fruits has been reported to be capable of affecting the preference for light (Lutz, 1914).

In addition to the use of eye color mutants, a number of workers have explored the behavioral capabilities and reactions of flies performing phototaxis. McEwen (1918) removed the tibia and tarsus from the midlegs and found little effect on phototactic response. Removal of the wings produced a decrease in photopositive response and the mutation vestigial was slower than wild type (McEwen, 1918; 1925). Campan (1964) confirmed McEwen's claim for the depressing effect of antennectomy on photopositive response, but found no effect of this operation on the augmentation of phototactic response by vibration (Campan, 1966). Removal of antennae could influence general locomotor activity and thus exert an effect of phototaxis. Medioni (1959c) reported a graded reduction of photopositive response, up to 43%, without one or more ocelli.

Dürrwächter (1957) reported an extensive study of phototaxis and geotaxis, testing flies that had been reared in each of three different conditions. One group was reared in a normal light–dark cycle, another was reared in constant light, while the third was grown in constant darkness and exposed to 20 sec of light when food was changed.

Adults were tested in a 50-cm^2 open field with two 6-volt lamps at opposite ends. The field was marked off in a grid pattern. A trace was made of the orientation path of individual flies. When a fly was near a wall of the chamber a light at the opposite end was turned on and the angle of movement to the light was calculated from the grid pattern. Positive phototaxis diminished during the course of an experiment. Wild type flies generally had straight paths towards the light source and ran faster than other strains tested (+/*ClB,e,y cv v f,cn,w sn*^{3}*,B,L;Cy,v;e,vg,cu*). Dark adaptation had little effect on performance. The orientation of the mutant vestigial was good though inferior to wild type, but flies with the mutation curled showed tiny wobbles in the path that was traced for them. The orientation of a *vg;e* strain was less exact than the other strains.

Another series of tests was performed using groups of 15 flies in 60-cm tubes of 0·8 cm diameter, closed at one end. Counts were made of the number of flies in each 15-cm section of the tube at 2, 4, 6 and 10 min. Flies were run three times in each tube for the initial characterization of the strains. The section nearest the light was given a weighting factor of 3, the next section 2, etc., and the weighting factor x number of flies/section constituted a running index. Each strain tested had its own performance curve and index. In general, short wing mutants had a performance level below that of other strains. Mechanical stimulation altered the behavior of many strains as did changing the connection to the starting tube. After 50 or so trials, mechanical stimulation no longer had an effect. The running index began to decrease after 20 trials, although the speed of movement in the tubes remained at about 120 cm min^{-1}. Flies tested for a phototaxis reaction for 90 trials nearly fail to react. Phototaxis and geotaxis could be exhausted independently of each other and flies failing to respond to one would, if tested in the other condition, perform at normal levels. *Drosophila melanogaster* reared in darkness for several generations apparently showed stronger phototaxis and a greater sensitivity to light orientation as opposed to geotactic orientation than flies reared normally. Payne (1911) reared 69 generations in darkness and while such flies did not respond significantly faster, they did show reduced activity. Flies maintained in constant light showed a diminution of phototaxis and greater sensitivity to geotactic orientation. Differences in behavior were accentuated by shifts to different environments.

D. melanogaster wild type and mutant individuals in a horizontal tube tended to run with their dorsal side downwards. In a vertical tube these flies moved with their ventral side to the light and in an oblique tube with their dorsal side to the light. A species difference may be involved in this behavior since *D. funebris* individuals in a horizontal tube apparently always ran with their ventral side down. Additionally, flies of this species reared in constant darkness tired more easily, perhaps suggesting selection for inactivity. In all rearing conditions, *D. funebris* showed none of the effects attributed to *D. melanogaster* reared in the different conditions, and in general was less subject to environmental effects. Individual *D. funebris* flies tended to stay at the end of a tube while *D. melanogaster* flies would remain 2–3 min and then move away from the light. Finally, *D. funebris* flies moved more slowly, taking 2 min to move a distance covered by *D. melanogaster* individuals in 34 sec.

The use of *D. melanogaster* and its mutants in phototactic assays has demonstrated a considerable amount of variation among strains. As has been noted above, even known visual system mutants have, on occasion, been reported to perform as well as wild type in some tests. The effect of various morphological mutants on phototaxis (see Table I), unless affecting physiological capability in a predictable fashion, should be taken as provisional. Those studies comparing isogenic lines differing only in the chromosome region of interest are less problematical to evaluate.

3. *Species*

In addition to demonstrating differences in activity between widely divergent species in particular assays, and differences among strains of the same species, phototaxis has also been used to characterize variation between pairs of closely related species. A comparison of numbers of flies moving along a tube (Design 1) in bright and dim light showed *D. melanogaster* to be more active than *D. simulans* in both conditions (McDonald and Parsons, 1973). Various strains of *D. melanogaster* revealed consistently different responses but strains of *D. simulans* demonstrated differences among them only in bright light. Comparison of four strains of each of these species in a gradient of light intensities (Design 2) demonstrated that both species preferred the higher available intensities with *D. simulans* showing the greater phototactic response and *D. melanogaster* showing a broader spatial distribution among intensities (Parsons, 1975). The detailed studies by Koch (1967) characterized differences between another pair of closely related, European, species and demonstrated that the activity of *D. subobscura* is decreased by bright light while that of *D. obscura* is increased. Directional differences in photoresponse have been demonstrated as well for a North American pair of sibling species of the *obscura* species group. An open field design (Rockwell and Seiger, 1973a) allowed flies to choose among portions of a light gradient of three intensities perpendicular to a temperature and humidity gradient. The responses of strains of *D. pseudoobscura* and *D. persimilis* were not homogeneous within species. While the overall data did not permit a direct comparison, the

distribution profiles of the various strains could be successfully used to characterize populations of the two species. In later work (Rockwell *et al.*, 1975) populations of these two species were compared under "at rest" and "disturbed" conditions in an open field two choice situation at constant relative humidity. Significant intrapopulation differences in the "at rest" photoresponse for both species were found. There were no such differences after mechanically agitating the chamber and measuring the "disturbed" photoresponse. A higher mean photoresponse was found for this measurement for both species. The species showed a greater difference between them in the undisturbed condition. *Drosophila persimilis* showed a higher mean response for both conditions. An interesting corollary of this analysis was the finding, based on morphometric analysis, that the differences found for the photoresponse of the two species resulted from their behavioral architecture which was not the same as that underlying morphological species characteristics *per se*.

Drosophila persimilis was also shown to be more positively phototactic than *D. pseudoobscura* in a maze (Design 3) photoresponse assay (Spassky and Dobzhansky, 1967; Polivanov, 1975), and sampling of various strains of the two species revealed considerable intraspecific variation. *Drosophila pseudoobscura* was very close to a neutral photoresponse (Dobzhansky and Spassky, 1967).

A wild type population of *D. subobscura*, given a choice of five light intensities, distributed itself preferentially among three intensities with 60% going to bright light, 10% to the dimmest light and the remainder to intermediate intensities (Kekic and Marinkovic, 1974). A preference for an optimum light level of white light has also been shown for a species of *Calliphora* (Lipinska-Skawinska and Chmurzynski, 1968).

Drosophila robusta has been characterized as showing a low level of spontaneous phototaxis (Carson, 1958). Males were more active under all test conditions. In some strains no flies moved in 15 seconds of a test. *Drosophila hydei* showed considerably higher levels of photoresponse. Differences between *D. melanogaster* and *D. funebris* in the position assumed in a phototaxis tube represent alternate choices of motor response. The accentuation of behavioral differences that occurs when flies are shifted to a new environment may reflect a "disturbed" level of response. It is not known whether this choice of position can be altered in a disturbed condition.

For several species then, a preferred light intensity seems evident in laboratory tests. The light preference may differ between closely related species and may or may not be associated with a higher activity level *per se*. Differences in photoresponse between strains of a species may disappear under conditions where an escape response is incorporated into the testing regime. This may suggest that although a high response level capability is present, it is not manifested unless the individual is under stress.

B. Genetics of Photoresponse

The visual system mutations affecting receptor cells and higher order neurons involved in visual physiology have been discussed elsewhere (Pak and Grabowski, Ch. 9), while the effect of various morphological mutants on photoresponse have been presented earlier in this chapter.

When Hecht and Wald (1934), using *D. melanogaster*, determined the intensity of light required to elicit the optomotor response, a significant degree of individual variability was noted in the stimulus intensity necessary for the response to occur. Siegel (1967) used a selection regime of 30 generations to produce three strains which showed low, middle, and high optomotor scores. He then measured the minimum light intensity required to elicit a response in these strains and found that the threshold function (plot of visual angle *vs.* intensity) was identical to that of wild type. These three different strains, however, showed different thresholds necessary to elicit the response. Thus, the basic stimulus response relationship was identical, in that the visual system processed the information in the same way in both wild type and the selected lines, but the minimum light level required was different for different lines. Gotz (1970), using inbred lines, did not achieve any selection response in 8 generations but each strain showed a consistent level of optomotor response.

Populations may therefore be expected to show variability in responding to visual stimuli of various kinds each of which may involve processing by different portions of the visual system. The species differences noted above may involve, in part, different set points at which particular elements of the system are operating. This in turn reflects the genetic organization of the system as translated to developmental and physiological pathways.

Efforts to unravel the genetic complexity of the system have used several approaches which have provided information that may be useful in different ways. Mutations affecting physiological function can be used to dissect the function and structure of the visual system. It might be noted that isolation of visual system mutants was effected by use of three different assays for phototaxis (Hotta and Benzer, 1969; Pak *et al.*, 1969; Gotz, 1970). Assays of the photo-behavior of populations may provide insight into the overall genetic architecture of photoresponse and its relevance to the behavior of the organism, which may have implications for population and ecological genetics.

Phototaxis of some visual system mutants, even when outcrossed to various marker stocks, is sufficiently different from the panoply of responses

designated wild type as to allow conventional genetic mapping of the non-phototactic mutant (Merriam and Benzer, 1969; Grossfield and Pak, 1971).

Hirsch and Tryon (1956) and Hirsch and Boudreau (1958) suggested photo- and geotaxis as heritable traits and proposed use of a multiple unit maze. Hadler (1964a, b) explored use of the technique, stressed the population aspect of its measurement, and demonstrated that while genetic control was polygenic, the X-chromosome was implicated. Other workers, using selection in mazes, have demonstrated the polygenic nature of genetic control of phototaxis in *D. melanogaster* (Walton, 1970; Oshima and Choo, 1972; Choo and Oshima, 1973; Markow, 1975). It has been suggested that selection might be more effective using older flies (Elens, 1972b). One study (Walton, 1970) reported negative phototaxis to be partially dominant, but interpretation is difficult since mutants affecting photoresponse were employed. Markow (1975) selected for maze photoresponse in populations having one or more chromosomes heterozygous for inversions which restricted recombination. Selection in the presence of inversions in any one of the three major chromosomes was as effective as selection in an inversion-free population. Restricting recombination in the first and third chromosomes reduced effectiveness of selection for positive phototaxis and the presence of inversions on all three chromosomes restricted selection response for negative phototaxis. This is in agreement with studies of *D. robusta* photoresponse (Carson, 1958) where selection was not as effective in populations with high inversion heterozygosity. Sex linkage for genes determining negative phototaxis has been reported (Markow, 1975b) and negative phototaxis has been found dominant to positive phototaxis (Choo, 1975). This latter study showed that photopositive populations respond to reverse selection twice as rapidly as photonegative populations.

Studies with *D. virilis* (Oshima *et al.*, 1972) are in agreement with the work reported above for *D. melanogaster* in suggesting that negative phototaxis measured in a maze was partially dominant. Individuals in populations selected for positive phototaxis weighed less and were smaller and faster while the negative phototaxis line deposited 20 % more eggs and included a fraction (25 %) of flies that were inactive (Oshima and Choo, 1972, 1973).

Analysis of lines of *D. pseudoobscura* differing in maze phototaxis demonstrates that genes responsible for phototaxis are on the autosomes (Woolf, 1972). Additional studies (Dobzhansky *et al.*, 1975) indicate that the third chromosome exerts the strongest effect on phototaxis, with the second, X, and fourth chromosomes following in order of effectiveness. Individuals of negatively phototactic populations tend to have increased eye size while sexual dimorphism for phototaxis is reduced in positively phototactic populations (Pasteur, 1969).

Relaxation of selection resulted in a convergence of phototactic scores in mazes which was almost as rapid as the initial divergence (Dobzhansky and Spassky, 1969; Dobzhansky *et al.*, 1972), indicating that the architecture of the trait, while permitting rapid and marked response to selection in both directions, does have a homeostatic set point. Heritability of phototaxis in maze populations selected for positive or negative response tends to decline as selection progresses (Dobzhansky *et al.*, 1969; Richmond, 1969).

In contrast to *D. pseudoobscura* which tends to be neutral when tested in a phototaxis maze (Dobzhansky and Spassky, 1967), *D. persimilis* tends to be photopositive (Polivanov, 1975). This species showed selection to be effective in both directions but unlike *D. pseudoobscura* the response was asymmetric, with photopositive behavior showing some directional dominance over photonegative behavior. Interspecific differences were almost obscured by the attained level of response to selection.

Drosophila subobscura selected for the ability to choose among five light intensities showed the greatest selection response initially. This response declined in subsequent generations. Over 19 generations the proportion choosing the dimest light went from 8 to 30 %, while those choosing the brightest light rose from 60 to 78 % and the middle range proportion rose from 32 to 55 % (Kekic and Marinkovic, 1974). The rise due to selection was thus roughly 20 % in each case. Since the proportion originally choosing dim light was smallest, selection intensity in this line was commensurately the greatest. Heritability declined during the course of the selection regime. Analysis of hybrids between the two extreme lines showed that the mother's genotype influences the behavior of their progeny. The use of micronized dusts to mark individual flies demonstrated that 33 % of flies chose the same light intensity in both of two 24-h tests and 31 % chose an intensity contiguous to that of their first choice.

In summary, in *D. melanogaster* and *D. virilis* negative photoresponse is dominant, with X-linkage for the trait in *D. melanogaster*. The polygenes influencing *D. pseudoobscura* photoresponse are mainly on the autosomes. Thus the genetic architecture of photoresponse differs among species. There can be correlated morphological changes to selection for photoresponse. Heritability of the behavior is low and it may be well to consider the meaning of heritability at this point.

Heritability is an estimate of the genetic component of the observed phenotypic variance for any particular trait. The remaining phenotypic variance is the environmental component of the phenotype. A heritability of 100 % suggests that the observed phenotype is entirely genetic in origin. A value of zero suggests that the phenotype in question is entirely due to environmental effects. A low value of heritability for a trait indicates a small genetic contribution with respect to that trait in that environment.

An alternative explanation would be a high level of environmental variation for that trait. The greater the genetic variability for a certain trait, the greater the effect of selection can be in altering the frequency of genes controlling the trait. If a population in a particular environment were completely homozygous for all genes determining a particular trait, then selection could have no effect. If selection is effective in altering the expression of a trait then the population contains genes affecting the expression of the trait. A population which no longer responds to selection, or reaches a selection plateau, has little remaining genetic variation; the population has been rendered essentially homozygous for genetic variants affecting the selected trait. A decrease in heritability over the course of a selection regime indicates that the genetic variability for the trait has been reduced. The decrease does not mean that the trait no longer has a genetic component. Heritability has been computed in a number of ways which need not be summarized here.

Thus although there is a genetic component to phototaxis, it is small. Given the fact that mutations which may affect photoresponse were used to determine which chromosomes had an effect on the behavior and that environmental effects are quite large, the use of phototaxis as an assay has not been that informative with respect to the mechanism of the behavior itself. There is no question that populations can more easily be characterized by behavioral assays and that population assays provide information useful both in the analysis of population phenomena and in developing assays to screen for mutations perturbing specific systems.

At the level of the individual organism, the operation of physiological mechanisms at different thresholds and CNS control points raises the question of phenotypic variability. Different genotypes can give rise to similar phenotypes for photo- and geotaxis, activity and larval feeding. This suggests homeostatic mechanisms affecting the degree of observable plasticity. The extent of individual variability has not been clearly delimited. Selection for phototaxis has produced effects, while work on behavioral control mechanisms has defined some aspects of stimulus response parameters. Yet the precise target of maze selection is not clearly known. The effects of selection on large numbers of individuals have differentiated collections of individuals, while information on the exact response of those individuals has been blurred. An exit from this Procrustean logic would seem to lie with the analysis of individual behavior.

One other aspect of phototaxis which may be relevant and useful to population genetics lies with an assessment of photoresponse in a number of different species. There is evidence that species do differ in the genetic architecture of photoresponse and this may be related to their natural environment.

C. Geotaxis

Geotaxis is defined as a directed movement mediated by gravity. Since an organism performs in an environment replete with other sensory inputs the directive effect of gravity alone is difficult to dissect. The proximal cue for orientation with respect to gravity may in some cases be a function of the apparatus used to measure the response.

Carpenter (1905) first noted that *D. melanogaster* was negatively geotactic and that this response was accentuated by mechanical stimulation. Cole (1917) reported that gravity could have a kinetic as well as a directional effect. McEwen (1918) found that removal of antennae had a slight effect on geotactic response while removal of the wings, unlike the case for phototaxis, had no effect on geotaxis. Dürrwächter (1957) demonstrated that phototaxis and geotaxis were controlled independently and that both responses would decrease with repeated trials. Geotactic orientation was stronger for individuals reared in constant light. Flies tested in oblique tubes (40°) gave responses characteristic of phototaxis. Negative geotaxis gave smaller responses than positive phototaxis, and odor was more effective a stimulus than mechanical shock in producing a geotactic response.

