activity data. However, only the main effect due to illumination was significant ($F = 5.92$, $p < .02$).

The results of this study provide evidence for a major gene effect on the quantitative traits of open-field activity and defecation. Analyses of variance of the behavioral scores of albino and pigmented animals in the F_2, F_3, and F_4 generations indicate that this single gene difference at the *c*-locus may account for approximately 12 percent of the variance in both traits. As compared to pigmented animals, albinos show a pattern of higher defecation and lower activity when tested under white light. This behavioral pattern, which is interpreted as indicating heightened emotionality (*6*), largely disappears when animals are tested under red illumination; thus, the differences observed under bright illumination appear to be the result of a fear reaction. Therefore, it is concluded that this single gene effect is mediated through the visual system and that albinos are more photophobic than pigmented animals.

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Entrainment of Circadian Rhythms by Sound in Passer domesticus

Abstract. *The circadian locomotor rhythm of house sparrows was entrained by a sound stimulus. The birds were maintained at a constant temperature in dim green light. The entraining agent was 4½ hours of tape-recorded bird song played each day. Variations in the response to this stimulus have been correlated with individual variations in free-running period. This is the first clear demonstration that a biological clock can be influenced by sound stimuli.*

Light and temperature cycles of various durations and magnitudes can entrain the circadian rhythms of many organisms (*1, 2*). But the effectiveness of an agent other than light or temperature has not been adequately demonstrated, although several reports indicate such a possibility (*3*). Enright (*2*) observed that a loud buzzer served as a weak entraining agent for the activity rhythm of one house finch. Data of Halberg *et al.* (*4*) suggest that blind mice may have been entrained by normal mice that were entrained to a light cycle in the same room. Human rhythms can be entrained by social and psychological factors, but these factors are at present poorly defined (*5*). Attempts to find other agents for various organisms have failed (*6*). There are no published reports in which circadian rhythms in any organism have been rigorously shown to entrain to any clearly defined environmental factor other than light and temperature.

In order to demonstrate that a signal is an effective entraining agent, one must force the rhythm examined to assume the same frequency as that of the signal. In addition, to exclude the possibility that the rhythm is masked (that is, the measured parameter is forced but not the underlying timing system) it is necessary to show that the phase of the rhythm has been shifted during entrainment. The free-running period of the organism must always be examined under constant conditions in order to verify phase shifting by the entraining signal and to rule out coincidence between the free-running period of the organism and the period of the signal.

Our experience with house sparrows (*Passer domesticus*) housed in individual light-tight but not sound-proof boxes suggested that bird song might act to entrain the circadian rhythm of locomotor activity and led us to investigate this possibility systematically. The stimulus consisted of tape recordings of the sounds made by a colony of sparrows in the field in February as they began their activity in the early morning and as they went to roost in the evening (*7*). The sound was played continuously for approximately 4½ hours per a 24-hour day and was repeated each day at the same time. Its intensity was between 70 and 80 db; the background sound in the incubator was 60 to 70 db.

Ten sparrows (five males and five females) were examined for ability to be entrained by this stimulus. The responses did not vary according to sex (Table 1). Three birds produced activity records which satisfy all the rigorous criteria for entrainment. All three had circadian free-running periods preceding entrainment. During entrainment (26, 30, and 38 days), the stimulus controlled both the phase and the period of the rhythms. When the sound was discontinued, all three ran once more with a circadian period, the phase of which indicated that the rhythm had been phase shifted by the entraining signal (Fig. 1A).

Two other birds showed phase and period control by the sound stimulus until it was discontinued, but they failed to satisfy rigorous criteria of entrainment. In one case the subsequent free-run was indistinguishable from 24 hours, and in the other the sound was discontinued too soon to adequately demonstrate that it had shifted the phase of the rhythm.

Three other birds showed good phase and period control by the sound but subsequently broke away from the entraining signal and assumed circadian periods in its presence (Fig. 1B). In these three cases the sound caused a shift in the phase of the rhythm. In the remaining two cases the sound stimulus had no influence on the phase or period of the locomotor rhythm.

