Table 1. The receptivity of *D. melanogaster* females following various treatments of the antennae.

Treatment	Receptive	Unreceptive
Etherized but unoperated	72	3
Both antennae removed	23	57
One antenna removed	68	25
Funiculus and arista removed from both sides	23	59
Arista removed from both sides	22	64

(day 0 being the day of eclosion); the animals were tested for receptivity on the following day at an age when almost all normal females are receptive (*4*). The results agree with those of Petit to the extent that the loss of both antennae reduces the number of receptive females much more drastically than the loss of one does ($\chi^2 = 33.9$; $P < .001$), although the latter operation also has a marked effect (compared with controls, $\chi^2 = 15.6$; $P < .001$) (Table 1). However, in contrast to her findings, there is no significant difference between females whose antennae have been totally removed, those which have lost the funiculus and arista, and those which have simply lost the arista. This latter result is striking because removal of the arista involves very little damage or disturbance to the rest of the antenna; in particular, Johnston's organ and the olfactory receptors on the body of the funiculus remain unaffected.

This result suggests that the presence of the arista is essential for the normal perception of wing vibration and that an intact Johnston's organ is not sufficient. There are two ways in which the arista might operate. Hertweck (*3*) describes a single sensory neuron running from the arista, and a male's wing vibration might induce movements of the arista with respect to the funiculus. Alternatively the arista may act as a lever arm or "sail" which causes the whole funiculus to oscillate in response to wing vibration, thus stimulating Johnston's organ. Burkhardt and Schneider (*5*) have shown that the arista does act as a sail when the antenna of *Calliphora* is exposed to air currents.

For the perception of courtship stimuli one can distinguish between these two alternatives with fair confidence by fixing the funiculus so that it cannot move while still allowing free movement of the arista itself. This was done by running tiny drops of Eastman 910 adhesive from a fine glass needle onto the lower side of the distal end of the funiculus, and then gently pressing it back into the antennal socket. If successful, this held the funiculus fast without the adhesive's affecting the pedicel, and it left the arista projecting normally, though admittedly rather less exposed to air currents because of the backward position of the funiculus.

Table 2. The receptivity of females whose antennae have been treated with adhesive. Results are given for females that were found after testing either to have one or both antennae free or to have both antennae fixed. (χ^2 with Yates's correction = 19.7; $P<.001$).

	One or both antennae free	Both antennae fixed
Receptive	18	1
Unreceptive	2	13

Drosophila females proved to be extremely adept at freeing their antennae within a few hours of such treatment, but this enabled about half the treated group to be used as controls. Flies were treated with adhesive, and their receptivity was tested on the next day. They were then examined to see how far the treatment had been successful. All the flies showed extensive areas of dried adhesive on the funiculus, but in more than half the cases at least one antenna was free from its socket. Most females with one or both antennae free were receptive; few were if both antennae remained fixed, although in this latter group the arista was free to move (Table 2).

This finding suggests that a female's perception of wing vibration depends on the arista and funiculus acting as a unit that twists and thus stimulates Johnston's organ. Recently, Bennet-Clark and Ewing (*6*) have shown that the wing vibration display has two components which are, at least in part, synergistic. The vibration serves to drive a stream of air—a tonic component, and it also provides a phasic auditory stimulus with brief pulses repeated 30 times per second whose frequency within pulses is 180 to 350 cycle/sec. Burkhardt and Schneider (*5, 7*) found both tonic and phasic receptor units in *Calliphora* antennae, but they report no behavioral response to auditory stimuli. It seems most likely that the antenna's responsiveness to sound is important in courtship for a variety of sounds are also produced during the brief sexual displays of related flies such as *Sarcophaga* (*8*).

If the mechanical properties of the arista and funiculus in *Drosophila* are "tuned in" to resonate at the male's courtship sound frequency, it should be possible to hamper their action by loading or clipping the arista. In fact, preliminary experiments indicate that neither operation has much effect on receptivity. This finding suggests that, rather than following precisely the frequency within pulses of the male's vibration, the important stimulus may be the frequency of pulse repetition. So long as some kind of a sail is present to move the funiculus, there is adequate pickup of the pulse train, and the antennal nerve transmits a signal which is registered by the central mechanisms responsible for sexual acceptance.

