



Fig. 1. A copulating pair of cicada killers. The smaller male has begun flight while the female behaves as is typical in this situation by continuing to hold or cling to the substrate. The result is usually an aborted flight attempt by the male or ultimately the breaking away and termination of the copulation by the male.

resist the females, but immediately began flight. Escape was thus facilitated by this behavior.

Females apparently can communicate the presence of potential danger to males and elicit flight in them. However, the information is not precise, because the males' response is the same when females begin flight "spontaneously." Males are unable to, or at least do not, distinguish flight elicited by potential enemies from flight elicited "spontaneously" in the female. Thus the major differences in the two roles appear to be largely dependent on the differences in threshold for flight behavior. Communication is also unidirectional (that is, from female to male).

Other adaptations seem associated with these two necessarily exclusive roles. Separation may be enhanced by the male's considerably more frequent attempts at flight and, when the substrate permits, the male's frequent tendency to dangle free in space. On vertical surfaces, the male is almost always lower than the female, consequently gravity may facilitate separation. One apparent adaptation aiding in raising the female's threshold toward flight is a strong tendency toward cleaning behavior which apparently is much aggravated after repeated approach and contact stimulation by the observer. This behavior seems to inhibit flight.

There appear to be several "undesirable" consequences of conflicting selection pressures. The males have a greater ability to perceive or respond to danger, as indicated by attempted flight, without being able to communi-

cate the presence of danger to the female, and there is an understandable incongruity of the female's escaper role and her considerably higher threshold for flight in response to danger. Both of the above appear to be indirect consequences of the female's remaining still when the male attempts flight, thereby fostering or perhaps even making possible the eventual separation of the couple. Thus the female's considerably higher threshold for either "spontaneously" or nonspontaneously induced flight aids in separation. The dilemma arising from these conflicting selection pressures appears to have been satisfactorily resolved by behavioral evolution of the female. A balance appears to exist between the two conflicting behaviors (separation and escape). The female's generally lowered responsiveness to mild stimuli enables her to act as a counterweight against attempted flights of the male thereby facilitating separation, while her tendency to respond to strong stimuli by flight enables the pair to escape potential enemies. Centripetal selection probably opposes much oscillation in shifting the mean in favor of either behavior since the efficiency of the opposing behavior would be greatly curtailed. This balance illustrates behavioral homeostasis at the level of the copulating pair. The balance, however, is probably dynamic; and under changing conditions, such as in the importance of enemies, directed selection may be expected to shift the mean in favor of one or the other behavior.

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References and Notes

1. N. Lin, in preparation.
2. E. T. Nielsen, *Spolia Zool. Mus. Haun.* 7, 1 (1945); K. Tsuneki, *Mem. Faculty Liberal Arts, Fukui Univ.* 6, 77 (1956); H. E. Evans, *Studies on the Comparative Ethology of Digger Wasps of the Genus *Bembix** (Comstock, Ithaca, N.Y., 1957), p. 64.
3. G. P. Baerends, *Tijdschr. Entomol.* 84, 68 (1941); G. E. Bohart and G. E. Knowlton, *Proc. Entomol. Soc. Wash.* 55, 100 (1953).
4. A. Huber, *Zool. Jahrb. Abt. Syst. Okol. Geogr. Tiere* 89, 43 (1961).
5. G. E. Bohart and P. M. Marsh, *Pan-Pacific Entomol.* 36, 115 (1960).
6. H. E. Evans, *The Comparative Ethology and Evolution of the Sand Wasps* (Harvard Univ. Press, Cambridge, Mass., 1966), p. 229.
7. F. E. Kurczewski, *J. Kansas Entomol. Soc.* 39, 436 (1966).
8. N. Lin, *Behaviour* 20, 115 (1963).
9. —, *Anim. Behav.* 14, 130 (1966).
10. —, thesis, University of Kansas (1964).
11. This research was partially supported by a Sigma Xi grant-in-aid of research during the summers of 1965 and 1966.