In each case the effect of the sound stimulus can be clearly related to the free-running period of the bird. Table 1 summarizes the period lengths and entrainment behavior of all ten birds. Note that in all situations in which entrainment failed (the subsequent periods of birds 69, 5, and 74, as well as the periods preceding entrainment of birds 4 and 7) the length of the period falls outside the range 23 hours 35 minutes to 24 hours 45 minutes. All other free-running periods fall within this range. The particular stimulus used in these experiments (presented with a period of 24 hours) apparently will entrain only those birds whose free-running periods fall within these limits.

With the exception of birds 4 and 7, there were differences in free-running period between the beginning and the end of the experiments. In all but one case (bird 72) the period lengthened. (Table 1). Some of these changes in period length resemble the after effects which often follow entrainment with light and temperature cycles (*8*). However, we do not wish to make such an interpretation at present since spontaneous lengthening of period during the first months of laboratory confinement under constant conditions is a common feature of the activity rhythm of this species (*9*).

Table 1. Relationship of free-running period to entrainment response of *P. domesticus.*

Bird number and sex	Period before stimulus (hr : min)	Song stimulus	Response		Subsequent period (hr : min)
			Entrainment	Duration (days)	
72, F	24:20	Evening	Yes	38	23:35*† 24:10
73, M	24:15	Evening	Yes	30	24:45†
9, F	23:45	Morning	Yes	26	24:20†
8, M	23:45	Morning	Yes	12	24:00†
3, M	24:20	Morning	Yes	11	24:45†
69, M	24:15	Evening	Broke away	18	25:30‡
5, F	24:30	Morning	Broke away	18	25:00‡ 25:30†
74, F	24:25	Evening	Broke away	7	24:55‡
4, M	23:30	Morning	None		No change
7, F	23:35	Morning	None		No change

* Period changed spontaneously after 13 days to 24 : 10. † Period after stimulus was discontinued. ‡ Period in the presence of the stimulus.