AUBREY MANNING
Department of Zoology,
University of Edinburgh,
Edinburgh, Scotland

References and Notes

1. E. Mayr, *Evolution* **4**, 149 (1950); H. T. Spieth, *Bull. Amer. Mus. Natur. Hist. N.Y.* **99**, 401 (1952).
2. L. Petit, *Bull. Biol.* **92**, 248 (1958).
3. H. Hertweck, *Z. Wiss. Zool.* **139**, 559 (1931).
4. A. Manning, *Anim. Behav.* **15**, 239 (1967).
5. D. Burkhardt and G. Schneider, *Z. Naturforsch.* **12b**, 139 (1957).
6. H. C. Bennet-Clark and A. W. Ewing, *Nature* **215**, 669 (1967).
7. D. Burkhardt, *J. Insect. Physiol.* **4**, 138 (1960).
8. H. T. Thomas, *Proc. Roy. Entomol. Soc. London* **25**, 93 (1950).
9. I thank Marion Hill for assistance with these experiments, H. C. Bennet-Clark and A. W. Ewing for criticizing the manuscript, and Science Research Council for research support.

21 June 1967

Decay of Visual Information from a Single Letter

Abstract. *If the trace of a letter can be matched more rapidly with a physically identical letter (as in the pair AA) than it can be with a letter having only the same name (as in the pair Aa), then the trace must preserve the visual aspect of the letter. The visual information from a single letter decays in about 1.5 seconds if the task provides little incentive for preservation.*

A number of studies have found that information from complex arrays of visually presented items shows rapid decay in the 1st second after presentation (*1*). Such studies have led to the notion of a storage system for visual information which holds material for a brief period during the process of naming the stimuli (*2*). In this paper we present a technique which makes

Table 1. Mean reaction time (msec) and standard errors (S.E.) for responding to letters which are physically identical (P), have the same name (N), or are different (D), as a function of time interval between letters. Data are shown for performance on the second day only.

Mean and S.E.	Interval (sec)			
	0	0.5	1	1.5
	Type P			
Mean	879	505	582	609
S.E.	23	22	20	21
	Type N			
Mean	966	563	629	628
S.E.	25	26	22	22
	Type D			
Mean	928	558	615	629
S.E.	24	18	14	22

it possible to observe the decay of visual information from a single letter which has already been named.

In previous work (*3*), pairs of letters were exposed simultaneously within the fovea. The subject was instructed to respond, as rapidly as possible, whether the letters had the same name or different names. The time to respond "same" depended upon whether the particular letter pair was physically identical (for example, AA) or whether it was not physically identical but had the same name (for example, Aa). The results indicated that subjects are able to respond to physical identity 70 to 100 msec more rapidly than to name identity, even for highly overlearned figures such as letters of the alphabet.

The present paper takes advantage of the differences in speed of response to physical identity and name identity. The first letter is always in memory while the second letter is present in the foveal field. If the differences in speed still obtain, it is possible to infer that visual information of the first letter, as distinct from the name, is in store. Changes in the relative speeds of physical and name identity over time can then be used to infer the availability of visual information from the first letter.

The stimulus population consisted of capital and lower case typewritten letters, A, B, F, H, and K. The letters were typed on a tape and viewed from a distance of about 46 cm on a Stowe Memory Drum. The ambient lighting approximated normal reading light and did not vary during the experiment. The first letter was exposed on the left side of the tape and remained present during the entire trial. Either simultaneously or 0.5, 1, or 1.5 seconds later a shutter was automatically raised and the second letter appeared at the right side of the tape. The first letter was always capital while the second letter could be either upper or lower case. The distance between the letters was 8.4 cm, subtending a visual angle of about 10°.

The subjects were 12 right-handed males who participated for 1 hour on each of 2 successive days. They were positioned in front of the drum with the index fingers of each hand resting upon microswitches. They were instructed to respond as quickly as possible after the second stimulus appeared. They were to respond "same" if the two stimuli had the same name and "different" if they did not. The "same" key was always assigned to the left hand.

Each trial began with the word "ready" presented verbally by the experimenter. About 0.5 second later the first stimulus appeared and was followed, after the indicated interval, by the second stimulus. The experimenter recorded the response, elapsed time, and provided feedback concerning errors and reaction time. The time between trials was about 6 seconds.