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Recovery of Masked Visual Targets by Inhibition of the Masking Stimulus

Abstract. *Theories of visual backward masking all assume that a masked target is eliminated from the visual system. Experiments on reaction time to masked signals suggest otherwise, as does a recent demonstration that a masked target can be restored to phenomenal awareness by backward masking of the target's mask. Two experiments are reported here that substantiate the possibility of recovering a masked target, by using different stimulus materials and a more elaborate design than was employed in the first demonstration of this effect.*

Visual backward masking consists in the retroactive interference with the perception of one visual stimulus, the target, by another visual stimulus, the mask, closely following the target in time. The primary issue for theories of backward masking has been to explain why such a masked target is not perceived. Hence, theoretical efforts (1) have been devoted to postulating mechanisms whereby the target might be removed from the visual system. However, some experiments (2) have shown that reaction times to masked targets are not increased, even though reaction time is ordinarily inversely related to target luminance. This finding indicates that masked targets retain some representation in the visual system despite their phenomenal absence.

The present research follows another approach to assessing the status of a masked target. It bears close resemblance to a recently reported experiment by Robinson (3), who concluded that a masked target could be recovered if its mask were itself suppressed through backward masking. In that experiment the target was an illuminated disk; mask No. 1 was a larger disk, and mask No. 2 was a still larger disk. Subjects indicated via phenomenal report what they saw when the target was followed only by mask 1 and also when the target was followed by mask 1 and mask 2 in sequence. The latter condition yielded more reports of the target than the former.

One weakness in the Robinson experiment is the failure to present data on a possible direct effect of mask 2 on the target. It most likely would be inhibiting, if at all effective, but it con-

ceivably could have been directly facilitating. Thus, some question can be raised about the conclusion that the apparent recovery of the target resulted from the inhibition of its mask by mask 2, that is, from "disinhibition." However, if substantiated, Robinson's dramatic findings provide in a simple and direct fashion convincing evidence for the registration and at least temporary storage of a masked target.

In the present study, the target stimuli were the letters D and O, each 21' (minutes) of visual angle in height, 18' in width, and with a strip width 4½', drawn in black ink on a white background. Mask 1 was a solid black disk, 36' in diameter. Mask 2 was a black ring, with an inner diameter of 36' and an outer diameter of 1°12'. The target letter was centered on the disk, and the ring fitted snugly around the disk. The stimuli were presented tachistoscopically (Scientific Prototype, model GB) in the center of a dark fixation field containing in its periphery four back-lighted, red pinhole dots arranged in a diamond pattern and designed to help maintain fixation in the center of the stimulus field. Target and mask fields were illuminated at about 10 footlamberts (10.8 mlam); all interstimulus and intertrial intervals were dark. Viewing was monocular. The subjects were 25 volunteers from introductory psychology classes, naive about the purpose of the experiment. All had normal vision or were corrected to 20/20.

After a 5-minute dark adaptation period, each subject was exposed to four conditions in a single half-hour session, with 50 trials per condition presented in random order. To assure proper attention and fixation, the subject was allowed to initiate each trial after a ready signal from the experimenter. The subject's task throughout was to say whether the target letter had been D or O.

The four conditions were: T, target alone; T + 1, target followed by mask 1 (the disk); T + 1 + 2, target followed by mask 1 followed by mask 2 (the ring); T + 2, target followed by mask 2. Target duration was 1 msec. The interstimulus interval between target and mask 1 was 50 msec. The duration of mask 1 was 5 msec, and the interstimulus interval between it and mask 2 was 30 msec. The duration of mask 2 was 50 msec. In condition T + 2, the interstimulus interval between target and mask 2 was the same as in condition T + 1 + 2, namely, 85 msec.

The percentage of correct recognition was computed for each subject in each condition and was corrected for guessing. A mean percent recognition score was then computed for each condition, yielding the following values: T, 0.78; T + 1, 0.32; T + 1 + 2, 0.32; T + 2, 0.47. While the means in T + 1 and T + 1 + 2 are equal, it is also evident from the difference between T and T + 2 that the ring alone had a substantial direct masking effect on the target. That effect must also be reflected in T + 1 + 2, thereby concealing possible disinhibiting effect. To assess whether there was indeed recovery evident in T + 1 + 2, the following argument was pursued.