The sensory input for geotaxis is poorly defined, yet a negative geotactic reaction is observed in many species. The magnitude of the response is clearly sensitive to modification by light stimuli and the two interact in a complex fashion. There has been some work on gravity orientation in Diptera which suggests that the antennae are involved (Horn, 1975; Horn and Kessler, 1975) but do not entirely determine response to gravity. Walking blowflies hold their antennae out at nearly 20° while at rest the antennae are at about 7°. Immobilization or amputation of the antennae diminishes the ability for gravity reception. Proprioceptor bristles on the first antennal segment (scapus) detect the position of the second segment (pedicellus) and the mobility of the joint between the two segments allows the bristles to control a constant amplitude of movement of the joint. Elimination of antennae results in an increase in photopositive turning, and other stimuli do affect the strength of a geotactic response. This is in agreement with McEwen's suggestion that antennae are involved in geotaxis. Geotactic response is thus closely tied to integrative centers which process other modalities of sensory input. In contrast to phototaxis, the range and capability of receptors involved in geotaxis is far from known. The minimum angle required for geotactic response in *Drosophila* has not been determined in a fashion analogous to the determination of threshold for photoresponse. Horn has used a number of methods for assessing geotactic response with *Calliphora* including tilt boards and measurement of antennal movement. With *Drosophila* however, the same

basic designs have been used to measure the response as have been used in phototaxis, but mazes have been used for all of the selection experiments.

D. Genetics of Geotaxis

Hirsch (1959) demonstrated that populations of *D. melanogaster* isogenic for different chromosomes showed consistent differences when tested for geotaxis in a vertical maze. Directional selection of a heterogeneous population for geotaxis was effective in both directions, thus reversing, in one line, the normal negative response (Hirsch and Erlenmeyer-Kimling, 1961a). Maximum separation of response occurred at 48 generations. Genetic control of geotaxis was found to be polygenic with the X and second chromosome factors leading to positive geotaxis and the third chromosome factors to negative geotaxis (Hirsch and Erlenmeyer-Kimling, 1961b). Selection of this base population for negative geotaxis reduced the effect of the X and second chromosomes and enhanced the effect of the third, while selection for positive geotaxis reversed the effect of the third chromosome (Hirsch and Erlenmeyer-Kimling, 1962). Hybridization analysis, after 65 generations of selection, confirmed the interaction of X and autosomal factors, suggested partial dominance of positive geotactic factors, and revealed considerable genetic variation remaining in the population (Erlenmeyer-Kimling *et al.*, 1962).

Analysis after 133 generations of isolation of the lines, using a technique in which morphological mutants identifying the various chromosomes did not appear in the flies tested, revealed that dosage compensation was present for the X chromosome factors and that males and females differed in the amount of genetic variation for geotaxis present in the X and second chromosomes (Hirsch and Ksander, 1969). Analysis of positive and negative geotactic lines of *D. pseudoobscura* revealed that a major proportion of the genes responsible for positive geotaxis are in a discrete region of the X chromosome (Woolf, 1972). Selection for negative geotaxis in *D. melanogaster* showed continued response after generation 65 but the positive selection line showed no further response. Selection of the positive line for negative geotaxis and *vice versa*, demonstrated that these reverse selection lines achieved nearly the same scores as the lines originally selected for a response in one or the other directions (Hostetter and Hirsch, 1967). Thus, different genetic constitutions may produce the same phenotypic expression of this trait.

A diallel analysis (Walton, 1968) confirmed both the polygenic control of the trait and the dominance of positive geotaxis. No morphometric changes were associated with geotactic selection in *D. melanogaster*. In *D. pseudoobscura*, however, selection lines of positively geotactic flies tended to be larger and have more branches on the arista (Pasteur, 1969). Relaxing selection in *D. melanogaster* lines selected in both directions revealed that reversion to baseline scores occurred more rapidly when flies were maintained on an impoverished food medium than when they were reared on an enriched medium (Walton, 1969). Watanabe and Anderson (1976) found their selection lines of *D. melanogaster* showed a response to bidirectional selection with a heritability of 13% and a suggestion of dominance for positive geotaxis. No loss of productivity, measured as number of progeny, was observed in 10 generations of selection. They observed changes in the frequencies of chromosomal inversions which are in agreement with the results of Hirsch and coworkers in assigning polygenes affecting positive or negative geotactic behavior to specific chromosomes. The clustering of genes affecting this behavior in chromosomal regions is a feature of the genetic architecture of geotaxis.

Selection of *D. pseudoobscura* for positive and negative geotaxis demonstrated that although this species is neutral (Spassky and Dobzhansky, 1967) for the trait in the three karyotypes tested, rapid divergence of behavior can occur (Dobzhansky and Spassky, 1962). Older flies were slightly more geopositive and no effect of temperature in the range 15–27°C was discerned (Dobzhansky *et al.*, 1974) Reversal of selection for positive geotaxis tended to favor *AR* chromosome homozygotes while negative selection tended to favour *AR/CH* heterozygotes.

Estimates of heritability of geotaxis in *D. pseudoobscura* range from an upper limit of 17·5% (Richmond, 1969) to 2·8% (♀♀) and 2·8% (♂♂) for positive geotaxis and 2·4% (♀♀) and 3·4% (♂♂) for negative geotaxis (Dobzhansky and Spassky (1969). As with phototaxis, heritability declines as the number of generations of selection increases (Dobzhansky *et al.*, 1969).

Some strains of *D. persimilis* were found to be neutral for geotaxis (Spassky and Dobzhansky, 1967) but other strains are apparently slightly geonegative (Polivanov, 1976). Unlike the case for phototaxis, no clear differences between geotactic scores of *D. persimilis* and *D. pseudoobscura* were observed. Bidirectional selection for geotaxis was effective in both directions and was more efficient than in *D. pseudoobscura* (Polivanov, 1975). In *D. persimilis* the heritabilities of positive geotaxis, 9·8% (♀♀) and 5·2% (♂♂), and negative geotaxis, 6·4% (♀♀ and 4·2% (♂♂), were practically the same as similar estimates for phototaxis. In *D. pseudoobscura* the heritability of phototaxis is higher than that for geotaxis. These two species then, have different genetic architectures for geotaxis.

The overall picture to emerge from the data is that heritabilities are low, decrease with the number of generations of selection and seem to be somewhat higher for maze studies than for open field designs (see Table III).

TABLE III. Heritability of positive and negative phototaxis in *Drosophila*.

Species	Heritability estimate (in %) Positive	Negative	No of generations	References
D. melanogaster	57		29	Hirsch and Boudreau, 1958
	41·2	66·8	30 (bright light)	Hadler, 1964b
	56·4	65·8	30 (dim light)	Hadler, 1964b
	59·7	36·8	25	Oshima and Choo, 1972
	1·6	2·4	35 (selection relaxed)	Choo and Oshima, 1973
	4·5 (♀♀) and 4·2 (♂♂)	4·8 (♀♀) and 3·8 (♂♂)	20	Markow, 1975
D. virilis	17	46	30	Oshima *et al.*, 1972
D. pseudoobscura	9·9 (♀♀) and 10·0 (♂♂)	9·1 (♀♀) and 7·6 (♂♂)	15	Dobzhansky and Spassky, 1967
	9·9 (♀♀) and 10.0 (♂♂)	9·0 (♀♀) and 6·3 (♂♂)	15	Dobzhansky and Spassky, 1967
	16·7 (♀♀) and 15·4 (♂♂)		1	Richmond, 1969
D. persimilis	6·8 (♀♀) and 5·3 (♂♂)	8·0 (♀♀) and 6·4 (♂♂)	10	Polivanov, 1975
D. subobscura	13·0		2 (dim light)	Kekic and Marinkovic, 1974
	1·9		19 (dim light)	Kekic and Marinkovic, 1974
	11·0		2 (bright light)	Kekic and Marinkovic, 1974
	1·9		19 (bright light)	Kekic and Marinkovic, 1974

Higher heritabilities are probably a result of the intense selection possible with the mazes. Selection for geotaxis does not appear to produce large correlated effects. Most of what is measured in these experiments is environmental rather than genetic in origin. Different genotypes can give rise to similar phenotypes. This suggests that there are homeostatic mechanisms operating in populations which affect the degree of observable plasticity. Since the precise target of maze selection is not known, the value of geotactic selection for analysis of the behavior and its underlying physiology is tenuous. Modification of the technique to detect mutations or discrete alterations in response would seem to offer an approach with higher predictive value for studies of behavioral mechanisms.

E. SPONTANEOUS LOCOMOTOR ACTIVITY

Motor activity which has no immediate significance can be designated as general or spontaneous activity. This is not to ignore internal physiological changes or subtle environmental inputs but rather to illustrate the difficulty of stipulating the proximate causality responsible for alteration of motor output of a complex system. It may well be that foraging or arrestant behavior involved in habitat selection relies on precisely this kind of motor output. The correlation between satiation and activity supports this view. The level of spontaneous activity can easily be altered by a number of stimuli including mechanical shock, light, odor, temperature and interaction with animate or inanimate features of the environment.

The level of activity can vary considerably among strains of a species or among species. *Drosophila immigrans* has been characterized as intermediate in activity between active species—*D. melanogaster*, *D. simulans*, *D. hydei*, *D. repleta*—and sluggish species—*D. robusta*, *D. funebris* (Spencer, 1940). Young adults of *D. virilis* have been described as being more active than those of *D. americana* (Stalker, 1942). Use of a maze (see Phototaxis, Section IV, A) to measure the rate of activity has shown that 93 % of *D. persimilis* (*or*) complete the maze in 24 h with 90 % doing so within 8 h, while only 59 % of *D. pseudoobscura* (*gl*) complete the maze and 60 % of them pass through in 8 h (Levine and Kessler, 1965). A population of crowded *D. subobscura* given a series of cages showed 30–50 % of the flies moving to the next cage within 2–3 h. Once the initial crowding was relieved, no further movement to the next cage in the sequence was observed (Wallace, 1968b).

In addition to the effect of spontaneous activity on measurements of other behaviors such as photo- or geotaxis and dispersal, the effect of domestication on spontaneous activity itself is a feature of laboratory strains. Activity levels of wild flies are generally much higher than strains

kept in the laboratory for many years. Accentuation of this effect may have been produced by rearing in conditions reducing activity (Dürrwächter, 1957). Many mutations may affect the level of activity (see Table I), but the route by which they do so cannot in all cases be ascribed solely to spontaneous activity. Some mutations may simply alter sensory input or reactivity.

Barton Browne and Evans (1960), using *Phormia*, found that locomotor activity was a function of crop volume and not of metabolic state or blood sugar concentration. The mechanism involved was different from that whereby feeding of sugars altered tarsal taste thresholds. Green (1964a, b) observed that locomotor activity was immediately depressed when flies were fed to repletion and that, on subsequent deprivation, activity increased at a rate dependent on the concentration of sugar ingested. He determined that the foregut receptors (see Feeding Behavior, Section IV, I) monitored the contents of the alimentary tract and controlled the release of a hormone from the corpus cardiacum to the hemolymph. Locomotor activity can thus be considered, in part, a feeding response.

Connolly (1966) found that locomotor activity in *D. melanogaster* was also dependent on food deprivation. He used an open field apparatus consisting of a Plexiglass box (10 × 10 × 0·5 cm) with the top marked in a grid of 1-cm squares. The measure of activity was the number of squares crossed in 5 min. Selection for active and inactive strains using the ten pairs scoring at either extreme in this apparatus succeeded in producing significantly divergent lines. By generation 25 the inactive line had little margin for further change. Heritability, calculated as regression of offspring on midparent, was 51 % for spontaneous activity. This suggests that considerable genetic variation influencing activity exists in this population. Connolly demonstrated the reality of the changes in activity with tests of the same lines in three different pieces of apparatus: a system of channels, a circular runway intersected at 5° angles by lines which are counted as flies cross them in a one minute test, and in a series of funnels. All tests were in agreement as to the significantly different strains produced by selection.

Ewing (1963) had selected lines for high and low activity and found a response only for lessened activity. He determined that selection had affected reactivity, or the interactions between flies or between flies and their environment. In these strains the flies reacted to visual stimuli from the sides of the apparatus. Connolly (1967) analysed his selection lines for the rate at which they cease to respond as a measure of reactivity. Both selection lines showed greater reactivity than a control line but the primary difference was in the level of spontaneous activity *per se*. Activity and reactivity were interpreted as being under the control of two separate systems.

Ewing (1967) found that the pattern of inheritance for activity depended on whether activity was measured in a circular runway or in a series of funnels. He commented that the spontaneous activity may not reflect the underlying genotype. A modification of the latter piece of apparatus was used in a selection regime that was effective in both directions (Grant and Mettler, 1969; Coyne and Grant, 1972). A series of connected chambers (30 ml dropping bottles) was tapped twice every twenty seconds for five minutes and high and low responding flies were used to produce the next generation. This response was interpreted as an escape reaction. The heritabilities for the low response line ranged between 3·6 and 7·6 % for 1–18 generations, while the high escape line heritabilities ranged between 5·8 and 14·3 %.

Hay (1972b, 1973a, b) applied the techniques of biometrical analysis to activity as a response to mechanical stimulation. By testing large numbers of individuals with a time sampling technique he was able to analyse diallel crosses of six inbred lines as well as F_1, F_2 and back-cross generations of the extreme strains. The time sampling method involved scoring the activity of single flies in glass tubes as activity, preening or inactivity every 6 sec for a period of 60 or 120 sec. Flies were stimulated by a tap prior to obtaining the time sample record. Dominance for high activity was found and it is suggested that the genetic architecture of activity is the result of directional selection for high activity. Activity declined over the first 15 days of adult life. In unfavorable conditions the least active flies showed the highest mortality. The inbred lines were less active when tested in groups. Angus (1974a, b, c) confirmed these findings and noted that dispersal increases when flies are starved. He observed a change in the level of activity in response to a shadow passing over the flies. Luchnikova (1966) analysed the progeny of two extreme inbred lines and concluded that both the X chromosome and the autosomes were involved in the control of activity. A reduction in the level of activity, and consequently in the amount of desiccation, was observed in irradiated *D. melanogaster* (Lamb and McDonald, 1973). This behavioral response was thought to have increased heat tolerance of flies in the experimental conditions used.

Choo (1975) selected two lines of *D. melanogaster* for slow and rapid "walking behavior". Flies were given 5 min to traverse eleven connected 150-mm test tubes. Each tube was separated from the next by a 5-mm aperture in a black background. The apparatus was illuminated at one end and movement was toward regions of increasing light intensity. Flies remaining in the starting tube were designated slow while those reaching the terminal tube were designated fast. Hybridization of the two lines after each had reached a consistent level of response, 3 generations for the slow line and 6 generations for the fast line, showed relative immobility to be

"dominant" to rapid movement. These results are in agreement with those cited above in that they demonstrate that both high and low rates of movement can be selected for. They also underscore the fact that, experimentally, it is difficult to require flies to move less than the minimal amount permitted by the apparatus. Since the apparatus used by Choo confounded walking, phototaxis and olfaction it is not surprising that the response to selection was far more rapid than that in Connolly's (1966) selection lines. Choo's results are not in agreement with Hay's results which suggested dominance for high activity. Given the differences in apparatus and the complexity of the stimuli in Choo's apparatus, it may be assumed that quite different responses were being measured in the two cases.

These analyses illustrate that the genetic architecture of locomotor activity seems to play a role in dispersal under poor conditions. The difference in heritabilities found in the several studies of selection lines may suggest that the escape response represents a "disturbed" reaction which is under different control from the "at rest" measurement of spontaneous activity. Similarly, the biometrical analyses were performed with mechanical stimulation and, while a change in light level did alter the response in one set of measurements, no systematic set of data comparing "at rest" and "disturbed" activity has yet been obtained. The sensitivity of this mode of analysis in dissecting genetic architecture might resolve the question of whether a real difference exists in activity measured under the two conditions as was shown for "at rest" versus "disturbed" photoresponse (Rockwell, *et al.*, 1975). The fact that the selection lines did not drift back to control values, as is the case for maze phototaxis, suggests that different homeostatic mechanisms may be operating.

Analysis of Connolly's selection lines for a number of biochemical correlates of activity revealed several consistent differences between inactive and active strains (Tunnicliff *et al.*, 1969). No differences between inactive and active lines, each selected for over 100 generations, were found for serotonin, cholinesterase or γ-aminobutyric acid (GABA). On the other hand, noradrenaline levels were highest in the active strain and lowest in the inactive strain and dopamine levels were highest in the inactive strain and lowest in the active strain.

A balance between these two compounds was suggested as a mechanism for mediating the level of activity. Rearing flies of the high activity strain with γ-hydroxybutyric acid, which increases dopamine levels, resulted in a decrease in spontaneous activity of these flies (Connolly *et al.*, 1971). Control lines were unaffected. Thus a balance of the two amines, noradrenaline and dopamine, may control spontaneous activity levels. The relationship of these to the secretion of the corpus cardiacum which stimulates movement in starved flies (Green, 1964a, b) is not currently

known. On the basis of this hypothesis, poor environmental conditions would alter the biochemical balance in the direction of increased spontaneous activity.

Another aspect of the biochemical basis for activity is present in the work of Geer *et al.* (1971) who found that maximum adult activity resulted from raising *D. melanogaster* on a diet supplemented with choline and carnitine. While feeding choline to adults increased activity, the activity level was not as high as that of flies raised on a supplemented diet. Carnitine alone enhances activity levels. Choline is thought to be involved in phosopholipid synthesis while carnitine may exert its effects by serving as a substrate for mitochondrial enzymes. While these dietary supplements do increase the growth rate of larvae, nothing is known of their effect on larval behavior.