On each of the 2 days subjects received 160 trials each. The trials were divided into blocks of ten. For each block a given time interval between the first and second letter was used. The list of 160 trials consisted of 80 different letter pairs, 40 physically identical pairs, and 40 pairs which were not physically identical but had the same name. Within each session, subjects responded to 40 pairs at each interval. Each subject was assigned to one line of a random Latin square so that for a group of four subjects each particular pair was used once with each interval.

Mean and median reaction times for correct responses were calculated for each subject. Table 1 shows the overall means and standard error of the means for the second day's performance. Values are shown for each type of letter pair (physically identical, name identical, and different) at each delay interval. The data of Table 1 are based on ten letter pairs per subject at each time interval for physical identity and for name identity and twenty letter pairs for the "different" condition. Since error responses are excluded, these numbers vary slightly from subject to subject, depending on the number of errors which they made. However, overall error rate on the second day was only 4.8 percent. The general trend was for more errors to occur with the longer times. Results for the first day and for data based on medians are quite similar to those shown in Table 1.

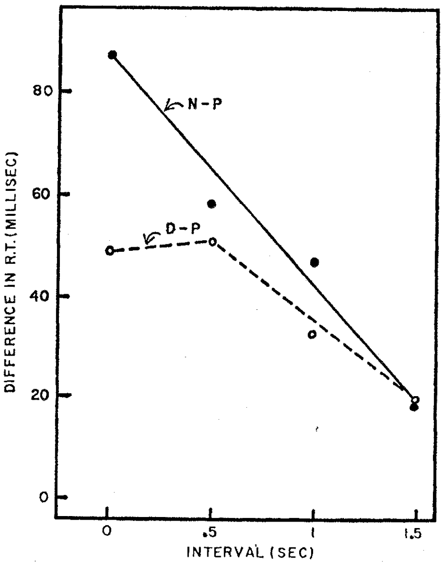

Fig. 1. Decay functions for visual information obtained by use of two different subtractive methods: $N - P$ is name identity minus physical identity, and $D - P$ is different minus physical identity (see text). *R.T.*, reaction time.

In order to analyze the loss of visual information over time, two subtractive methods can be employed. The first involves subtraction of the time for physical identity responses from the time for name identity responses. This same-same method eliminates any differences between the time to respond with the same versus the different key. Another subtractive method is to subtract the physical identity "same" responses from the "different" responses. This subtraction is based on the assumption that the time to respond "different" includes time to check both physical and name identity. However, this method does involve differences between the time to use the left and right hand and other things that differ between the two responses (*4*). Figure 1 shows the results of these two subtractive methods. In both cases there is the steady decline in the relative advantage of the physical identity response over the name identity or different response.

The data for the same-same method seemed to be somewhat more orderly than for the same-different method, but both provide roughly similar functions. At time zero, the difference between physical identity and name identity is approximately 80 msec, which was about equal to that obtained with simultaneous foveal presentation.

The orderly subtractive data are obtained despite wide fluctuations in the absolute levels of the times obtained with different intervals. The mean time to respond to a physically identical pair when the two stimuli are simultaneous is nearly 900 msec. Of course, this must include the time for an eye movement from the first stimulus at the left side to the second stimulus at the right side of the tape. The time for the eye movement is removed when there is a delay period. Thus the delay conditions have mean times for physical identity which are close to half as long as that for the zero condition. There is also a tendency for all times to increase between 0.5- and 1.5-second delays. This increase in the absolute level of the times presumably reflects the increasing temporal uncertainty when subjects are required to wait for the second stimulus. This is a frequent finding in studies of reaction time (*5*).

The results described in the preceding paragraph are borne out by statistical analyses. An analysis of variance was performed on the data presented in Table 1. The analysis showed that the effects of interval (0, ½, 1, and 1½ seconds) and of type of stimulus pair (physical identity, name identity, and different) were both significant $P < .01$. A linear trend analysis was run on the interaction between intervals and type of pair. This interaction is the curve displayed in Fig. 1. The results showed a significant linear interaction between types and interval $(.025 > P > .01)$.

Not all subjects showed the orderly linear relationship reflected in the means. This may be owing to the relatively little data obtained from individual subjects and the local effects of order which were different for different subjects. There is, however, considerable uniformity, since out of 24 comparisons of name identity minus physical identity at zero and 0.5 second, 22 show a positive sign and only one shows a negative sign. A similar comparison of 12 subtractions of name minus physical identity at 1 second gives nine positive and three negative, and at 1.5 second, seven are positive and five negative.