Assume, contrary to our hypothesis, that the dot and the ring function as independent sources of target masking. Assume that condition T + 1 (compared with T) provides an estimate of the probability that the disk will mask the target and that T + 2 provides the same estimate for the ring. Then the joint masking effect of the two masks, as presented in T + 1 + 2, should be predictable from the well-known formula for combining independent probabilities, namely, $p_{1+2} = (p_1 + p_2) - (p_1 \times p_2)$.

The value of p_1 was obtained by expressing the difference between mean recognition scores of condition T and T + 1 as a ratio of the score in condition T, that is, $p_1 = (0.78 - 0.32)/0.78 = 0.59$. Similarly, $p_2 = (0.78 - 0.47)/0.78 = 0.40$.

The predicted probability of masking for condition T + 1 + 2, if the two masks are independent, $= 0.59 + 0.40 - 0.236$, or 0.754. To estimate the mean recognition score for condition T + 1 + 2, under the independence assumption, we then invert the operations that yielded the estimates of p_1 and p_2 . That is, we compute the probability that a target will be masked in condition T + 1 + 2 as 0.754×0.78 , or 0.588. Then $0.78 - 0.588$, or 0.19, gives the probability of target recognition in T + 1 + 2, if masks 1 and 2 were independent. The difference between 0.19 and the obtained recognition score in T + 1 + 2 of 0.32 is statistically significant ($t = 2.64$; $P < .01$), allowing us to reject the independence hypothesis. The two masks do interact, and in a manner compatible with the hypothesis that mask 2 vitiates the inhibiting effect of mask 1.

However, the above manipulations of the data do require assumptions that might be questioned, and so a

second experiment was performed. Experiment 2 exactly replicated the first experiment, except that in an attempt to decrease the rather large effect of the ring on the target, the interstimulus interval between target and mask 1 was increased from 50 to 80 msec. Twenty-five new subjects were run exactly as in the first experiment. The mean recognition scores were: T, 0.86; T + 1, 0.56; T + 1 + 2, 0.65; and T + 2, 0.74.

As anticipated, the ring had very little direct inhibiting effect on the target (comparing T and T + 2). Furthermore, despite that effect, condition T + 1 + 2 now yielded a significantly greater mean recognition score than T + 1 ($t = 2.56$, $P < .02$). If the analysis applied to the first experiment is used here, the predicted recognition score for condition T + 1 + 2 is 0.48; the obtained value of 0.65 is also, of course, significantly greater than 0.48 ($t = 3.66$, $P < .001$).

Thus, the two experiments provide convincing evidence of target recovery, substantiating Robinson's finding, with different stimulus materials and an improved design. Exactly how this recovery is effected is still an open question. Our original notion was that the target enters the visual system, is suppressed from having phenomenal impact by the masking disk, but is still "in the system," perhaps in some sort of short-term storage. When the ring is introduced, it in turn suppresses the disk, thereby releasing the target for entry into phenomenal awareness. However, we are now, like Robinson, impressed with the potential applicability of the concept of lateral inhibition (4) to both backward masking and recovery. It may prove possible, with the aid of the lateral inhibition concept, to replace the above general notion with an explicit neural model.

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References and Notes

1. E. Averbach and A. S. Coriell, *Bell System Tech. J.*, **40**, 309 (1961); C. W. Erikson and J. F. Collins, *J. Exptl. Psychol.*, **70**, 343, (1966); J. H. Thompson, *ibid.*, **71**, 580 (1966).
2. E. Fehrer and D. Raab, *J. Exptl. Psychol.*, **63**, 143 (1962); E. Fehrer and I. Biederman, *ibid.*, **64**, 126 (1962); K. Harrison and R. Fox, *ibid.*, **71**, 162 (1966).
3. D. N. Robinson, *Science*, **154**, 157 (1966).
4. F. Ratliff, *Mach Bands: Quantitative Studies on Neural Networks in the Retina* (Holden-Day, San Francisco, 1965).
5. Based on a master's thesis by D.G.P. Supported by NIH grant NB 07622.

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