The response of *Drosophila* to electrical and magnetic fields constitutes one aspect of activity which may possibly be found to be relevant to both laboratory and field studies. Given the kinds of apparatus used in some learning paradigms and in measurements of the capabilities of flies held in fixed positions in various "open loop" experiments, the individual experimental subjects may be exposed to unscheduled stimuli which they may be able to detect. The number of flies moving at 10-sec intervals in experimental and control periods of 15 min duration was used as an assay for the effect of an electric field on *D. melanogaster* activity (Edwards, 1960). A variable potential difference across the experimental chamber resulted in flies being exposed to gradients ranging from 10 to 540 volts/cm, depending on the applied voltage and the position of a fly in the chamber. Activity of both *Drosophila* and *Calliphora* was temporarily reduced by exposure to a gradient of constant polarity as low as 10–62·5 volts/cm. Reversing the polarity at 5-min intervals prolonged the reduced activity of *Drosophila* but not of *Calliphora*. *Drosophila melanogaster* is thus more sensitive to alterations of electric field than *C. vicina*. Size considerations may play a role in this sensitivity but the mechanism of detection is unknown. Picton (1966) exposed *Drosophila* to a 2G magnetic field and 3 volts/cm electrostatic gradient and reported a tendency for flies to run to the left, which was accentuated by these fields. If confirmed, these tendencies may play a role in evaluating the performance of flies in maze or choice situations. There is a suggestion for a slight turning bias in *Drosophila* (see Learning, Section IV, O), but any such bias can too easily result from details of the apparatus.

In summary, activity has been measured in a variety of ways and is found to vary among species and strains. The concept of activity level includes a number of variables, some environmental, others intrinsic to the fly. There is genetic variation in populations for both high and low activity

levels. Some measures of activity may include an escape response, the reactivity of flies to features of their environment, or the confounding of multiple variables in assessing activity. Some biochemical correlates of activity are known; both putative neurotransmitters and compounds involved in anabolic aspects of metabolism show effects. The response of flies to physical forces other than temperature and visible light has not been explored in detail. Neurologically, the control of activity is unknown, extirpation experiments of specific portions of ganglionic centers have not been performed, nor have stable electrophysiological recordings from such centers been reported. Since activity is in a very real sense an operationally defined behavior, it is certain to be used to measure a wide range of behavioral capabilities from drug responses to ecological parameters. Hopefully future work will attempt to assess the variables as well as to quantify the norms of reaction associated with any particular genotype. Only in rare instances will apparatus-specific activity be of general utility.

F. Locomotion

Flight in *Drosophila* has been studied by means of observations and measurements of both tethered and free-flying insects. Tethered flies can be induced to fly by removing tarsal contact and subjecting the fly to a puff of air. When tarsal contact is lost, normal flies open their wings, tuck their pro- and mesothoracic legs against the underside of the thorax and extend the metathoracic legs on opposite sides of the abdomen (Vogel, 1966). The rear pair of legs may serve a steering function as they project downward (see Vogel, 1967; Weis-Fogh, 1973). Vogel determined that *D. virilis* achieves level flight (lift = weight) at 200 cm/sec and a body angle of +10°. The head is thus pointing up at this angle from the horizontal. Lift was found to vary directly with body angle and Vogel suggests that the direction of output force, or thrust and lift, is controlled by altering the body angle. Parameters of wing articulation such as the amplitude or stroke angle of the extreme wing positions, stroke plane, wing pitch and stroke frequency were independent of body angle.

Flies without experience in moving air performed more steadily in still air (= zero airspeed or simulated hovering) than those with prior exposure to a wind tunnel (Vogel, 1966). Turning off the wind tunnel usually caused experienced flies to loose flight posture and initiate grasping movements with the legs. Flights in still air, even when steady, resulted in the tarsi of the first two pairs of legs hanging down rather than being pressed against the body. No effect on flight reactions was found for body volume or hind legs measured in still air (Gotz, 1968). Hocking (1953) noted that loss of

tarsal contact was a dominant stimulus for flight, followed by visual stimuli and airflow. In this respect *Drosophila* relies on visual stimuli more than some other higher Diptera. Individuals flew faster if an object were visually overtaking them but flight was inhibited by stripes beneath them. Flies tried to land on black and white patterns but flew well over uniform black or white backgrounds.

Observations on freely flying *Drosophila* support the visual nature of their guidance system (Kellogg *et al.*, 1962). Upwind migration to an odor source was only possible when flies could see fixed reference points. Movement of objects past a fly and especially under it was intimately related to its orientation. Upwind guidance was effected by orientation of the apparent movement parallel to the body axis to minimize apparent velocity. Downwind guidance maximizes apparent velocity. Across-wind orientation maximizes apparent motion perpendicularly to the body axis. Flies would follow a projected pattern away from an attractive odor if the pattern speed was higher than wind speed in a wind tunnel. Flies would also pass the bait if pattern motion was at an angle to the wind direction. The guidance of flying *Drosophila* was shown to involve a sequence of responses. Perception of an attractive scent induces upwind movement mediated by vision to establish the direction of movement relative to wind direction. Within roughly 0·1 sec after losing an odor, a fly turns and flies perpendicularly to the wind. If the scent is regained, it turns upwind. If not, it may fly across wind in the reverse direction or up or down. The across-wind trials last about 0·3 sec. Failure to regain the scent results in a downward flight of 15 to 60 cm before resumption of across-wind trials. Darkness results in a reduction of flight and that which does occur is very close to the ground. Little flight occurs in the absence of attractive odor. Such flight is generally straight, without reference to wind direction. A uniformly diffuse odor with no wind induces flies to land on the nearest surface and crawl about.

Measurement of the flight reaction of tethered flies has confirmed the role of visual input (Gotz, 1968). Motion detectors control the magnitude of the force of flight. Pattern motion from below will thus increase the thrust. The wing articulation parameters are not influenced by pattern motion, with the exception of wing beat amplitudes or stroke angle on either side. The torque responses to pattern motion could be attributed to the differences of wing-beat amplitude on the two sides of a tethered fly. The articulation of the two wings involves common frequencies of wing beat but not common amplitudes. Visual mediation of independent torque and thrust control is interpreted by Gotz as involving a minimum of two contralateral and two ipsilateral nerve connections between the visual system and the effector system.

The landing reaction of flies is mediated by visual stimuli (Braitenberg and Ferretti, 1966). When an object appears to approach a fly the legs are lowered from their characteristic flight position and extended toward the landing site. A landing response is evoked when a stimulus appears to be an expanding image as determined by the change in light intensity at successive ommatidia, the number of ommatidia stimulated and the rate of their successive stimulation. A rotating disk with a black arithmetic spiral on a white background can produce a pattern of expansion or contraction, depending on the direction of rotation. The landing reaction has a threshold in terms of the angular velocity of expansion of the pattern; an increase in distance between fly and disk necessitates an increase in either velocity of rotation or width of spiral to produce the reaction. Similarly, a decrease in distance gives the reaction at lessened velocity and narrower spirals. Decreased light intensity facilitates the reaction, thus accounting for the tendency of flies to land in corners or shady spots. The preference for a particular landing site is determined by many variables, including the wavelength and intensity of light reflected from a surface.

The halteres of flies are involved in stabilization of flight (see Tracey, 1975). Angular rotation of a fly about any of the body axes generates a torque at the base of a vibrating haltere. Campaniform sensilla detect this stimulus and generate input which results in a compensatory alteration of wing pitch to produce a postural change. The halteres vibrate at the same frequency as the wings but in opposite phase. Flies lacking halteres rarely attempt flight and are incapable of maintaining altitude. If induced to fly they lack the minor fluctuations in wing-beat frequency seen in normal flies (Chadwick, 1953). Tracey (1975) described an additional haltere reflex, in *Musca*, involving a compensatory rotation of the head when a fly experiences a rotation about its longitudinal axis. The wing pitch reflex stabilizes flight against small deviations about the axis while large deviations produce a rotation of the head about the axis. The apparent rotation of the visual field produces an additional effect on wing pitch. If compensatory head movements to stabilize the visual field were prevented by fixing the head to the body, flies crashed immediately on release.

Flight in *Drosophila* is powered by singly innervated muscle fibers. The fibrillar indirect flight muscles compress the thorax, providing power to the wings during flight. The indirect wing elevator and the direct and accessory indirect muscles, including leg muscles, are of the tubular type. The ability to jump is impaired if the mesothoracic legs are removed. This is a function of the tubular type tergotrochanteral muscle which is also involved in initiation of flight, producing the first upstroke after the initial downstroke (Pringle, 1957). Hocking (1953) suggested that one-third more

power is required on the downstroke since the ratio of the weights of the muscles involved is 1·36.

When *Drosophila* are flown to exhaustion the wing beat frequency decreases rapidly at the termination of flight but wing movement ceases before dropping below 70–100 double beats/second, or $\frac{1}{2}$ to $\frac{2}{3}$ initial frequency (Williams *et al.*, 1943). Flies may cease wing movement with the wings in the extended position (Wigglesworth, 1949). Flies may rest with increasing frequency but can be restarted by feeding sugars. Different sugars will support flight with varying degrees of efficiency. The normal reserve substance is glycogen and flies will fly faster on it than on glucose (Hocking, 1953) but glucose will restore continuous flight in an exhausted fly within 30–45 sec of feeding (Wigglesworth, 1949). Sucrose may take 1–1·5 min and galactose will support brief but not uninterrupted flight.

Endurance is age dependent, with 18–20 h *D. melanogaster* capable of 133 min of flight, 7 day flies of 278 min and 4 week flies of 100 min. The comparable figures for *D. funebris* are 26, 110, and 26 min (Wigglesworth, 1949). Similar figures are reported by Williams *et al* (1943).

Williams and Reed (1944) reported the effect of a number of mutations on wing beat frequency (see Table I) and Reed *et al.*, (1942) reported that wing beat frequency could be used to distinguish among species and strains of a species. Wing beat frequency is temperature dependent, 150/second at 16°C and 250/second at 37°C for *D. melanogaster* (also see Gotz, 1968), and a positive correlation was found for higher frequencies in species having higher optimal temperatures. If muscle volume is held constant, wing beat frequency increases as wing size decreases. The relationship implies that increased wing loading decreases the wing beat frequency. Similarly, wing mutilation increases the wing beat frequency.

Wing beat frequency (see Chadwick, 1953) is low after emergence, increases to a plateau and remains there until senescence. Males tend to have a higher frequency. Wing beat frequency is positively correlated with temperature until roughly 32°C where it then decreases before reaching the thermal death point. In a water saturated atmosphere, wing beat frequency increases steadily till death at about 40°C. *Drosophila* equilibrates rapidly, within seconds, to shifts of 10°C. There is some evidence that flies reared at 20°C have larger wings and lower wingbeat frequencies than siblings raised at 25°C; larger species may show lower frequencies.

Genetic analysis of wing beat frequency showed polygenic control. The general changes involved affect alterations of the relationship between the volume of wing muscle and wing size (Reed *et al.*, 1942). Harnly (1941) found that various vestigial alleles, when reared at temperatures permitting some wing development, could support weak or controlled flight, while other alleles provided no lift into the air. The vg^{hem} mutant was reported to

be able to jump and run, but not fly. Since this mutation produces degeneration of the right or left mesothoracic imaginal disc, the wing muscles are absent. The tubular muscles of the legs, however, would be present, permitting some movement. This suggests that mutations causing appropriate developmental lesions could be quite useful in dissecting the interaction and control of the musculature involved in movement. Levine and Wyman (1973) have determined that the mutation stripe, which had been reported as being incapable of flight, affects the motor output of flight. Flies carrying this mutant, when given the same stimuli that initiate flight in wild type, show only a partial opening and slight fibrillation of their wings and a lateral extension of all three pairs of legs. The effect of the mutant is interpreted as altering the firing pattern of the motor neurons driving part of the flight system. It seems likely that additional mutants affecting flight capability will be isolated.

Although flight characteristics and capabilities have received a great deal of attention, *Drosophila* and other flies do spend a portion of their lives walking. Walking flies have been used in several assays of visually mediated behavior (see Vision, Section II, A). Detailed investigations of walking (Gotz and Wenking, 1973) reveal that this mode of locomotion is also under visual control. The effect of visual cues on walking can be assessed by holding flies fixed in position and thus disengaged from their environment. This "open loop" condition differs from the "closed loop" activity of freely moving flies since movement of the fly cannot change its visual environment and any motor output reflects the sensory input presented by a controlled visual environment. In the case at hand flies walk on the surface of a small ball while pulling a small metal sledge which keeps them from flying. The ball moves freely on a system of rollers and its movement is controlled by a servo system which counteracts displacements of the fly and maintains the fly in fixed orientation with respect to moving dark and bright stripes on either side. Displacements of the fly are monitored by virtue of the metal sledge deforming a magnetic field of 50 kHz. Thus if a particular stimulus pattern causes a fly to move to the left, the ball rotates to bring the fly back into a forward heading again. A read-out terminal records the components of the fly's locomotion. Most of the locomotor activity is spent in forward motion or longitudinal movement. The terminal also records the rotatory response or tendency to follow stimulus movement or to move in the opposite direction. An average fly moved 55 meters in about 8 h. One fly moved 670 meters in 36 h of continuous walking. In general, flies lost 50% of their body weight during an experiment. The movement detection systems in the eye respond to the horizontal component of the stimulus and respond equally well no matter what portion of the eye is stimulated. There is no functional specialization

of the legs; partially amputated flies could respond with the fore-, mid-, or hind-legs. The motion detecting systems control the thrust of the ipsilateral legs in wild type flies. Thus, front-to-back movement of the striped pattern decreases walking speed. The white eye mutation w^a reacts in just the opposite fashion, with movement controlling the thrust of the contralateral legs and front-to-back movement increasing the walking speed. While flight involves both vertical and horizontal components, walking uses only the horizontal components of the motion detection system. Both flight and walking systems however, have the same resolving power and dynamic range for detecting the horizontal component of the stimulus. Gotz and Wenking (1973) propose that the feedback in the neural interactions linking motion detectors and motor output is of opposite sign in wild type and w^a flies.

Both airborne and terrestrial locomotion of *Drosophila* are thus under the control of visually mediated guidance systems. The information from these processing systems is integrated to produce the appropriate motor output on one side of the body or the other, so that oriented movement continues. The thrust of wings or legs provides power for the orientation. The reflexes involved in orientation and landing are also visually mediated. The visual information is integrated with factors such as olfaction and mechanoreception to achieve continuous directed movement. The degree of motor output can be affected by other factors: rearing conditions, age, sex, temperature, humidity and the composition of the air or walking surface. The decision to locomote, however, involves still other factors such as hunger, sex drive, stress, or escape.

G. Dispersal Activity

Dispersal of *Drosophila* may be active or passive, contingent on the forces that bring an individual to a particular location. Long distances are regarded as examples of passive dispersal while short distances may be considered active dispersal. The relative meaning of these terms is defined by the behavioral component of dispersal. The passive transport of *Drosophila* by winds or other agents has been well documented (Holzapfel and Harrell, 1968; Johnson, 1969; Gressit, 1970; Dobzhansky, 1974). Individual flies have been found up to 900 m in the air over land and up to 430 km at sea, where *Drosophila* spp. were the prevalent Diptera in transoceanic catches. Most individuals were taken between 5 and 22 km from land. The extent to which passive movement of *Drosophila* occurs over short distances is not known.

Active dispersal may include a random movement component as well as directed movement. The latter infers perception of stimuli, integration of

the information and resultant movement towards or away from the perceived source of stimulation. The stimuli thus far known to induce movements towards a source can be visual (Koch, 1967) or chemosensory as demonstrated by many studies with natural or artificial bait. The degree to which random movement may be involved in directional flight is not known. It is not clear whether a particular threshold of activity, other than restrictions imposed by light, temperature or humidity, must be achieved before an individual is amenable to distance stimuli. It is probable that activity can be elicited from inactive individuals by appropriate stimuli acting at a distance, just as random movement can be converted into directional movement by the proper signals. In this latter sense, foraging or substrate localization (arrestant) behavior might be a more appropriate term. The relationship of each species to its habitat will determine the relevance of any one of the factors involved in the balance of inputs producing directed movement.

In presenting the ensuing studies the dispersal rate has been given as meters/day where feasible. Much of the original data is presented as mean squared distance from the point of release to indicate the fact that the movement of flies may be omnidirectional rather than along any one radius at a collection site. For estimation of population characteristics with respect to dispersal this is an excellent precaution against weighing too heavily the occasional outlying individuals. In considering the behavioral capabilities of the individuals in a population it seems preferable to direct attention to individual performance and variability as well as population effects on dispersal.

Release of mutants of *D. melanogaster* in the center of a refuse heap with grids of 63 baits (70 × 90 m) or 121 baits (110 × 110 m) at 10-m intervals demonstrated that the flies barely reached the boundaries of the heap after 2 weeks (Timofeeff-Ressovsky and Timofeeff-Ressovsky, 1940). There was a distinct movement in one direction rather than a uniform distribution of recaptured flies.

Release of a different mutation of this species (Gordon, 1935) indicated that mutant genes could be recovered from a population and that most released flies apparently remained at the point of release. Some descendant individuals carrying the marker gene were captured up to 0·8 km away from the point of release. Rapid dispersal away from the point of release was noted for ^{32}P tagged flies with some individuals recaptured up to 150 m from the point of release. Most recaptures were within 15 m of the point of release (Pimentel and Fay, 1955). Other field tests have shown that tagged flies can move up to 7 km in 24 h but the bulk of released flies were within 0.3 km to 1.9 km of the point of release (Yerington and Warner, 1961). Flies released when marked with flourescent stains dispersed rapidly

and individuals were recovered at distances up to 4.8 km (Wave *et al.*, 1963). In these studies a marked clustering of individuals at attractive sites was noted. Wallace (1970) demonstrated limited dispersal of 1–2 m in field trials for a number of strains and noted that wild populations moved more quickly than laboratory strains when tested for movement through a tube. He also noted that, given a particularly attractive site, flies will travel tens of meters to reach it. Additionally, flies released in an unfavorable environment will disperse extremely rapidly while those released in appropriate conditions show highly localized movement of under 1m. At high population densities flies were observed to spread beyond their breeding sites (McCoy, 1962).

In a study of vineyard populations of *D. melanogaster* and *D. simulans*, McKenzie (1974, 1975) found that the behavior of the two species was differentially affected by the presence of alcohol odor with mean distances travelled of about 2–7 m/day but higher, 8–13 m/day, during vintage. He describes a population of *D. melanogaster* whose individuals move toward a wine cellar during vintage and where overwintering occurs in the cellar, with the overwintering individuals responsible for building up the outside population in the spring. Wallace (1966, 1968a) has estimated that 60–80 % of flies in an area may come from within 25 m. Estimates of dispersal of *D. melanogaster* thus range from 1m or less to roughly 5 km, depending on conditions.