It seems reasonable to conclude from the functions shown in Fig. 1 that the visual information from the first letter shows a significant decay over time. The statistical analysis indicates that under these conditions the advantage of physical identity is lost after 1 to 1.5 seconds' delay.

Two objections might be raised to this conclusion. In the name identity condition the second letter is always lower case, and it could be that lower case letters are processed more slowly. This suggestion seems unlikely in view of the decay found over time. Moreover, there is no tendency for different responses which involve a lower case letter to be slower than those involving capitals only. The second objection concerns the fact that the first letter is present in the periphery of the visual field during the whole trial. It could be that subjects look at the first letter for a variable time as the interval increases. Subsequent studies have employed intervals which varied randomly over trials and conditions in which the first letter does not remain present. They have generally confirmed the findings presented here. It should be possible, however, to obtain much more accurate determinations of the decay functions than presented in this study.

The study reported in this paper differs considerably in methodology from previous reports concerning decaying visual information. Two differences appear to be crucial. All previous studies have used bright tachistoscopic flashes and have presented large amounts of information which cannot be encoded immediately. This study used reading light and only a single letter. The low error rate suggests that the subject has ample time to encode the letter. In view of these differences it is somewhat surprising that the decay rate obtained is so high and so closely resembles that in previous studies (*1*).

We believe that this rapid decay occurs only when the subject does not attempt to preserve the visual information from the first letter. In this experiment, the subject was given little or no incentive for preserving the visual information. He never knew whether he would receive a capital or small letter as the second stimulus. Thus, as the subjects report, the major way of preserving information seemed to be by way of verbalizing the letter and retaining the name during the interval. This should not be taken to mean that subjects would be unable to preserve the visual information of the first letter if, in fact, they desired to do so.

Michael I. Posner
Steven W. Keele
Department of Psychology,
University of Oregon, Eugene 97403

References and Notes

1. E. Averbach and A. S. Coriell, *Bell System Tech. J.* **40**, 309 (1961); G. Sperling, *Psychol. Monogr.* **74**, (whole No. 498) (1960); S. Keele and W. Chase, *Perception and Psychophysics* **2**, 383 (1967).
2. D. E. Broadbent, *Perception and Communication* (Pergamon Press, New York, 1958); G. Sperling, *Human Factors* **5**, 19 (1963).
3. M. I. Posner and R. F. Mitchell, *Psychol. Rev.*, in press.
4. D. Bindra, J. Williams, S. S. Wise, *Science* **150**, 1625 (1965).
5. E. T. Klemmer, *J. Exptl. Psychol.* **54**, 195 (1957).
6. Supported in part by NSF grants GB 3939 and GB 5960 to the University of Oregon.

19 July 1967

Trans-2-Hexenal: Mating Stimulant for Polyphemus Moths

Abstract. *The volatile compound from oak leaves which stimulates the female polyphemus moth to release her sex pheromone has been isolated and identified as* trans-2-hexenal. *Although leaves of other food plants contain* trans-*2-hexenal, they also release masking odors which block the activity of the hexenal.*

Polyphemus moths (*Antheraea polyphemus*) will not mate in the laboratory unless a volatile substance found in red-oak leaves is present. When the female receives the emanation via her antennae, she releases a sex pheromone, which attracts the male (*1*). Vacuum distillation, either of aqueous suspensions of frozen leaves or of fresh leaves, followed by preparative gas chromatography, has led to the isolation of the volatile oak-factor and its identification as *trans*-2-hexenal.

Vacuum distillation of freshly ground oak leaves under a reduced pressure of 70 to 80 mm-Hg produced a biologically active distillate (distilling temperature 40° to 46°C) which was collected in a bath of dry ice and acetone. When analyzed by gas chromatography (Barber-Colman; 1.8-m by 3.5-mm glass column packed with Poly-pak-2, at a column temperature of 140°C), this fraction contained at least four components with short retention times. The three major components were isolated by preparative gas chromatography on a glass column (2.4 m by 14.5 mm) packed with Poly-prep-pak-2 (F and M Scientific) at a column temperature of 212°C with nitrogen used as the carrier gas (300 ml/minute). Only one compound (retention time 13 minutes) provoked mating.

The characterization of this compound was greatly simplified by the