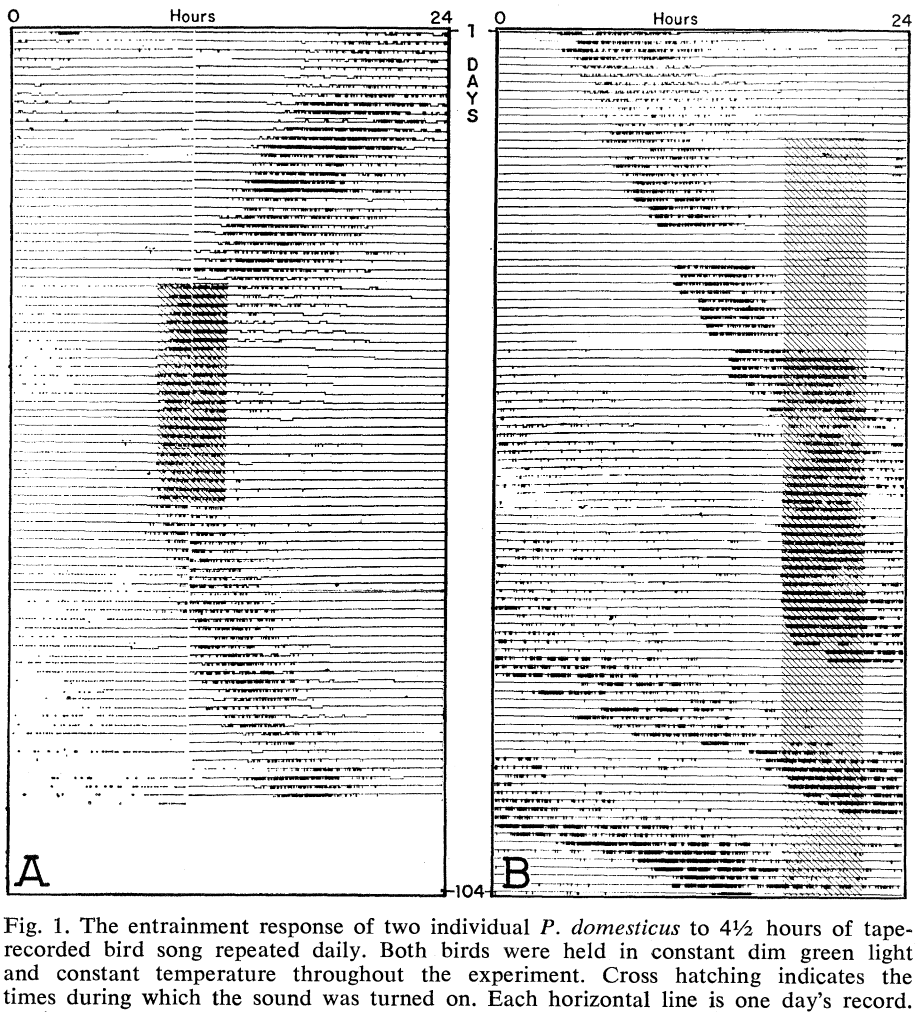

Fig. 1. The entrainment response of two individual *P. domesticus* to 4½ hours of tape-recorded bird song repeated daily. Both birds were held in constant dim green light and constant temperature throughout the experiment. Cross hatching indicates the times during which the sound was turned on. Each horizontal line is one day's record. Each day's record appears under the record of the day preceding it. Dark bands indicate intense activity. Bird 9 (A) was entrained for 26 days until the sound was discontinued. The sharp cutoff of activity when the sound is turned off each day is not a general feature of such records. Bird 69 (B) had the sound for 33 days before entraining to it. Note the gradual transients as he breaks away from entrainment and the slight shortening of his period as he goes completely through the sound a second time. The complete lack of activity on some days is due to failure of the apparatus.

In seven of the eight cases in which the period was controlled at 24 hours by the tape-recorded sound, the phase of the onset of activity was within ± 45 minutes of the beginning of the sound, regardless of whether morning or evening sound was used as a stimulus. The phase of bird 8 was about 3½ hours in advance of the onset of the sound for the 12 days during which it was entrained.

In six of the ten experiments the sound stimulus was presented to the bird at or very near the onset of its activity. As this was very close to the final entrained phase relationship, there was no opportunity, in such cases, to observe transients. In the four cases in which the sound was first presented at other than the final relationship with the activity rhythm, no transients were observed until the final phase had almost been reached (Fig. 1B).

Attempts were also made to study the mutual interaction of the rhythms of two birds. A pair of birds were placed in a double-breeding cage in which they were separated by a wire screen partition. The activity of each bird was recorded separately. In some cases very little interaction was observed, but in others significant effects were noted. In the case shown in Fig. 2, entrainment of bird 70 lasts for 21 days but it subsequently breaks away. Bird 79 has a period of about 23 hours 45 minutes, and bird 70, after breaking away from entrainment, has a period of about 24 hours 30 minutes as compared with a period of about 24 hours 20 minutes before bird 79 was introduced. If we assume that bird 79 is providing some entraining signal with the same period as its activity rhythm, the difference between the period of this signal and the period of the activity rhythm of bird 70 after breaking away from entrainment is about 45 minutes. These data coincide well with the limits of entrainment to the tape-recorded signal (Table 1). In such experiments the entraining stimulus may consist in part of visual cues. However, the fact that sound by itself can entrain makes it necessary to exercise extreme caution when interpreting free-running rhythms of birds in experimental situations in which they may be visually, but not acoustically, isolated from one another.

The significant feature of our results is not that bird song per se will entrain,

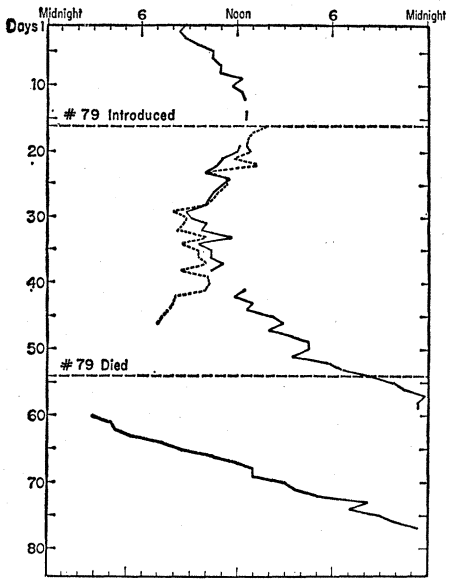

Fig. 2. Entrainment of one bird's activity rhythm by another bird. Lines have been drawn connecting each day's onset of activity (solid line, bird 70; dotted line, bird 79). Gaps indicate days on which the activity onsets were not clearly defined. Bird 70 occupied half of a double-breeding cage. On day 16 bird 79 was introduced into the other half. On day 46 the activity of bird 79 became diffuse and on day 54 it died.