Release of mutants of *D. funebris* (Timofeeff-Ressovsky and Timofeeff-Ressovsky, 1940) in the same sites used for the *D. melanogaster* studies yielded an estimate of 5 m/day but release of flies carrying inversions as markers (Dubinin and Tiniakov, 1946) in a less favorable environment at a different time of year yielded estimates of 50–100 m/day.

Extensive work with *D. pseudoobscura* produced estimates of roughly 56–103 m/day (Dobzhansky and Wright, 1943, 1947) with a mean of 88 m/day for day 1 of recapture. Dispersal on the first day of recapture was higher than on succeeding days and the effective radius of population movement was estimated to be roughly 2 km. Wright (1968) has noted the tendency of these flies to cluster at particular sites after release. Crumpacker and Williams (1973) found dispersal rates 50 % higher (204 m/day) than those in the early studies as well as a non-uniform distribution of the population. Dobzhansky and Powell (1974) found dispersal rates for *D. pseudoobscura* and several related species to be roughly three times higher than the original estimates, with a mean distance of 183 m/day for the first day of recapture, and an increment of 96·5 m/day for the second day of recapture. Flies were recaptured up to 440 m from the point of release. Faster dispersal was demonstrated for the first day of release. In another study (Powell *et al.*, 1976), values of 263 m for the first day and 361 m for the

second day were reported. Wallace (1966, 1968a) estimated that 25 % of *D. pseudoobscura* flies at a site have originated within 25 m of that site, while a figure of 60–80 % would estimate the movement of *D. funebris*.

Work with the European *obscura* group species *D. obscura* and *D. subobscura* (Greuter, 1963) yielded estimates of 101–114 m/day. *Drosophila obscura* oriented towards woodland and dispersed more rapidly there while *D. subobscura* was relatively indifferent. The latter species crossed a wide river more easily, survived desiccation better and in general is more ecologically flexible. *Drosophila obscura* is found mainly inside forests while *D. subobscura* is at the edge of forests or in open meadows. Field observations of flies in transparent arenas (Koch, 1967) revealed that in daylight *D. subobscura* orients toward the forest and at night towards an open field, *Drosophila obscura* orients towards the forest day and night. Similar orientation of these two species occurred in the laboratory where the arenas were surrounded by a cylinder that is half black and half white. For *D. subobscura*, bright light, high temperature and low humidity produce orientation to the dark and low locomotor activity. In the same conditions, *D. obscura* increases its activity and decreases its orientation to the dark. For both species morning activity only occurs above 13°C and both react to temperatures below 10°C with decreased activity and increased orientation to dark. High temperature and light intensity increase activity. Rapid decreases in light intensity increase activity of both species but *D. subobscura* shows a lower threshold to light and temperature for activity *per se*. *Drosophila obscura* is more sensitive to desiccation and responds more quickly to rapid increases in temperature. This study by Koch provides laboratory confirmation of factors involved in dispersal in the field and may be taken as a model system for exploring the ecological differences between sibling species.

The importance of visual input to dispersal is also noted with respect to *D. mimica* (Richardson and Johnston, 1975a) where movement only occurred during daylight. Tagging studies showed movements of 5–14 m, with some flies moving 45 m in one day. Laboratory tests established that flies move into air currents at air speeds below 3·3 km/hour, with a maximum response at 1·5 km/hour. Above 3·3 km/hour flies move with the current and are blown involuntarily at velocities over 8 km/h. Dispersal in this species is thought to occur as a response to wind with olfactory guidance to locate the unique attractive areas provided by their food plant.

Burla *et al.* (1950) estimated dispersal rate for *D. willistoni* in the range of 16–28 m/day. A non-uniform distribution of flies was observed in the areas collected. *Drosophila aldrichi* was found to move roughly 2·6 m/day with most individuals not moving beyond 4·5 m and a few more than 100 m (Richardson, 1969).

Estimates of dispersal for *D. repleta* using ^{32}P label indicate rapid initial movement and a maximum distance of about 300 m with the majority of individuals recaptured at 15 m or less (Pimentel and Fay, 1955).

In an important study, Johnston and Heed (1975) demonstrated that baiting estimates of the dispersal of *D. nigrospiracula*, a cactiphilic species, were an order of magnitude below the actual movement of unbaited natural populations. Bait estimates produced an estimate of 4·8 m/day, while unbaited individuals could move more than 250 m/day.

Thus the dispersal rates of various *Drosophila* spp. are roughly: *D. nigrospiracula* > *D. pseudoobscura* ⩾ *D. subobscura* ⩾ *D. melanogaster* upper range ⩾ *D. repleta* ⩾ *D. willistoni* > *D. aldrichi* ⩾ *D. funebris* ⩾ *D. mimica* > *D. melanogaster* lower range.

It appears that the species with the greatest oligophagy shows the greatest effective mobility while the cosmopolitan *D. melanogaster*, although possessing the broadest range of mobilities, yet is capable of remaining sedentary when localized resources are available.

Conditions under which these estimates are made may vary in a number of physical and biological variables. Temperature, wind, humidity and light level will set upper and lower limits for activity *per se*, but within those boundary limits a normal level of activity may be expected. Experimental design, use of natural or artificial recapture sites, initial distribution of released flies and time to reach maximum recorded distance are contingent variables to be considered in evaluating behavioral components of dispersal.

A laboratory approach to the measurement of dispersal has been suggested by Sakai *et al.* (1958). The apparatus consists of a set of tubes or vials with three radially spaced arms projecting perpendicularly halfway along the length of a tube. Flies are introduced into a tube and stored for 24 hours. Three more vacant tubes are then connected by short lengths of plastic sleeving over the arms of the respective tubes, the assembly is placed in darkness for a specified time and the flies in each tube are counted. These workers consider movement from the central tube to consist of both a random movement of individual flies and a mass movement component resulting from population density. An inbred line of *D. melanogaster* showed movement of 2·3 % of the population per day, while wild strains showed 14 to 22·5 % movement with different strains apparently having different threshold densities for movement, ranging from 40 to 150 individuals. The inbred line required the highest density to elicit movement. Takada (1959) presented some data indicating that different species had different critical densities requisite for movement. The order of species from the lowest density producing movement to the highest was *D. nigromaculata* (30) > *D. ezoana* (50) > *D. melanogaster* (40–50) > *D. virilis* (50–80) > *D. funebris* (250).

As with phototaxis, *D. funebris* was least sensitive to environmental effects. Narise (1962) showed that strain differences exist and selection was effective in increasing movement. Activity of strains of *D. ananassae* and a sibling species, *D. pallidosa*, differing in body color was altered when flies of different origin were mixed in the apparatus (Narise, 1966). Movement of light coloured flies was stimulated by the presence of dark flies while that of dark individuals was reduced by the presence of light colored flies. The magnitude of the effect was dependent on the relative frequency and origin of the flies used. The maximum change produced by any combination was about 10%. Larger effects were produced when combinations of various strains and wild type and vestigial *D. melanogaster* were tested (Narise, 1969). In some cases, activity of vestigial was promoted by the presence of wild type flies while activity of wild type individuals was reduced by the presence of vestigial flies. A similar effect was noted in combinations of different strains of wild type and vestigial (Benzer, 1967).

Tests of combinations of various mutants indicated that the strain of sepia was stimulated by all other strains while the white-eyed double mutant *cn bw* reduced its activity except when mixed with the slightly pigmented w^a strain (Narise, 1974).

Measurement of the dispersal rates of *D. obscura* and *D. subobscura* in this apparatus (Koch and Burla, 1962) demonstrated that the latter species moved less at 25°C than at 18°C while the reverse was true for *D. obscura*. Maximum dispersal of this species occurred at lower relative humidity while the reverse was true for *D. subobscura*. For both species, dispersal was greater on fresh food, and when starved or young. del Solar (1970) has devised a spiral tube apparatus for measuring dispersal and reported some effects of density on the behavior.

The relationship of such measures to field studies is not clear, although the characterization of the two *obscura* group species in the apparatus has been substantiated by field tests (Koch, 1967).

Dispersal occurs within boundary conditions of temperature, light, wind and humidity. The European species *D. obscura* and *D. subobscura* have been shown to orient visually to their preferred habitat. Movement was at rates well above those of the original *D. pseudoobscura* studies. They also showed no crowding effect (Greuter, 1963). Work with the European members of the *obscura* group (see Koch, 1967 and references therein) has concentrated on visual orientation, activity levels and rhythms with respect to light, temperature effects, desiccation and differential movement of species with respect to their habitat. The North American *obscura* group species have been studied from a genetic point of view, with emphasis on dispersion measured by baiting studies and analysis with respect to potential gene flow and population size. Density estimates for these North American flies include 0·38/100 m^2 (Crumpacker and Williams, 1973), 0·61/100 m^2 (Dobzhansky and Wright, 1943) and 0·66–4·4/100 m^2 (Powell *et al.*, 1976). Estimates for the European species have been given as 100/100 m^2 (Begon *et al.*, 1975). While workers on both sides of the Atlantic may be dealing with flies whose population density differs considerably, a synthesis of both approaches would provide detailed information that would be useful in analysing data for all species. It would not be surprising to find that *D. pseudoobscura* and *D. persimilis* differ in their visual orientation in the field. Indeed, given the ecological differences shown by the European sibling species in the *obscura* group and with other groups (see Habitat Selection, Section IV, H) such differentiation would be expected.

The sequence involved in dispersal seems to involve the use of visual stimuli to orient towards a preferred site followed by olfaction subject to visual guidance and finally chemoreception for feeding with the same or possibly different chemoreceptors choosing an oviposition site. Such a combination of stimuli may render explicable the distances traversed by some species without making unrealistic assumptions of olfactory sensitivity. Threshold differences in olfaction among *Drosophila* species appear to exist, but little is known of chemoreception in species other than *D. melanogaster*. Oligophagic species may be of value in exploring the mechanism of discrimination at the integrative level. In contrast to polyphagic species, the difference in sensitivity may be analogous to a threshold shift produced by mutation.

An unused parameter in dispersal studies is the flight capacity of the several species used in field experiments. The change in wing loading noted for species from different climatic regions suggests that local adaptations of the flight system exist in populations. The long wings of the temperate zone radiation of the old world *Scaptodrosophila* in Australia, e.g. *D. inornata*, may represent such an adaptation. Alterations of behavior seen at different temperatures involve, in part, changes in wing beat frequency. Selection for wing size or vibration may reflect changes in wing loading and the ratio of components of wing musculature respectively, both of which may modify wing beat frequency. Biometrical analyses of aspects of locomotion may provide a clearer view of the evolutionary history of these components.

Additional information on the natural movement of specialized species will undoubtedly emerge from studies of the Hawaiian *Drosophila*, as well as from species which show a patchy continental type of distribution such as *D. buzzatii* in Australia, which is restricted to *Opuntia* cactus (Barker, personal communication) and the endemic Australian *Drosophila* (Grossfield and Parsons, 1975).

While measurement of dispersion rates will aid analysis of particular population movements, what emerges in a broader sense is the need for comprehension of how the decision to disperse, or not to disperse, is made. If a population varies with respect to threshold for several modalities, or if the integrative control points responsible for summing the various inputs show variation, then the factor to be incorporated into population models must be an expression of the variance of behavioral plasticity of the population. This may or may not be the same as the proportion actually dispersing since other factors may, firstly, limit movement of those that are sensitive to dispersal stimuli and, secondly, increase dispersal of those not sensitive to these stimuli, but susceptible to other inputs which increase movement.

It might be noted that flies have been shown to disperse rapidly when conditions are too dry, too wet, at stress temperatures, too bright, too dim, or when food is absent. Flies in a situation where conditions are appropriate do not disperse greatly. Flies may leave an area for different reasons depending on the spread of thresholds for each input and its reference control point in different members of a population. Migrants may thus be quite heterogeneous and may represent not only the most active members of the population. Some flies may be more sensitive to all inputs and will depart when a summation has been reached, while others may show a high threshold to a certain input. If that particular input changes, such flies would detect it last. Similarly a high sensitivity would induce a fly to leave before conditions were poor. Thus, depending on prevailing conditions, the most fit individuals would either remain or disperse. This *threshold balance* hypothesis suggests that flies disperse when they are unhappy and remain sedentary and in non-uniform distributions when they are content. Species differ in the effective strength of the individual modalities that are summed to produce movement.

H. Habitat Selection

Drosophila and related genera occupy a wide variety of habitats including rotting fruit and plant parts in deserts and tropical forests, slime fluxes, fungi, flowers, ferns and crabs. A few are parasitic on various hosts. Of the more than 2000 species, very few (10–20%) can be cultured in the laboratory. Many species have a narrow range of host plants, or in some cases a single host plant, which serves as an oviposition or larval substrate. A major problem in rearing such species is inducing females to oviposit. Different species may show different distribution patterns and seasonal frequencies, ranging from a tight nuclear distribution at a food source to a uniform low density distribution (Carson *et al.*, 1970; Dobzhansky and Pavan, 1950; Shorrocks, 1974).

Some species can use various related substrates but show clear preferences for particular host plants or yeasts in the field (Fellows and Heed, 1972; Dobzhansky and Da Cunha, 1955). Preference for the yeast found in the crop of the adult may be shown by some species but not by others (Da Cunha *et al.*, 1951). Adults of some species may be polyphagous on a general type of substrate and show specificity for a single substrate for oviposition (Kaneshiro *et al.*, 1973). The same site may attract different species as the microflora changes with age and sibling species may differ in their order of attraction to the site (Burla, 1955). From these data it would seem that olfaction plays a major role in the general distribution of species and chemoreception operates at the next level where the decision to oviposit is made. The more host specific the species, the greater the degree of host discrimination. The polyphagic species, after initial attraction, sample the substrate in more detail before using it for purposes other than feeding. Some cactiphilic species do not show preferential oviposition among several types of substrate but do show differential survival (Fellows and Heed, 1972). This may suggest that larval behavior may be a factor operating in differential utilization of resources.

Another difference in habitat preference emerges from studies on alcohol tolerance (McKenzie and Parsons, 1972). *Drosophila melanogaster* females with a choice of media containing 0 and 9% alcohol showed a slight oviposition preference for the alcohol medium, while *D. simulans* females showed a distinct aversion to the alcohol-containing medium. McKenzie (1974, 1975a, b) has demonstrated that these two species are differentially distributed and differentially utilize available resources in a vineyard. Of these two species, *D. melanogaster* is the sole resident in the wine cellar where alcohol concentrations are highest. This illustrates laboratory confirmation of a behavioral difference observed in the field.

The effect of dealing with only laboratory strains of a species may be seen in tests of a compound chromosome strain in field experiments with a natural population of *D. melanogaster*. The compound chromosome strain was unable to use the substrate of the natural population (tomato) as an oviposition site (Cantelo and Childress, 1974). In laboratory experiments the compound strain was successful in replacing wild type at ratios above 4:1.

In addition to olfaction, chemoreception, oviposition and larval behavior as parameters of habitat selection, there is good evidence that visual cues are involved (see Grossfield, 1968). Comparisons of *D. obscura*, a woodland species, and *D. subobscura*, which is found at the edge of forests, showed that the former species visually orients towards its usual habitat and disperses more rapidly there (Greuter, 1963; Koch, 1967). For some species there may be a shift in the sensory modality used to determine location at

any point in time. Such a shift may also be involved in microhabitat choices. This implies that once an individual is in a certain environment, or balance of sensory inputs, there is increased sensitivity to particular stimuli. The same stimuli would be ineffective at other times.

One example of a particular stimulus modality overriding an established preference based on a different sensory input is present in the work involving habitat selection among the Hawaiian *Drosophila* (Richardson and Johnston, 1975). In laboratory tests, *D. kambysellisi* is the most photopositive of three species which constitute the major portion of the *Drosophila* community in an isolated area, Kipuka Puaulu. Males of all three species select brighter areas than females of the same species. The response of *D. mimica* and *D. imparisetae* is the same as that seen in field studies where females are on the ground and males are on leaves a meter or more above the ground. *Drosophila kambysellisi* however, is found in the most densely shaded microhabitat where the odor of its oviposition substrate conteracts the photoresponse of this species. The light preference of the other two species is reinforced by the location of the plants which constitute their oviposition sites. In the evening all three species move up into the overstory. At this time *D. kambysellisi* shows a strong negative response to very low light levels which overcomes its attraction to its substrate. These species show niche separation correlated with spatial separation of the species based on differential utilization of resources. Spatial separation of the species and of the sexes within a species are maintained in part by a response to light intensity. This community of the sibling species *D. kambysellisi* and *D. mimica* with *D. imparisetae* environmentally intermediate between them has been analysed in terms of relatively few genetic changes in behavior possibly giving rise to sympatric speciation (Richardson and Smouse, 1975).

A variety of behavioral factors are involved in habitat choice and it is clear that different species rely on different sensory modalities to varying degrees in deciding their direction of movement. Differences between generalized and specialized species may involve rather discrete alterations in information processing in either sensory input or integrative mechanisms determining sensitivity to particular stimuli. Similarly, differences between sibling species may be akin to shifts in threshold. The problem of whether these changes are in the peripheral or central nervous system is unresolved. The fact that individuals utilize sequential sampling of the environment, via visual, olfactory and chemosensory cues before deciding where to leave their eggs suggests the intimate relationship between the behavioral and population biology of *Drosophila*.

I. Feeding Behavior

Given the interest in *Drosophila* ecology and laboratory husbandry, it is surprising that no detailed examination has been made of a basic facet of behavior, namely eating. The mechanisms involved in feeding are presented here with respect to another Dipteran and in general features may be taken to apply to *Drosophila*. The extensive work with *Phormia* deserves at least some repetition with *Drosophila* species to determine the precise extent to which threshold values and preferences are in agreement. This is especially relevant to studies of *Drosophila* ecology as well as neurobiology.

The feeding response of the blowfly consists of extension of the proboscis, spreading of the labellar lobes and sucking (Dethier, 1969). The proboscis extension response can be elicited by bringing the tarsi into contact with a sugar solution above a minimum concentration, the acceptance threshold. If concentrations just below threshold are applied to the tarsi only the rostrum and part of the haustellum are extended (Shiraishi and Tanabe, 1974). Test solutions applied directly to the labellum elicit slight extension of the haustellum, extension of the oral disc and spreading of the lobes. Behavioral threshold determinations agreed with electrophysiological determinations for labellar stimulation but determinations using the tarsal response did not fit behavioral thresholds quite as well. The difference in response between tarsal and labellar threshold distributions implies that impulses from these two inputs are processed to control different effector systems of the proboscis. Summation of impulses for each tarsal sugar receptor may be necessary for proboscis extension, in contrast to a response on stimulation of a single labellar sugar receptor (Dethier, 1969).

Fredman (1975) has determined, in *Phormia*, that the regulation of both peripheral and central nervous system sensitivity varies from fly to fly and with the nutritional state of each fly. He provided evidence for interactions between receptors on the labellum of the fly in producing the motor response of proboscis extension. Simultaneous stimulation of two water receptors produced a motor response. Separate stimulation of two receptors did not produce a response. Stimulation of salt receptors influenced the response to water and sugar. The response to sugar could be enhanced by antecedent stimulation of a different receptor. Since each sensillum on the labellum contains receptors sensitive to monovalent cations and anions, sugar and water, these results indicate cross channel summation between receptor types and between pairs of sensilla. A portion of the interaction involves modification of the central excitatory state of the fly. This change in level of responsiveness by the sequence, type and intensity of stimulation suggests, on a physiological level, the integration of excitation and inhibition involved in producing the behavioral pattern observed in

feeding. These results do indicate the level of complexity to be expected when sensory input from the tarsi are incorporated into the integrative mechanism. The existence of at least two different types of labellar taste setae (Maes and Den Otter, 1976) may aid analysis by offering the possibility of organizing integrative mechanisms in the form of classes of interactions.

While tarsal and labellar stimuli promote feeding behavior, two internal receptor mechanisms have been found which inhibit feeding (Gelperin, 1971). The foregut stretch receptors monitor peristalsis of a region of the foregut. The abdominal stretch receptors are nerve cord stretch receptors in branches of the abdominal nerves around the crop. These nerves do not innervate or connect with the crop. As crop volume increases, the output of these receptors increases. The frequency of foregut peristalsis is inversely related to the rate of crop emptying so that digestion of a dilute sugar solution, which empties from the crop rapidly, results in less output from the foregut stretch receptors than digestion of a concentrated sugar solution which empties from the crop more slowly. The output of either of these sets of receptors acts on the brain to reduce feeding. Gelperin suggests that the foregut receptor may be more effective at low crop volumes while the abdominal receptors may be more effective at high crop volumes.

On this basis, the distribution of behavioral thresholds by tarsal stimulation should not vary in appropriately starved animals (Shiraishi and Tanabe, 1974). Since feeding behavior is determined by integration of inputs from the tarsal and labellar sugar receptors and two sets of internal inhibitors, the variation seen in tarsal threshold determinations would seem to be ascribable to differences in sensitivity of the central nervous system. This raises the question of the extent of inter-individual variability in processing diverse stimuli with presumably the same circuitry in each animal. It seems possible that different individuals may vary in the level at which control points are set. Feeding of a high concentration of a particular sugar elevates the tarsal threshold to that sugar (Dethier, 1969).

Sotavalta *et al.* (1962) measured the feeding rate of a number of insects including the Diptera *Calliphora*, *Sarcophaga* and *Lucilia*. The flies favored strong sugar solutions, over 20%, and fed fastest on the weakest solutions. They favored the monosaccharides glucose and fructose, and the disaccharides, sucrose and maltose. Lactose has no nutritive value for Diptera.

Field studies have demonstrated that adult *Drosophila* will feed on the substrate used by the female for oviposition, but may also feed on other substrates that are not oviposition sites (Carson *et al.*, 1970). Species may vary in the extent to which there is a separation of these two functions and specialization of site. Several species of Hawaiian *Drosophila* may feed on a species of mushroom but only one will use it as an oviposition site (Grossfield, 1968). Similar results emerge from studies of Australian fungivores (Grossfield, unpublished observations).

Fellows and Heed (1972) have demonstrated that cactiphilic species show high but not absolute host plant discrimination for feeding. They also observed that adults tended to feed on a different portion of the cactus than that supporting larval feeding. The degree of monophagy or oligophagy of these cactiphilic species seems to be correlated with active host plant selection of a continuously available feeding resource. The polyphagic species on the other hand appear to use passive selection of whatever host plants are available. Based on observations during summer drought periods, Fellow and Heed suggest that, for some species, host specificity operates during periods of host plant availability while polyphagy is operative during stress periods. The behavioral mechanism involved in this shift in preference is not known, nor is the basis for host plant discrimination. Presumably the set point of CNS sensitivity for particular inputs can act as a trigger for the release of feeding. Olfactory stimuli would appear to be involved in attracting flies to a feeding site. The degree of stimulation subsequently required to release feeding once at the site is not known, but may involve tarsal and labellar summation of input. Knowledge of the extent to which the initial olfactory stimulus sensitizes the feeding response *per se* would be useful in probing the mechanism of feeding site specificity. Other than foregut receptors controlling release of a hormone from the corpus cardiacum (Green, 1964a, b), the general role of hormonal involvement in feeding specificity or information processing is unknown. The contribution of hormonal factors in establishing the central excitatory state is also unknown.

There are two receptor sites, for pyranose and furanose, on labellar sugar receptors. The P II isozyme of α-glucosidase is currently a candidate for the pyranose site (Amakawa *et al.*, 1975) where the interaction of the enzyme and substrate may produce the excitation required for sensory input. If sugar specificity operates in a similar fashion on the tarsi, then some alterations of protein structure may affect tarsal and labellar receptors.

The variation in threshold for individual flies may be environmental, genetic or a product of gene–environment interaction. *Drosophila*, with the possibility of isogenic lines and specific mutants, may offer unique approaches to the general problem of integration. Analysis of the components of feeding behavior (Thomson and Holling, 1974) may offer the possibility of developing assay systems to detect mutations affecting integrative mechanisms. Mutations affecting either tarsal or labellar receptors may be anticipated. It is possible that some mutations affecting both groups of receptors may involve perturbations of integrative portions of the feeding pathway. The relationship of particular ecological situations to

the receptor and integrative components of the species involved may well be approached by use of *Drosophila* species existing in special habitats. Behavioral assays will of necessity be the first step in uniting physiological and ecological data.

J. Preening

Preening or cleaning behavior has been viewed in part as a displacement activity, performed as a substitute for some other behavior that a fly does not perform. Connolly (1968) has investigated the extent of preening behavior of individuals and groups by observing the number of bouts of preening and the time spent in preening within a 3 min period. After the initial observation period, a door in a chamber was opened thus exposing an individual fly to 10 other individuals of the same sex, and observation was continued for a further 3 min. Individual females in a 3-min period showed an average of 10·4 bouts lasting 47·5 sec. When shifted to a group the comparable figures were 16·2 bouts and 65·9 seconds. Data for males was 7·3 bouts (20·9 sec) for single individuals and 11·6 bouts (27·9 sec) in the group situation. The increase in preening when individuals were shifted from a solitary to a group environment was greater for females (5·8 bouts and 18·4 sec) than for males (4·3 bouts and 7 sec), but both sexes showed a significant increase in both the number of bouts and total time spent in preening. Significantly, *w* eye mutants showed no increase in preening in a group situation which suggests that vision seems to be the sensory modality involved in detecting the presence of other individuals. Connolly (1968) thus interprets preening as serving as a signalling device and notes that the amount of preening is not a function of physical contact between individuals nor is it restricted to becoming dirty.

The parts of the body preened include the front, middle and hind legs, head, head and first pair of legs, wings, abdomen, thorax, proboscis, and genitalia. Szebenyi (1969) has classified preening behavior into 7 leg cleaning and 20 body cleaning components. He notes that a fly apparently requires at least three legs for support at any moment. He also points out that there are two basic movements by which macroscopic particles are removed from a fly's body: a sweeping movement of the legs over the body and a rubbing motion of the legs along the tarsal joints. Szebenyi discusses the problems inherent in securing an accurate ethogram for this kind of behavior. The use of videotape records (Grossfield and Smith, 1971) may obviate some of these difficulties. Bennett and co-workers (1970, 1971, 1972) have compared isogenic Oregon-R strains constructed by substituting *w* for w^+ in one line over 60 generations. They report that the frequency with which certain cleaning actions are performed is significantly different

in two strains. Of a total of 14 actions observed, the wild type strain rubbed forelegs, antennae, head and eyes and combed wings more than the *w* eye strain. The *w* strain showed a higher frequency of anus pulling.

Few data on preening exist for species other than *D. melanogaster*. Loeblich (1971) records that ethograms for six species tend to be stock specific and that the body parts cleaned varied between individuals. Generally, the order of cleaning was head > forelegs > hindlegs > wings. Different species are reported to show three levels of cleaning behavior. At the first level, all individuals spend the same proportion of time cleaning, e.g. *D. heteroneura* and *D. planitibia*. Individual strains of *D. robusta* and *D. virilis* spend one or another of the different fraction of time cleaning, e.g. either 79 or 168 sec of a 10-min period. *Drosophila grimshawi* and *D. nannoptera* are examples of species where any one of three different time periods may be spent preening.

In field observations it has been noted (Carson *et al.*, 1970) that individuals of some of the larger Hawaiian species will bathe in water droplets by dragging their wings, one at a time, through the water and then pull them along a length of branch to dry out.

The extent of preening in the field compared to that in the laboratory has not been measured. It may be that a portion of the behavior which is observed is an artifact of spacing conditions in the laboratory. The marked social facilitation of the behavior in *D. melanogaster* suggests such an effect. A biometrical analysis (see Spontaneous Locomotor Activity, Section IV, E, for details) of preening demonstrated dominance only when density was low, suggesting directional selection for low preening as part of the genetic architecture of the trait (Hay, 1972b). High density cultures reduced differences between the strains used in the diallel analysis. Preening activity did not vary with age over the first 15 days of life as much as did activity (Hay, 1973a).

The presence of individuals from two strains in the same group accentuated the differences between the strains in the amount of time spent preening (Hay, 1972b). The spacing of the flies also became more uniform in all groups containing individuals of two different strains. Both the spacing and preening effects were greater among individuals left in the original culture bottle for at least ten days before testing. Another biometrical analysis using a time sampling technique revealed dominance for high levels of preening (Angus, 1974b). This effect disappeared after stimulation by a shadow passing over the flies. Thus dominance for a high level of preening before stimulation disappears after stimulation. Hay (1972b) found either no dominance or dominance for a low level of preening in his experiments which involved mechanical stimulation. Both sets of experiments agree in that flies respond to the low levels of stimulation

employed in these experiments by reducing their level of preening. The architecture of the trait indicates that the function of preening is intimately involved in fending off other individuals and distributing flies over the available space.

One aspect of body posture that has been examined using a selection regime is wing folding behavior (Purnell and Thompson, 1973). Individual flies showed a strong tendency to fold their wings right-over-left or left-over-right. Two lines were selected for asymmetrical bias in the direction in which they folded their wings. Progenitors of ensuing generations were chosen from among the 100 flies each generation which were observed for which wing was drawn in first. Both lines showed significant response, but after 6–10% bias was achieved, the accumulated response was lost. There was some intimation that the relevant alleles may have been sex-linked.

Overall then, preening is a signaling and spacing behavior which may be species and strain specific in duration, intensity, and patterning. It is affected by the presence, density and type of other flies involved as well as by the general level of stimulation.

K. Spacing Patterns Between Individuals

Few studies have been made of fending behavior or the mechanism by which flies occupy a space either in the field or in laboratory cultures. Stalker (1942) noted that *D. virilis* adults maintain relatively isolated positions while *D. americana* adults tended to form grouped aggregates. Sexton and Stalker (1961) found that *D. paramelanica* females space themselves uniformly by means of avoidance reactions if approached within 5 mm. Each fly occupies 17 mm^2, of which 9·3 mm^2 is fly. This space is mainly at the front and sides and extends a distance of 2 fly legs' length. The spacing of individuals tended to become more uniform as density increased. This spacing was achieved by virtue of moving flies avoiding one another, as well as stationary flies. Stationary flies would rarely move out of the way of moving flies. Groups of *D. melanogaster* have been reported to increase aggregation with decreasing temperature (Navarro and del Solar, 1975). Under the conditions of this test, 50% of the flies in any one area of a globe moved to a different area in ten minutes. No data are presented as to the effect, if any, of interactions with other flies preceding any changes in distribution. Individuals of some species will use all three pairs of legs in fending off other individuals, even if the first pair of legs is used infrequently, e.g. *melanogaster* group. Other species will never use the forelegs and will undergo peculiar postures to avoid doing so. Certain Australian species (*D. enigma*, *D. lativittata*) use only their mid and hind legs for non-sexual interactions between individuals. In some cases the midleg may be extended and held out for up to 30 sec after another individual has passed by (Grossfield, unpublished observations). Some Hawaiian *Drosophila* are known to establish defended territories (leks) for sexual behavior (Carson *et al.*, 1970). Clearly, more detailed study is warranted of the behavioral components responsible for allowing individuals to coexist in the same area.

L. Oviposition

Control elements involved in the regulation of oviposition include intrinsic and extrinsic components (Grossfield and Sakri, 1972) The physiology of ovarian maturation and concomitant hormonal and nutritional factors are intimately related to the capability of females to deposit eggs. The degree of distension of the ovaries as measured by abdominal stretch receptors may also constitute an input to the thoracic ganglionic center from which neural control of the ovipositor musculature is exercised. The brain (head ganglia) participates in processing some stimuli required for oviposition. Anesthetization and/or decapitation of fecund females of some species (*D. melanogaster*, *D. pseudoobscura*, *D. tripunctata*) results in the immediate extrusion of an egg. Decapitation of insects generally results in a removal of central inhibition and exaggerated reflex responses. This type of reflex oviposition is not shown by certain other species (*D. virilis*, *D. palustris*) and suggests that, for these species, the brain is required for the performance of this motor pattern. Thus there may be alternate circuits in different species for the control of oviposition. Of the species tested, only *D. melanogaster* was capable of post-reflex oviposition, or the deposition of eggs by decapitated females.

Among extrinsic factors that have been identified as affecting oviposition are substrate conditions, temperature, mating, light and other environmental cues as well as circadian rhythms. Spencer (1937) noted the importance of humidity as a major factor determining proper substrate condition for oviposition. In one field study, oviposition was exclusively on moist surfaces of fresh cracks in the skin of tomatoes (McCoy, 1962) with no eggs deposited on unbroken skin. In the laboratory many workers routinely scarify the surface of fresh food medium to achieve the same effect. The condition of the food surface has been shown to be of importance in the choice of oviposition site by *D. melanogaster* and *D. simulans*. Moore (1952) has demonstrated, using food cups in population cages, that when both species are present, *D. simulans* prefers to oviposit in the center of food cups and on food cups with a surface crust to a greater extent than do *D. melanogaster*. The same preferences were found not to be as strong in

other strains of these species (Soliman, 1971). In pure species cultures, Barker (1971) has found that *D. simulans* demonstrates a greater preference than *D. melanogaster* for oviposition in the center of the medium, while in mixed cultures *D. simulans* still showed preference for this site when *D. melanogaster* was present at low frequency. Other workers (Sameoto and Miller, 1966) have found that desiccation of the medium decreases oviposition more by *D. melanogaster* than by *D. simulans* and Bakker (1961) reported that a surface crust decreases suitability of medium for use by *D. melanogaster*. Using this species, Palomino and del Solar (1967) found that 72 to 92% of all eggs laid were deposited in only 50% of available sites in a population cage. They also found an inverse relationship between density of females and number of eggs laid per female. Parsons (1968), however, using the Canton-S and a yellow mutant strain found fewer eggs deposited per female at low adult density. Barker (1973) has suggested that decreased fecundity of female *D. simulans* may be a behavioral response to crowding. Godoy and del Solar (1971) reported that *D. melanogaster* deposited the highest number of eggs in sites that already contained eggs. del Solar and Palomino (1966) suggested that these females preferred oviposition sites containing preadult forms, whether they were *D. melanogaster* or *D. funebris* larvae. With *D. pseudoobscura* del Solar (1970) found that females do not discriminate among sites containing different numbers of eggs but do prefer clean food cups in a population cage more than cups that had previously been occupied. The degree to which females will aggregate at oviposition sites can be modified by selection (del Solar and Palomino, 1968). After 20 generations of selection the aggregation index was shifted in populations monomorphic for *AR* or *CH* inversions as well as in a population maintained as *AR*/*CH* heterozygotes. The *CH* population for example, with an initial aggregation index of 183, showed an index of 66 in the low line and 233 in the high line. *Drosophila melanogaster* females have been reported to prefer to oviposit in sites previously occupied by males (Mainardi, 1968, 1969) but this preference was found to be reversed when tested with another strain of flies (Ayala and Ayala, 1969). There are sufficient differences between the experiments with respect to temperature, yeast, and the possibility of males depositing yeast on the food surface, to suggest that more effort will be needed to resolve the problem. David *et al.* (1971) have found that oviposition behavior varies with the age of the female, with females more readily depositing eggs in an unsuitable medium if they are forced to remain in a cage fouled by the presence of other flies.

Begon (1975) has determined that for *D. subobscura* and *D. obscura*, which bury their eggs when ovipositing, soft media are preferable to hard media as oviposition sites. On this basis, although certain fruits are present in the flies natural environment, they would be unavailable for oviposition.

In nature, *D. subobscura* shows a peak oviposition in mid September. The species studied by Begon show a separation of feeding and oviposition sites. However, this separation is not as marked as that demonstrated by the Hawaiian *Drosophila*.