but that the sparrow's clock can be influenced by way of auditory pathways (*8*). Biological clocks appear to be phylogenetically ancient adaptations, and environmental cycles of light and temperature must have impinged upon them continuously from their earliest beginnings (*10*). The mechanisms for entrainment to these cycles are thus likely to be a fundamental part of the organization of whatever oscillations underlie expressed circadian rhythms. On the other hand, auditory entrainment, no matter how unspecific the required sound may be, is predicated upon a high degree of organization of the central nervous system and must therefore represent a relatively recent evolutionary addition to the entrainment repertoire of these oscillations. A comparison of the pattern of entrainment to light cycles with the pattern of entrainment to auditory stimuli may thus provide insight into the phylogeny of biological clocks.

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7. The field recordings were transferred to a Cousino Audio Vendor which allowed continuous repetition of the tape loop. Variations in playing time for one revolution of the loop (2 seconds in some experiments, up to 20 minutes in others) did not affect the results. The tape recorder was controlled with a time switch, making it possible to present birds with a continuous signal of any duration automatically. Data was processed, and birds were housed in activity cages as previously reported [M. Menaker, in *Circadian Clocks*, J. Aschoff, Ed. (North-Holland, Amsterdam, 1965), p. 385]. The cages were placed in light-tight and relatively soundproof B. O. D. incubators at 23 ± 1°C in constant dim green light (approximately 0.1 lux) provided by electroluminescent panels. The birds were fed at approximately 14-day intervals at random times of day with no accompanying increase in light intensity. The sound stimulus was presented to each bird individually through a speaker mounted inside the incubator.
8. This is based on the reasonable assumption that the sound is not being sensed in some other undetermined way.
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Visual Adaptation: Increased Efficiency Resulting from Spectrally Distributed Mixtures of Stimuli

Abstract. *Visual adapting stimuli having different spectral distributions are used alone and then mixed together. It is found that the mixture is more effective, as an adapting field, than either component when used alone. This experiment, along with others, supports the following: although the most efficient stimulus for eliciting a visual sensation is "compact" in space, time, and wavelength, the most efficient adapting stimulus tends to be dispersed in each of these dimensions.*

The most efficient input for exciting a visual sensation can be characterized as being "compact" in space, time, and wavelength. For short, small flashes of fixed spectral distribution, the relation $L.A.t = C$ holds nearly exactly, meaning that luminance, area, and flash duration are interchangeable. This product is proportional to the energy content of the flash. As area or duration or both extend beyond the so-called "reciprocity" range, energy must be increased to maintain a constant visual effect. This generalization is based on very many experiments; there are none known to us indicating that an opposite result ever occurs when a *direct visual effect* (defined below) is under investigation. In other words, a long, large flash is never more efficient than a shorter, smaller one. Similarly, efficiency is either unchanged or reduced when flashes are broken up, spatially or temporally, into discrete components (*1*).

The "direct visual effect" has most often been a threshold probability of seeing, but the generalization holds also for those relatively fewer experiments where suprathreshold brightness has instead been the response criterion.

Much less work has been done on the spectral aspect of this problem (*2*). The approach that we have used in previous work is as follows: (i) A threshold is determined for a flash of wavelength λ_1 and this is arbitrarily called 1 "S-unit" of radiance. (ii) Another threshold is determined for wavelength λ_2 and this also is called 1 S-unit of radiance. (iii) The two flashes are additively and simultaneously mixed together in some fixed ratio of their S-units. By proportionally varying the radiance of each, without altering the ratio, it is possible to determine a new threshold, and this is done for various ratios. In an eye containing only one type of receptor, like the human eye under scotopic conditions where only rods are functional, the number of S-units in the mixture, ΣS, must, within experimental error, always be unity at threshold for the mixture. Under photopic conditions, where at least three classes of cone receptors absorb light (each with a different action spectrum) it has been found experimentally that ΣS equals or exceeds, but is never less than, 1.0. This result implies that, when a direct visual effect is under investigation, the most efficient stimulus must be spectrally compact, as well as spatially and temporally so.

When ΣS exceeds 1.0, as it does in these cases, a failure of linear summation between the outputs of separate cone mechanisms is suggested as the