The importance of oviposition behavior in the ecology and population biology of *Drosophila* cannot be overstated. For this reason several workers have sought to determine whether selection for a different aspect of behavior produces any correlated change in oviposition behavior. Pyle (1976) tested lines of *D. melanogaster* selected for divergent geotactic maze behavior for differences in choice of oviposition site. Flies from geonegative, control and geopositive lines were allowed to oviposit in vertical cylinders with food and yeast at the upper and lower ends. Cylinders were kept in darkness for twenty successive 12 hour periods. Geonegative flies deposited more eggs on the upper surface than did control flies while geopositive females deposited a smaller proportion of their eggs on the upper surface than did control flies. Geotactically maze-divergent strains of *D. pseudoobscura* were also tested in this paradigm but demonstrated no differences among the three lines. Thus the two species appear to differ in their correlated oviposition response to geotactic selection. These experiments however did not measure the microenvironmental differences present at the respective food surfaces. Small differences in temperature or humidity could have produced a situation that altered the surface with respect to a threshold point for one or the other lines or species. This alteration rather than geotaxis *per se* may have influenced the results of the assay.

A correlated response in oviposition behavior was found in strains selected for positive and negative phototaxis (Markow, 1975) Photopositive lines deposited more eggs in constant light while photonegative lines oviposited more in constant darkness. This was true of both *D. melanogaster* and *D. pseudoobscura*. Thus these two species differ in their genetic architecture with respect to gene interaction for oviposition and photo- and geotaxis.

Temperature plays a decided role in egg laying behavior with oviposition rarely noted below 14°C (Michelbacher and Middlekauff, 1954). More detailed studies (McKenzie, 1975b) have shown that oviposition is severely restricted at or below 12°C. While virgins of many species will still lay eggs, insemination increases oviposition. This effect is mediated by a substance from the male paragonia probably acting on the brain (see Grossfield and Sakri, 1972). Some strains of *D. melanogaster* demonstrate that young virgins will lay almost no eggs (Cook, 1970), but the degree to which even young females will retain their eggs will vary with the strain and/or species tested. The oviposition rate for individual mated females may be quite variable (de Mazar Barnett, 1965). Virgins of some species

will deposit many eggs as soon as they are physiologically capable [e.g. some of the Australian *Scaptodrosophila* (*Drosophila*)], while inseminated females of other species will, if no suitable substrate is available, retain or even resorb their eggs. Mature females of the subgenera *Exalloscaptomyza* (*Scaptomyza*) and *Engioscaptomyza* (*Drosophila*) (Group 1 of Kambysellis and Heed, 1971) have been found to retain mature eggs in the vagina until a first instar larva is formed (Kambysellis and Heed, 1971). These flies deposit their eggs individually on walls of a glass vial or on paper in the vial. This is correlated with the possession of a small ovipositor and weak musculature of the female genital regions. Most *Drosophila* species will insert eggs into the surface of the food medium. Flies of the genus *Scaptomyza* will deposit eggs individually on surfaces with no attempt to insert the egg. They will scatter many eggs during one period of oviposition, e.g. *Scaptomyza australis*. Other species, in the sub-genera *Antopocerus* and *Drosophila* (Group II), deposit their eggs singly, one per site, by inserting the ovipositor into the mesophyllum of appropriate leaves so that only the egg filaments are exposed on the surface of a leaf. Still other species, in the genus *Ateledrosophila* and the subgenus *Drosophila* (*Drosophila*) (Group III) oviposit in clusters, with many eggs (up to 30) in each cluster. Several mutant strains of *D. melanogaster* showed a preference for clumped oviposition (Gress and Nickla, 1973) but only the mutant clot was significantly biased against solitary egg deposition to be behaviorally different from the other strains tested.

The association of these particular kinds of oviposition behavior with the natural substrate and with the morphology of the species may be of general significance since several Australian species of the subgenus *Hirtodrosophila* (*Drosophila*) have been found to match the oviposition behavior and ecology of a typical Group I species (Grossfield, unpublished observations).

Thus for certain species an apparently unique chemosensory stimulus must be present for oviposition to occur. Barton Browne (1960) has found that receptors on the antennae and/or palps can detect odors that stimulate oviposition in *Phormia* and suggests that receptors might be present on the ovipositor as well. It is known that electrical signals can be recorded from all of these sites, but the usual stimulus capable of eliciting an oviposition response has not been identified. In a study of a combination of specific substances which act at different receptor sites and induce oviposition in *Lucilia* it was found that higher concentrations of the same compounds were inhibitory (Barton Browne, 1965). Since one of the major problems involved in getting a species of *Drosophila* to breed in the laboratory involves oviposition as a first step, it may be anticipated that one of the groups actively working on *Drosophila* ecology will investigate the requisite specific

stimuli. Oviposition has been secured for some species by use of natural substrate or a high protein food medium.

Another aspect involved in establishing cultures of some species is the effect of day length on oviposition, which may be a problem either of reproductive physiology or of behavior. Oshima *et al.* (1972) have found that for twelve strains of *D. virilis* oviposition was accelerated by short light pulses interposed in otherwise dark rearing conditions. Interestingly this species showed a 20% depression of oviposition under a regime where sound of 3000 Hz was administered whereas *D. melanogaster* after an initial decrease was back at control levels after about a week. Additional work on this point could determine whether a real species difference in behavioral compensation exists.

In view of the processing of oviposition stimuli by either the head ganglia or the thoracic ganglia or both it appears that differentiating and identifying intrinsic and extrinsic inputs to these centers is the primary task. By use of substances inhibiting egg laying (Ovellet *et al.*, 1970) or mutants affecting ovarian maturation, the role of certain intrinsic factors could be clarified. Since the regulation of oviposition does have a number of control points (Grossfield and Sakri, 1972) each of which may have a set threshold, it may be anticipated that careful examination of female sterile mutants will reveal some that have normal reproductive function but are, in fact, behavioral lesions. Thus some may oviposit in spurts, irregularly, without an appropriate stimulus, or with an abnormal stimulus. It may be that investigation of the behavioral differences between species mentioned above as regards suitable substrate conditions may provide indications as to the kind of behavioral assays necessary to isolate mutants affecting the system or indications as to the specific olfactory or chemosensory stimuli involved. A study of actual oviposition behavior attendent with the behavioral components used to sample the environment may well provide the crucial information as to how the decision to oviposit is made.

The rerouting of information under alternate input states suggests that circuit selection operates as a mechanism subserving behavior. Different species may be served by different circuits while still possessing the capability of responding by use of a circuit that is not the usual one. This might be the case for oviposition, where alternate circuits appear to exist. The suggestion that *D. melanogaster* females can retain their eggs at high density (Barker, personal communication) does not appear as an isolated observation, but rather as part of a continuum, when the results of analysis of the Hawaiian *Drosophila* are considered. Some of these species, as well as some of the Australian *Hirtodrosophila*, hold their eggs until first instar larvae are present. Several known mutants of *D. melanogaster* cannot oviposit. Thus, what may be usual in one species is expressed under

stress or, in an exaggerated form, as a mutation in another. While no single factor seems to be overriding for oviposition (Adolph, 1920) the selectivity shown by some species would suggest that, for these species, sampling of possible substrates may involve discrete types of receptors or CNS comparator gate points.

Given the balance of extrinsic and intrinsic factors and the various points in the control system where interaction of these inputs occur, a shift in threshold or alteration of circuitry at any point could affect oviposition. The threshold for subsystems could include modification of sensitivity to external factors or a change in ovarian physiology manifested as perturbations of hormonal levels, protein synthesis or sensitivity of stretch receptors to abdominal distension. Mutations affecting discrete control points, perhaps including female steriles, could provide insight into the differences shown by various strains and species in the manner in which they regulate their output of eggs.

M. Mutations affecting Behavior

The screening of mutagenized populations for induced mutants affecting a specific physiological system in order to analyse the system constitutes an *a priori* approach. Depending on the assay, recovery of discrete perturbations of the system, or of gross effects may result. Both types are useful in exploring interdigitation of genetics, development, and physiology to produce behavior. Utilization of the mutations obviously relies on analysis of the effect. The mutations that have been induced in the visual system will be discussed elsewhere (Pak and Grabowski, Ch. 9).

1. Temperature sensitive

paralytic temperature sensitive (*para^{ts}*): There are four alleles currently known of this X-linked recessive which maps at 54.1. The phenotype is expressed immediately at 29°C (within 5 sec), but the induced paralysis is reversible on return to lower temperature. Different alleles may vary in sensitivity. No effect is seen at the permissive temperature of 22°C and the mutant flies are indistinguishable from wild type. At temperatures above 25°C there is progressive debilitation. Paralysed flies shifted back to 22°C recover immediately (Suzuki *et al.*, 1971). If *para^{ts}* flies are left at 29°C, they recover gradually over a 2 h period but remain debilitated. Mutant flies left at 29°C for several hours, transferred to 22°C for 5–10 min and then shifted back to 29°C, are immediately paralysed. If they are initially left at 29°C longer than 5–6 h they are relatively immune to reparalysis upon upshifting. *para^{ts}* flies can apparently develop a stable temperature

resistance (Suzuki, 1974). At least one allele causes larval paralysis at 29°C, while larvae carrying other alleles can be paralysed at higher temperatures. Adult heterozygotes, normal at 29°C, will show paralysis within one minute at 40°C while wild type flies show signs of debilitation at this temperature only after ten minutes (Hall, 1973). Double mutants of the constitution *Hk^{1} para^{ts}* shake under etherization at 22°C but not at 29°C. White eyed double mutants can be induced to jump when stimulated by a high intensity flash of light (Williamson *et al.*, 1974). Injection of picrotoxin, which blocks the putative insect inhibitory transmitter γ-amino butyric acid, causes wild type flies to become uncoordinated and active but permits some movement of *para^{ts}* flies at 33°C. Since the electroretinogram of *para^{ts}* flies is normal and propagated nerve impulses can elicit activity from motor elements it appears that sensory, neuronal and muscular components involved in vision, jumping and flying are normal in *para^{ts}* flies at 29°C. Use of gynandromorphs suggests that the mutation affects both the brain and thoracic ganglion and a current hypothesis for its mode of action suggests paralysis resulting from excessive inhibition (Suzuki, 1974). Reduced excitability of motor elements may also be involved and the question of pre- or postsynaptic action remains.

shibire temperature sensitive (*shi^{ts}*): This locus with eight known alleles and named with the Japanese word for paralysed, is sex linked at 52·2 (Suzuki, 1974). Adults are reversibly paralysed within 2 minutes of being transferred to 29°C as are heterozygotes of all combinations of allelic pairs. Flies will remain paralysed for over 12 hours, after which they die. No effects are seen at 22°C. The locus affects all developmental stages as well as adults. Different alleles each have a different spectrum of effects at 29°C, with *shi^{ts}* 1, 3 and 6 producing larval paralysis. These alleles also result in lethality to egg and pupa at 29°C while the other alleles do not paralyse larvae but do affect other developmental stages. *shi^{ts2}* causes transitory larval paralysis. Higher temperature accentuates the effects of *shi^{ts}* alleles and adult heterozygotes with wild type are debilitated within 1–2 minutes at 40°C (Hall, 1973). The time required for debilitation of heterozygotes decreases with increasing temperature. The *shi^{ts}* mutation affects receptor cells as well as neurons (Kelly and Suzuki, 1974). The transients of the electroretinograms are lost, fast decay of the receptor potential is attenuated, and spontaneous firing of flight muscle is induced by high temperatures. Thus both pre- and postsynaptic effects are observed. Phototaxis of individuals mosaic for *shi^{ts1}* reveals inability of the mutant tissue to process visual stimuli at the restrictive temperature. Tetrodotoxin (TTX) which blocks the regenerative sodium channel of the action potential, affects wild type flies, or wild type tissue in mosaics, to a greater extent than *shi^{ts1}* flies or tissue at 22°C. The resistance of *shi^{ts1}* to the effects of

TTX is temperature sensitive, with that of mutant flies doubling at 17°C while wild type shows only a small increase. It has been suggested that the effect of the *shi*^{ts} alleles is manifest via nerve membrane components which in turn may play a role in embryogenesis (Suzuki, 1974). Ikeda *et al.* (1976) have shown that the defect in *shi*^{ts1} involves a blockade of neuromuscular transmission.

stoned temperature sensitive (*stn*^{ts}): There are two currently known alleles of this locus. It is sex-linked at 66·3 (Grigliatti *et al.*, 1973; Suzuki, 1974). Mutant flies are sedentary but can climb and fly at 22°C, and stagger and buzz about when the vial is tapped. At 29°C they can kick and, although debilitated, never become completely immobilized. The debilitation is reversible at 22°C. *stn*^{ts2} flies reared at 29°C are permanently disabled. They are sensitive to a change in temperature more than the actual temperature *per se*. When transferred from 22°C to 29°C, mutants are debilitated but never lose their ability to kick and beat their wings, and recover within 15–60 min. The same occurs when adults grown at 17°C are shifted to 22°C. When shifted from 17°C to 29°C, or from 22°C to 35°C, they are paralysed for over 3 h. In contrast to *para*^{ts} and *shi*^{ts}, heterozygotes of *stn*^{ts} with wild type do not show the mutant effect at higher temperatures (Hall, 1973). Mutant flies jump when a bright light shining on them is turned off. This response diminishes with age but can be maintained for over a week, post-eclosion, by placing the mutation on a white eye background. The light must be left on for at least 10 seconds before the effect occurs and flies reared in darkness must have prior exposure to at least 30 minutes of light for the effect. Flies reared in the light and held in darkness for several days still jump when subsequently exposed to the off-light stimulus. The electroretinogram of *stn*^{ts} flies possesses an abnormally large off transient followed by a spike from flight muscle. This mutation may be an allele of the *unc* locus (uncoordinated, 1–65·9) which produces abnormal leg movements and an upheld wing position. Wings are frequently curled at the tips. Flies so affected die shortly after eclosion. The *unc* locus is a semi-lethal with three or more known alleles (Schalet and Lefevre, 1973), and the small proportion of *unc* flies that do hatch become entrapped on the medium.

Out-cold (*Ocd*^{ts}): Discovered in a classroom experiment, this X-linked mutation at 55·2 lies within salivary chromosome bands 14A1 and 14C8 (Søndergaard, 1975). It is a dominant reversibly paralytic mutation which is expressed when heterozygous females are shifted from 25°C to temperatures below 18°C–20°C. At 25°C hemizygous males walk in a reeling fashion, frequently fall over and usually die within 48 hours. They are more sensitive than females to downshifts in temperature. After transfer to lower temperature flies show a sequence of uncoordinated leg movements,

leg stretching and wing flutter. The last characteristic is not exhibited by 20% of heterozygous females. The proboscis is often extended and an egg is extruded. Flies are then completely immobile. The time course of the behavior pattern varies with the magnitude of the temperature drop and also varies among individuals. *Ocd*^{ts} has no effect on any developmental stages. Recovery of adults at permissive temperatures takes 1–5 min. Flies are sluggish if kept at low temperatures, but may regain some mobility depending on the temperature.

If given a sufficiently large cold shock, wild type flies show a similar behavioral sequence before cold induced immobility. *Ocd*^{ts} flies shake their legs when etherized but no gene interaction with the *Hk* mutation is evident. Similarly, no gene interaction with *para*^{ts} or *shi*^{ts} occurs. Flies homozygous for these mutations and carrying *Ocd*^{ts} are heat sensitive when given a heat shock and cold sensitive when given a cold shock. Mosaic analysis indicates that each leg is autonomous in the effect of *Ocd*^{ts}. The mutation increases the activation energy of mitochondrial succinate cytochrome *c* reductase at the restrictive temperature.

2. *Non temperature sensitive*

A number of other mutations have been recovered in the course of screening for temperature sensitive mutations. The selection assay allows recovery of adults whose mobility is impaired for any reason. These include a dominant autosomal mutation causing debilitation of only the posterior part of the adult as reflected in a phenotype of dragging the abdomen and the hind pair of legs (Grigliatti *et al.*, 1973). It was not possible to maintain this mutation in stock. It is possible that some of the mutations included here will, on closer inspection, be shown to be affected by temperature in some fashion.

The apterous^{4} (*ap*^{4}) mutation (King and Sang, 1958) is a second chromosome recessive at 55·2. Homozygous adults are active only during the first day or so, becoming paralysed with age and dying within 4 days. Wings and halteres are severely reduced. Vitellogenesis is retarded. Males have mature sperm but are inert.

The bang-sensitive (*bas*) mutation (Grigliatti *et al.*, 1973) sex-linked at 47·2, causes flies carrying it to be temporarily paralysed by mechanical shock. Paralysis persists for 30–40 sec after which the flies recover and are resistant to shock induced paralysis for at least an hour.

The drop-dead (*drd*) mutation (Hotta and Benzer, 1972) produces degeneration of the brain after a variable number of days (2–9) of adult life. Flies behave normally, but at some time individuals begin to walk in an uncoordinated fashion and die within a few hours.

A fly carrying a gene for the easily shocked phenotype (Benzer, 1971), when stimulated with mechanical shock falls on its back, flails its legs and wings and coils its abdomen under. Males exude a droplet of fluid, while females are likely to extrude an egg. Flies remain immobile for a few minutes and then recover. There is apparently no refractory period and several such loci are on the X chromosome.

The rapid exhaustion (*rex*) mutation (Grigliatti *et al.*, 1973), sex-linked at 17·0, produces temporary paralysis after rapid movement of flies carrying it. If adults are constantly shaken or rotated in a vial so that they move continuously, they fall paralysed within 20 seconds and remain in this state for 30–40 seconds. They then perform in an uncoordinated fashion after which they recover and are resistant to movement-induced paralysis for at least an hour.

3. *Shaker mutants*

Kaplan and Trout (1969), during the course of examing the F_2 generation in a study of sex-linked lethals, discovered a number of sex-linked mutants whose phenotypic expression consists of a rhythmic shaking of the legs when etherized. The Hyperkinetic mutants, Hk^1 at 30·9 and Hk^2 at 30·4, produce a vigorous steady leg shaking. Hk^1 gave a somewhat stronger reaction. Mutations at the Shaker^5 (Sh^5) locus (58·2) produce vigorous and erratic shaking associated with scissoring of the wings and twitching of the abdomen. The least vigorous shaker is Ether à go-go (*Eag*) which maps at 1–50·0. This mutation does cause an occasional abdominal twitch but resembles Hyperkinetic in its absence of wing activity. It is temperature sensitive, shaking vigorously at 30°C but not at all below 20°C (Trout and Kaplan, 1973).

The shaker phenotype has also been reported in *D. funebris* where it was apparently due to an autosomal dominant gene (Kiil, 1946). No such phenotype has yet been reported to be due to an autosomal locus in *D. melanogaster*.

The heterozygous combination of wild type and any of the four shakers showed that shaking, and scissoring in Sh^5, was dominant but still less vigorous than in the respective mutant homozygotes. The hyperkinetic Hk^1 and Hk^2 mutations, after some years in the laboratory, now act as recessives in crosses. All shaker mutants when unetherized, are more active than wild type flies, with Sh^5 and Hk^1 the most active. These mutants show an abnormally high metabolic rate, directly related to their increase in activity. Their lifespan is correspondingly shortened (Trout and Kaplan, 1970). Both Hk^1 and Hk^2 require a longer settling period after being disturbed than do wild type flies. All shakers show a kinetogenic response, jumping when their visual field is disrupted by, for example, a hand passing over the vial. Sh^5 and *Eag* have marginal expressivity for this trait while the *Hk* mutants respond vigorously. This behavioral component was shown to be recessive, since the response is absent in all combinations save Hk^1/Hk^2.

Both *Hk* and *Sh* larvae show a reduced feeding rate (Burnet *et al.*, 1974). Behavioral analysis has shown that adults carrying mutations show a lower rate of *sustained* locomotor activity. They may jump or fly and then fall over. *Hk* flies have difficulty in regaining equilibrium after falling and may thrash about. The shaker mutants differ in the mean duration of dyskinesis.

Ikeda and Kaplan (1970 a, b) have recorded intracellularly from these mutants and report that the neural mechanism responsible for the abnormal motor function of Hk^1 consists of rhythmic bursts of activity from motor neurons in the thoracic ganglion. Wild type flies show only irregular discharges. The impulses originate from three pairs of regions, the right and left sides of the pro-, meso-, and metathoracic portions of the ganglion. These regions contain two types of neurons controlling the behavior. The more frequently encountered Type 1 neurons discharge action potentials (8–10/sec) from a steady resting level, while the action potentials of Type 2 neurons (5–10/sec) are preceded by a slowly rising depolarization, or prepotential. The action potentials rarely displayed overshoot. Ikeda and Kaplan (1970a) suggested that Type 2 neurons may be the pacemakers for the Type 1 motor neurons. Type 2 neurons would then be the ones affected by the mutation. Studies with gynandromorphs reveal that the mutation is autonomous; motor regions of one side are unaffected by the genotype of the other side of the ganglion.

Each of the shaker mutants can be individually characterized by the rhythmicity of shaking, the number of bursts and the time spent shaking (Trout and Kaplan, 1973). The shaking rate increases with age to plateau at day 5 post eclosion. Hk^1 and Hk^2 show cyclic patterns of 3–6 periods of shaking/minute, with Hk^1 shaking more (63 % vs 23 %) and with longer periods than Hk^2. The heterozygote is intermediate and when either allele is heterozygous with a deletion for the locus, the fly shakes more. The shaking pattern of Sh^5 is quite different, with bursts of shaking of 2–3/sec. Combinations of these three alleles may produce a pattern that is typical of *Hk* or Sh^5 or both, depending on the exact genotype tested. Thus, the two *Hk* alleles may differ only quantitatively and the *Hk* and Sh^5 loci each has a different effect on the motor system. In combination, the *Hk* and Sh^5 loci have a normalizing effect on each other so that the double mutant is more normal than either mutant alone (Kaplan, 1972). There do not appear to be any differences between these mutants and wild type flies for the several neurotransmitter substances tested.

Hk^1 and *Hk*^{2} flies jump and fall over when an object passes near them. This kinetogenic response can be elicited by either a hand moving across or by high intensity light (Kaplan and Trout, 1974; Williamson *et al.*, 1974). It can be measured by noting the number of responses per 50 trials. The response is greater in *Hk*^{1} than *Hk*^{2} and when *Sh*^{5} is added to the genotype the response is reduced proportionately to the number of *Sh*^{5} genes present. The heterozygote between the two hyperkinetic loci also responds and the expression is accentuated when either allele is heterozygous with a deficiency for the region (Williamson and Kaplan, 1973). The *Hk* mutants are capable of flight but their wings begin beating before taking off.

The combination of *Hk*^{1} with *para*^{ts} produces flies which will give the kinetogenic response weakly at 22°C and not at all when at 29·5°C. When this double mutant is placed on a white eye background (Williamson *et al.*, 1974) which increases the effective light intensity of flash stimuli, a paralysed fly can be induced to suddenly leap into the air and may even perform a few wing beats before falling into a paralysed state again. The response may be incomplete and the extension of legs and wings may be brief and partial. These results are interpreted as indicating that the wild type products of both the *Sh*^{5} and *Hk* genes exert both inhibitory and excitatory effects and that the presence of the mutants (or their absence via a deletion) can sensitize central integrative pathways to respond to high intensity stimuli and temporarily suppress high levels of inhibition. One important aspect of these findings lies in the demonstration that it is possible to heuristically investigate the general integrative problem of summation of heteromodal stimuli. These observations may provide a basis for the construction of meaningful models of how the nervous system works.

The spastic (*sps*) mutation (Meyer and Edmondson, 1951), on the second chromosome at 63·6, was recovered as a pupal and young adult lethal. Many flies eclose and have normal wing expansion. They are "unable to walk or fly due to spastic contraction and jerking of leg and wing muscles". These flies flip over on their backs and become mired in food medium. They die within a day. When etherized, the muscles relax so that the flies are indistinguishable from wild type.

The technical knock out (*tko*) mutation (Judd *et al.*, 1972), at the tip of the X chromosome, has been localized to salivary chromosome band 3A2. Three alleles were recovered and all three are easily shocked; striking the culture container sharply results in adults falling and remaining immobile for a few seconds. After recovery there is a refractory period of reduced sensitivity to shock which lasts about an hour.

The uncoordinated-like (*uncl*) mutation (Schalet and Lefevre, 1973) at the base of the X chromosome, salivary chromosome region 20A–20B, with three known alleles is similar in phenotypic effect to the *unc* locus which is 10 functional units distant. It is semi-lethal, with flies dying prior to eclosion and showing uncoordinated leg movements in those few that do eclose.

The wobbly (*wob*) phenotype (Grigliatti *et al.*, 1973) represents a translocation between the X, second, and third chromosomes. No homozygous females have yet been produced. These flies show poor coordination of leg movements, often getting a leg or legs entangled with other legs, and are unable to climb.

The association of low rates of eclosion of mutants such as spastic, *unc* and *uncl* together with a general effect on coordination suggests that some pupal lethals may actually be behaviorally defective and unable to emerge from the pupa case. The range of thresholds seen with *para*^{ts}, *shi*^{ts}, and *Hk* alleles indicates the existence of slightly different degrees of expression of alleles at the locus of a neurological defect. The effect of cold shock on wild type flies and the variability of phenotypic expression among individuals carrying *Ocd*^{ts} suggests that the mutation simply raises the normal threshold for cold-induced immobility by about 10°C.

The temperature-sensitive mutations in several cases do seem to exert their effect by altering the normal threshold of responsiveness. The utility of conditional mutants is significant with respect to providing internal controls for experiments and maintaining lines that may otherwise be lost due to lethality. However, the shift in threshold that is part of the effect of such mutations suggests that neurophysiological probing of wild type animals over a range of temperatures may produce experimental preparations that could be useful in delimiting neural function and interaction.

These behavioral mutants, whether they affect neural tissue or other aspects of metabolism, have all forced a closer examination of the behavior and capabilities of wild type flies. The characterization of some of these mutants has invoked the application of neurophysiological techniques to genetically interesting material. The mutual facilitation between genetics and physiology stems from the discrete nature of the alterations of function provided by point mutations.

These behavioral mutants then are very useful in so far as they increase knowledge of normal behavior, provide insight into experimental approaches and aid in integrating neural function and behavior. But there may be a certain peril in that they become the object of interest *per se*, with characterization of each new lesion engendering a loss of perspective for the function of the organism as an integrated system.

4. *Morphological*

There are many morphological mutants that have been explicitly tested for their effect on behavior (see Table I). In some cases mutants that have been tested but found not to exert an effect have been included to serve as a baseline for the avoidance of repetition. The penetrance and expression of certain mutations is crucial with respect to any behavioral assay. Different genetic backgrounds can alter gross behavioral measurements and may be of even greater importance in detailed measurements. The use of strains isogenized, as far as practicable, for all but the chromosome region of interest or the use of inbred lines may avoid some of the problems of genetic background. However, such problems usually arise when polygenic rather than major gene effects are being studied.

Mutants affecting certain aspects of morphology such as sensillae, which have not been screened for behavioral effect, may, with use of appropriate techniques, be shown to be relevant.

The phenotype of wings-up (*wup*), in which both wings are raised vertically soon after eclosion and held permanently in that position, has been shown to be due to at least two different sex-linked genes (Hotta and Benzer, 1972). The first, wup^A, maps to the right of forked and has been shown to produce atrophic flight muscles. The second, wup^B, maps between vermillion and forked. In heterozygotes with wild type the wing position is normal but there is an absence of flight. The myofibrils are absent from both the longitudinal and vertical indirect flight muscles. The Z bands of the heterozygote are often irregular rather than organized in the usual pattern. Hotta and Benzer (1972) suggest that in this case the heterozygote fails to produce a normal number of the molecules required for proper structural organization, while in wup^A heterozygotes one dose of the wild type gene is sufficient.

The wup^A mutation, although a morphological as opposed to a behavioral mutation, underscores the relationship of certain morphological mutants to the neuromuscular basis of behavior. In addition to the effects of the wings up mutation on flight muscle, there are a number of other wing mutations (Lindsley and Grell, 1968) which may be worth investigating from the point of view of control of movement. These include outheld, heldup, upheld, heldout, raised, droopy and many other mutations which affect wing position.

A large number of wing mutations exist which affect the expansion of the wings rather than the position in which the wings are held. Since the wings are apparently expanded by active swallowing of air to increase pressure in the teneral adult (Perttunen, 1955), a behavioral malfunction might be responsible for some of these failures of expansion.

The effect of morphological mutants on behavior may be useful in behavioral analysis (see Grossfield, 1975 for the effect of such mutants on sexual behavior). The behavior of flies carrying wing mutations such as curled and curved indicates that photoresponse involves feedback from the wings but that geotaxis does not. These mutants might be used in an analysis of such feedback relations in developing systems models of behavioral components. The link between the visual system and the effector system has been noted above. The mutants stn^{ts} and $w\ Hk^1\ para^{ts}$ illustrate the same connection in a striking fashion. The vestigial wing mutations which showed different flight capability may involve alterations of musculature as a result of developmental changes at different temperatures.

Certain mutations result in the development of body parts in an incorrect location. These homoeotic mutations include several which result in the appearance of leg structures instead of antennal structures in the adult. Deak (1976) has demonstrated that one such mutation, spineless-aristapedia (ss^a), which replaces antennal aristae with tarsal segments, shows a functional connection between sensory neurons on the ectopic tarsi and the central nervous system. Proboscis extension was used as a measure of whether normal tarsi and antennal tarsi could detect a droplet of sugar solution placed on them. Although the response was weaker and not all flies responded, the sensory neurons of the antennal tarsi showed the same specificity and sensitivity to HCl inhibition as those in the leg tarsi. Neither leg tarsi or antennal tarsi of the ss^a mutation were as sensitive to salt as were normal flies. The mutations Antennapedia and Nasobemia both transform antennae into leg structures. The bristles on femoral or tibial structures do have nerve cells whose axons pass into the brain. Both of these mutations show a marked reduction in size of Johnston's organ. These mutants responded with proboscis extension when their leg tarsi were stimulated. The response was inhibited by both salt and HCl. Neither mutant responded to antennal leg stimulation since tarsi were lacking on these legs in the stocks used. Since the appropriate double mutants were not tested in this system any possible enhancement of the observed effect is not known. The results indicate that functional connections from sensory neurons to the central nervous system are established in a high proportion of individuals homozygous for certain developmental mutants.

There is no question of the importance of morphogenetic processes underlying the deposition of the neural elements subserving behavior. However relevant developmental studies are to behavior, there is a demarcation between those studies which answer developmental questions and those which address themselves to behavioral ones.

Some morphological mutants exert their effect on behavior as an obvious

mechanical difficulty. Other morphological mutants may so alter the physiological system subserving a behavioral component that the effect is meaningless in terms of analysis of the mechanism of the behavior. The analysis of morphological mutants which produce nontrivial perturbations of gross behavior constitutes an *a posteriori* approach which may be quite useful.

One way in which morphological mutants may be of unique use in analysing *Drosophila* behavior lies in applying the considerable body of existing genetic knowledge to a methodical probing of the genome for regions involved in regulating behavior. By sequentially manufacturing deletions and duplications of small regions of the chromosomes (Lindsley *et al.*, 1972), not only could each region be assayed for behavioral input, but possible dosage and consequently regulatory features of genetic effect on behaviors could be tested. Theoretically it would be possible to probe nearly the entire genome in this fashion. This may be of special interest in regions containing loci known to perturb behavioral functions. Until such time as this is feasible however, the use of behavior-specific induced mutations and mutations affecting neural function will unquestionably serve to unite *Drosophila* genetics with what may be termed classical neurobiology.

N. Anesthetization and Neuropharmocology

Early *Drosophila* workers used diethyl ether to narcotize flies and this substance has remained the mainstay for this purpose. Differences between strains and species are apparent. Newly hatched flies generally recover more quickly, as do females. Many mutant strains recover more slowly than wild type. Two recessive mutations, both designated ether sensitive (*es*), have been described. The first has been mapped to the region between 0·5 and 2·5 on the X chromosome (Peterson, 1947). The second mutation, hypersensitive to both ether and chloroform, has been localized on the second chromosome (Kidd, 1963). Both mutations show an overall poor viability. Parkash (1971) has described a temperature sensitive lethal which is very sensitive to ether. Ogaki *et al.* (1967) have reported a gene conferring ether resistance which is located at 61 ± on the third chromosome, with minor genes on the X contributing to the effect.

Other chemical substances can be used to narcotize flies, and one of these, methylene chloride (Hedgley and Lamb, 1973), produces a slight twitching and the typical wings held vertically over body posture of over-etherized flies, while not killing them. Other volatile chemicals may also produce body postures differing from the effect of ether which itself leaves etherized flies in a normal posture with the wings folded in resting position.

Drosophila melanogaster and *D. simulans* have been reported to recover more quickly than *D. subobscura* at low ether concentrations, with just the reverse occurring at high concentrations (Calloway and Kalmus, 1940). *Drosophila immigrans* will typically defecate as it succumbs to ether. This species is etherized faster than *D. melanogaster* but slower than *D. robusta* (Spencer, 1940). *Drosophila virilis* is etherized slowly and recovers slowly while a sibling species, *D. americana* reacts quickly to both facets of the procedure (Stalker, 1942).

Teissier first reported the use of carbon dioxide as an anesthetic. This gas avoids many of the effects, especially on behavior, that ether produces. There are some species whose females will extrude an egg as the gas takes effect. This kind of reflex oviposition (Grossfield and Sakri, 1972) has been noted for a number of species. Recovery from CO_2 is rapid and behavioral experiments have been performed within 30 minutes with no apparent difference. Other gases such as nitrogen, helium and argon (but not oxygen) will produce rapid and reversible anesthesia (Grossfield, 1972a). The major problem in using gas is the danger of desiccation which can be avoided by humidifying the gas prior to administration.

A virus-mediated sensitivity to CO_2 is known in *D. melanogaster* and several other species. A third chromosome (52·7) semi-dominant gene *Dly* has been reported which produces delayed recovery to CO_2 (McCrady and Sulerud, 1964). The mutation *shi*^{ts} shows extreme sensitivity to CO_2 (Suzuki, 1974) but nothing is yet known of the mechanism of the sensitivity. Another behavioral mutant, freaked-out, has been reported to be ether sensitive (Benzer, 1971). Until additional work has been done on the mechanism of anesthesia it will be difficult to assign any of these effects to a specifically neurological function. It may be anticipated that *Drosophila* will be used in studies of anesthesia. Luning (1966) has suggested that pharmacological testing of many agents be done with *Drosophila* as part of routine drug evaluation. The behavioral effects of any such agents may be worth noting, especially in respect of the finding of the shaker mutants by use of an anesthetic.

In an attempt to correlate behavior with its biochemical bases, Howard *et al.* (1975) assessed the toxic effect of a number of psychotropic and neurotropic drugs by feeding larvae, vacuum injecting adults or holding adults on drug containing medium. *Drosophila melanogaster* is sensitive to a number of drugs that affect neurotransmitter function in humans. Compounds that are putative mammalian neurotransmitters affected *Drosophila* at higher concentrations. Larvae are generally more sensitive to a particular dosage of these drugs than adults. An exception is the convulsant allylglycine where the adult lethal dose does not affect larvae. Several of the tested drugs reduced movement toward light while other

drugs had no effect on phototaxis, relative to control flies. In no case is the mode of action of any of these drugs known in *Drosophila*.

Selection over 30 to 50 generations produced strains specifically resistant to the initial toxic dose of a number of tested drugs. This indicates that genetic variability for drug resistance is present in the original population and that selection lines are resistant only to the agent used in the selection scheme. It remains to be seen whether any of these strains contain actual point mutations affecting the metabolism of specific drugs. Such mutants would be of considerable aid in isolating individual points in biochemical pathways subserving behavior. Even strain differences, however, may be useful in correlating certain pathways with aspects of behavior.

It is well to bear in mind that insects do possess a well developed blood brain barrier (Schofield and Treherne, 1975) which limits diffusion of water soluble substances between hemolymph and the fluid layer, which is the immediate environment of nerve cells. Metabolic activity of the perineurium and underlying glial elements can also regulate the composition of the neural environment. Seemingly trivial details such as the failure of drugs to be absorbed, or identification of the precise site of action in any behavioral effect must engender a certain caution towards interpretations of drug effects *per se*. Nonetheless, given the panoply of genetic techniques available with *D. melanogaster*, a drug effect, once noted, would be readily analysable. Whether or not the effect bore any relationship to its mode of action in vertebrates would remain to be determined. There is a certain logic in using *Drosophila* to evaluate those compounds which are thought to play a role in invertebrate nervous system metabolism. Use of conditionally sensitive mutants or those affecting only a particular developmental stage would negate the possible lethality of mutations affecting vital neurotransmitters.

O. Learning

The question of whether adaptive changes in the behavior of an individual can occur as a result of experience has attracted attention to a variety of experimental organisms. A number of demonstrations of learning have been made with insects (Alloway, 1973). Habituation, or a stimulus-specific decrement in response, has been noted for *Drosophila* reared on various larval media (see pre-imaginal conditioning). *Drosophila melanogaster*, with the amount of genetic information and techniques available, seems a logical subject for an analysis of the learning process.

Murphey (1967) reported instrumental learning of a maze by a negatively geotactic strain of *D. melanogaster* whose reinforcement consisted of

moving upwards. Instrumental conditioning implies that the stimuli or reinforcers are presented or removed contingent on the performance of an appropriate response. Murphey's results were not confirmed by Yeatman and Hirsch (1971), who reported that selection for performance of a conditioning test produced no response for either "good" or "poor" learners. Murphey (1973) noted that his original experiments had not used yoked controls and did not represent instrumental learning. Nelson (1971) indicated that *Phormia* would not show instrumental learning. These flies did not learn to associate food with a color or choice in a maze, nor did they respond to aversive conditioning using electric shock. However, Nelson did demonstrate classical conditioning in these flies by using sugar as the unconditioned stimulus and saline and water as the conditioning stimuli. Proboscis extension was the measure of response. The associative factors involved in conditioning were influenced by the central excitatory state (CES) of the fly. The CES refers to the level of excitation to particular stimuli at any point in time. This alteration of responsiveness due to an excitatory change somewhere in the central nervous system is subject to decay with time. This decay may be mediated by stimulus intensity as well as food and water deprivation and inhibitory stimuli. A hungry fly given sucrose will respond to a variety of unrelated stimuli for a short time after the sugar. This non-specific sensitization of excitation, or pseudo-conditioning, was controlled for by disassociating, in time, the reinforcement from the stimulus. A learning response depends on simultaneous presentation of stimulus and reinforcement. Nelson's experiments used several stimuli to fully discharge the central excitatory state as well as appropriate timing and sequencing of stimuli. Nelson reported that individual flies could be classified as good, fair or poor learners, with roughly 30% falling into the first category. Bidirectional selection of *Phormia* for good and poor learners over seven generations has been reported to be successful (McCauley and Hirsch, personal communication). Both lines were significantly different from each other and from the control line. These findings suggest that individual flies may differ in their learning capabilities and that genetic variation for these capabilities exists in a population of flies. Thus the central excitatory state may also involve a genetic component affecting threshold points for processing or integrating information.

Fukushi (1976) has reported classical conditioning in *Musca domestica*. Flies were exposed to a beam of monochromatic light. After several seconds they were given a sugar solution. This was repeated with varying intertrial intervals. A positive reaction was taken as proboscis extension to the light beam alone. Wavelength specific conditioning was reported with this system.

Spatz *et al.* (1974) and Quinn *et al.* (1974) have reported aversive conditioning of *D. melanogaster*. Spatz *et al.* used a T maze containing two funnels illuminated with either blue or yellow light in the long arm of the T and one illuminated funnel in each short arm of the T. One side was yellow, the other blue. As flies passed through the long arm of the T an electric shock was paired with one of the colors and the number of flies that subsequently choose either that color or the color not associated with the shock was recorded. The per cent choosing the "blue" arm of the T maze paired with electric shock at one of the colors was compared with a control population which chose "blue" in the absence of shock paired with either color. Learning was defined (conditioning index) as a non-zero difference between the two populations. About 30 % of the flies could pass through the long arm without experiencing shocks and over 50 % of the initial flies completed the maze. Spatz *et al.* note that the conditioning indices were small and demonstrate positive learning behavior for avoidance of either color when that color was paired with electric shock.

Quinn *et al.* (1974) exposed flies alternately to two different odors A and B, in four tubes of a countercurrent apparatus. A rest tube was used initially and for rest periods between odorant tubes. The first odorant tube, A, coupled shock with that odor. The number of flies subsequently choosing the shock associated odor in three successive cycles of presentation of the sequence A,B,A,B, was determined. The sequence of odors was reversed in half the trials. Habituation to odor was not a factor since temporal association of odor with shock was necessary for an avoidance response. Extinction of avoidance occurred when odor was presented without shock. Trained flies reciprocally mixed with naïve flies can be separated by the procedure although the two groups will exert some effects on each others movement (see Narise, 1974). A Y tube maze using quinine as negative reinforcement for one of two colors was also used to demonstrate selective avoidance. Roughly 30 % of a population demonstrated learning as defined by a learning index measuring the fraction avoiding the shock-associated odor minus the fraction avoiding the control odor. Quinn *et al.* note that the avoidance response is not strong but is apparently present in each fly.

Using the experimental paradigm outlined above, Dudai *et al.* (1976) have isolated a sex-linked incompletely recessive mutation designated dunce (*dnc*), which is incapable of demonstrating learning. Homozygous *dnc* females and hemizygous males are both deficient in learning. Heterozygous *dnc* females do not perform as well as homozygous wild type flies. Mutant flies can sense both odorants and shock. The appropriate neural mechanisms do not appear, however, to route this information to a learning center under conditions of this test paradigm. The flies are normal in other aspects of their behavior.

Hay (1975) has reported genetic differences in the ability of different strains to learn a training paradigm that involves no aversive conditioning. Flies were introduced into a modified 11 unit maze where the number of choices was reduced by blocking certain junctions, forcing the flies to use eight alternate pathways. The learning index consists of a comparison of the probabilities of going left or right at the initial choice point, and the probabilities of repeating this choice at a second choice point after the flies were trained to repeat their initial choice six times. If the behavior of the flies is unaffected by the training regime the probabilities at the second choice point should be equal to those at the first choice point. Flies were more likely to continue the sequence of turns they experienced during training. Strain differences in the efficacy of the training paradigm were found. About 90 % of the initial population completed the maze. Selection for a right–left bias in these strains was ineffective, and "wall-hugging" and following effects were tested and found absent, as was any odor effect. About 30 % of flies displayed learning in this paradigm, although genetically different strains varied from 15 % to 37 %. The lower figure is comparable to the results of Spatz *et al.* (1974). In response to comments of Bicker and Spatz, Hay (1976) stresses that apparatus differences can affect maze learning. The probability of turning right or left may be altered by the connection between the initial tube and the first choice point. In addition, alternation of choices or correcting behavior cannot explain Hay's learning paradigm since the behavior of the various strains undergoing forced turn training was unrelated to the performance of these same strains in following the outer walls of a maze. While flies of different strains do show varying tendencies to follow the outer wall and thus repeat their choices, the direction of the choices when the flies were trained was not in the direction expected if following were the only variable.

It is of interest to note that to date virtually every report of learning in a variety of training paradigms including proboscis extension with *Phormia* and aversive and non-aversive conditioning with *Drosophila*, yields a "good-learning" estimate of roughly one-third of the tested population. Kekic and Marinkovic (1974) reported that roughly 30 % of a population of *D. subobscura* would repeat their initial phototactic choice and 30 % would choose an intensity contiguous to their first choice. Walton (1968) found that 15 % of his populations repeated their sequence of choices.

Since Quinn *et al.* (1974) reported that learning is probabalistic in each fly and the results with *Phormia* indicate that good learners could be detected, the question of gene–environment interaction in the expression of learning arises. The existence of genetically different strains with respect

to learning, or of masochistic or bright mutants would help to resolve the question. It may be anticipated that *Drosophila* will be the organism of choice for such an analysis.

The population assay of learning in *Drosophila* has demonstrated that a certain proportion of all individuals can learn. The bias of flies for a left over right choice at the starting tube of a maze (Murphey, 1965) as well as the wing folding asymmetry of individual flies suggests that a certain fraction of a population will tend to repeat choices. Studies cited earlier confirm this point. The associative processes designated learning may reflect circuit selection, mediated by external stimuli, among an array of circuits available for repetitive choice. Variations in threshold among this array may be involved in producing the fraction designated good learners. The efficacy of selection for conditioning would suggest that genetic differences are distributed among members of a population.

The use of visual, olfactory and chemosensory paradigms in establishing a relatively weak learning capability suggests that *Drosophila melanogaster* may possess a degree of behavioral plasticity that, in nature, obviates the need for learning ability *per se*. It may be that the results to date illustrate manifestations of a central excitatory state and associated reflexes. Examination of learning potential in other *Drosophila* species which are less behaviorally flexible and are bound to a greater extent to unique modalities might be rewarding.

P. General Discussion and Prospects

An organism is bifunctional in that it must survive and reproduce. Yet it is the sexual behavior of *Drosophila* that has historically received the major share of attention. Consideration of those components of behavior other than sexual reveal that an astonishing amount is unknown about quite elementary functions. What is known does not fit conventional wisdom in implying that eating is eating or movement is movement. Species do differ among themselves in these more prosaic functions and are thus capable of demonstrating shifts in emphasis or threshold for unique sensory inputs. Evidence exists that CNS integration mechanisms differ as well.

A striking aspect of non-sexual behavior is its variation with experimental conditions. Superimposed on this is a degree of fixed response to specific stimulus conditions. A principal thrust of behavioral work therefore should be the delineation of variable and invariant components of behavior coupled with analysis of the organizational level and type of mechanism subserving each component. Stimulus identification, sensory filtering and CNS integration might be quantified at this stage. A model sequence to

accomplish this would seem to be a detailed description of a behavioral act which permits behavioral components to be recognized. This would be followed by physiological and anatomical studies to determine the circuitry and neuromuscular basis for the motor coordination producing the behavioral component of interest. Ideally, this phase of the analysis could be tied to a genetic approach and a concomitant evolutionary synthesis linking the behavior to that in related species.

The question that arises is where in the overall scheme of cellular, organismal and population approaches and mechanisms might *Drosophila* offer the greatest opportunity for analysis. It is clear that neurological mutations affecting sufficiently large identifiable cells which are amenable to electrophysiological probing have been and will continue to be of great relevance. Such mutations however, are unlikely to be found for all behavioral systems of interest. For some aspects of analysis then, the anatomy precludes use of *Drosophila*. Additionally, certain mutations may affect more than a single functional component. Certain components might be better approached through ablation or extirpation which may avoid possible manifold effects of single genes. The use of physiological analysis of wild type flies would surpass removal or destruction of tissue as an approach, and would provide a more detailed view of the modulation of a response by a particular stimulus. Mutations such as w^a, with certain visual stimuli, produce a locomotor response opposite to wild type. This could involve alteration of an integrative subsystem where, due to overlapping functional properties of different underlying genes, it may not be possible to use a single collection of mutations to dissect a component of neural function. Other single gene mutations may, as the simplest case, be straightforward in their effect by virtue of a discrete change in protein structure.

Behavioral components that involve the genetic separation of overlapping functions may include many systems that require integration of information. While this overlap confers an evolutionarily useful redundancy to the system, it might render difficult the detailed analysis of functional mechanisms. This would be especially true if genetic alteration occurred in cells too small for electrophysiological study. Thus, at the cellular level, there are limitations to the use of *Drosophila*.

The plasticity of response observed among individuals suggests that *Drosophila* might be quite useful in assaying individual behavior in terms of identification of variable and invariant components. Plasticity may be defined as a functional gene-environment interaction that varies with the genotype. Differences in plasticity can be analysed as a profile of response, or the norm of reaction for an individual, strain or species. The same evolutionary redundancy produced by the functional overlap of subsystems

under separate genetic control that might make some systems difficult to analyse may thus be quite useful in characterizing the extent and kind of genetic variation involved in a behavioral component. Biometrical and statistical techniques could be quite useful in this type of assessment. In a sense, such an approach could aid in establishing which systems would be worth investigating at the next level of organization. This approach would be limited without concomitant physiological or biochemical investigation. One other aspect of this approach deserves mention in connection with analysis of the behavior of individuals. This is the general problem of interindividual differences in behavior. Evaluation of plasticity can simultaneously reveal the extent to which environmental factors influence these differences.

The differences in threshold that exist between sibling species, among species, or between mutations in a species and the wild type behavior of the same or a different species must have a neurological or biochemical basis. Genetic changes that affect, as one example, the input/output relationships of neurons can produce the various shifts in threshold that are observed. Various integrative mechanisms may be altered by subtle changes in the processing of information. As a naive case, some mechanisms may involve an intrinsic or programmed reference point or comparator as part of an integrative loop. This reference point, say a temperature threshold for locomotion, may be subject to differential setting or shift in threshold depending on conditions obtaining at any instant in time. Alterations in the set point could be linked to other information sources such as light intensity and hunger. Thus although the genotype does not change, the output of the system may be altered. The functional overlap of different genes may establish redundancy for subsystems affecting the same behavioral component. If two such subsystems involve neural mechanisms in which one or both contains a variable threshold point, then observed plasticity may only be assessed in a range of environments. There are a number of facets of individual behavior that may benefit from this kind of examination, including performance intensity of behavioral components and the mechanisms involved in summation of heteromodal stimuli.

Analysis of individual behavior leads to consideration of the role of individuals in populations. The role of behavior in maintaining species in their habitats has been reviewed. The same microevolutionary changes that occur among individuals can also occur among collections of individuals constituting species populations. Some of the mutations affecting behavior are illustrative of the kinds of alterations that may be subjected to evolutionary pressures resulting in speciation. An evaluation of mechanisms may call for evaluation of each case, since a variety of behavioral differences can serve to establish ecological separation. The point of relevance lies

in extracting, from such species comparisons, the physiological mechanism that has been affected. Species comparisons, then, may be used in much the same fashion as evaluation of mutations affecting the same function within a species. The discreteness of the alteration is the important factor in determining the ease with which behavioral components can be used to analyse alterations of function, or trace an evolutionary lineage.

Some of the mutations affecting behavior appear to have rather general effects rather than constituting a discrete perturbation of a behavioral subsystem. These will undoubtedly be useful in probing the developmental basis of behavior. Other mutations producing discrete alterations in behavior may well represent altered responses of existing circuits. Thus, there may be differentiation of CNS as well as sensory mechanisms in the evolution of non-sexual behavior.

The phenotypes of mutations such as bang sensitive, *tko*, easily shocked in *D. melanogaster* are seen as part of the normal repertoire in other *Drosophila* species, where swooning, temporary paralysis, and the extrusion of an egg or fluid is part of the usual response to mechanical shock. Mutations affecting wing position and movement may also have a counterpart in other Drosophilid species, where the wings are waved (*D. tetraspilota*, *Chymomyza*), set slightly apart (*Leucophenga*), or held straight up (*Tambourella*).

These shifts of balance between mutations in one species which represent an accentuation of components of the normal repertoire of another species, are not restricted to widely divergent species. Many pairs of sibling species show a variety of differences: *D. melanogaster–D. simulans*, oviposition, larval behavior, pupation, phototaxis, dispersal (Parsons, 1975a, b); *D. subobscura–D. obscura*, orientation, activity, light, temperature; *D. virilis–D. americana*, activity, anesthetization, pupation, spacing; *D. pseudoobscura–D. persimilis*, humidity, temperature, light, activity. For those species where information is available, the generalization emerges that one species shows a higher degree of behavioral plasticity than the other. The quantitative and qualitative differences in behavior between sibling species constitutes a series of shifts in emphasis in stimulus processing. The generalization of threshold shifts between siblings may well hold for other pairs of species and may indicate the shifts in rerouting of circuitry caused by some mutations perturbing thresholds or control points. The shifts in threshold for the non-sexual behavior of pairs of sibling species parallels the differences found for light-dependent mating (Grossfield, 1972b).

Thus there may be an underlying pattern of neural networks present in many species among which the mechanisms of circuit selection choose a routing consonant for a particular species in a particular stimulus environ-

ment. Alteration of the intrinsic processing mechanisms may be reflected as a mutation, while an abnormal stimulus environment may be reflected in the expression of behavioral components not normally present in a species repertoire. The intertwining of studies of mechanism and evolution would seem to offer many insights into the shifts of control and threshold that have occurred in the development of behavioral responses.

This précis of *Drosophila* behavior may be useful in delimiting components of behavior which have not been analysed, and may indicate a variety of available approaches with which behavioral studies can pass from description to mechanism in an organism which offers a panoply of associated techniques for the detailed dissection of behavior.

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11. Sexual Behavior

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I. Introduction*

It is appropriate to devote a chapter to the sexual behavior of *Drosophila*; this is a behavior(s) which has been profitably exploited by biologists of assorted types since the early years of our century. Sturtevant (1915) considered:

> Much has been written on the subject of sexual selection since Darwin first developed the theory, and many remarkable observations have been recorded. There has, however, been very little experimental work in this field. Darwin and those who have followed him have obtained much of their evidence from the insects and within this group some of the most striking cases of elaborate mating habits have been reported in the Diptera, and here too there is to be found a most remarkable array of secondary sexual characters.

He then cited Barrows (1907) observations about odorous substances and the behavior of *Drosophila ampelophila* (now *D. melanogaster*), Lutz's (1911) work with experimentally mutilated but still-mating *Drosophila*, and Payne's (1911) studies on *D. ampelophila* bred without light for sixty-nine generations, among other historically fascinating references. If we then

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