where (R. M. Boynton, S. R. Das, J. Gardiner, *ibid.*, in press).

5. To do this requires very precise calibration of the optical wedges used to vary radiance. A five-channel, xenon-arc powered, Maxwellian-view optical system was used in this work. This apparatus and its calibration is described in detail by C. Ingling, "The receptor sensitivities of receptor systems in color vision," thesis, University of Rochester (1966).
6. This assumes a unit slope of the log threshold vs. log adapting radiance (t.v.r.) function.
7. I. T. Kaplan and H. Ripps, *J. Exp. Psychol.* **60**, 284 (1960).
8. G. Wald and A. B. Clark, *J. Gen. Physiol.* **21**, 93 (1937).
9. Supported by grant 00624 from the National Institute of Neurological Diseases and Blindness, U.S. Public Health Service.

* Work done while at the Center for Visual Science, University of Rochester, Rochester, N.Y.

26 September 1966

Pupil Diameter and Load on Memory

Abstract. *During a short-term memory task, pupil diameter is a measure of the amount of material which is under active processing at any time. The pupil dilates as the material is presented and constricts during report. The rate of change of these functions is related to task difficulty.*

In a recent series of articles, Hess and Polt have called attention to the fact that changes of pupil diameter can serve as a sensitive and useful indicator of mental state. The pupil dilates with pleasure and constricts with displeasure (*1, 2*). The pupil also dilates during mental activity, for example, when solving arithmetic problems (*2, 3*). Hess noted (*2*, p. 53) that the major constriction of the pupil occurs only after the subject reports his answer to a problem, even if this report is requested some time after the problem has been solved. This observation suggests that the pupil may serve as an indicator of the amount of load on memory, or, more precisely, of the amount of effort involved in storing information for report. Pilot experiments in our laboratory strongly confirmed this suggestion: in a short-term memory task, the pupil dilates while the subject listens to information, and constricts as he reports. The present study is concerned with this effect.

Subjects in this experiment were five female college students who reported adequate uncorrected vision in both eyes. The session began with practice on all experimental tasks (one additional subject was rejected at this point because of frequent failures in immediate recall of strings of seven digits).

The main experiment consisted of four blocks of seven trials: in each block the subject heard (i) strings of digits (three to seven digits per string) presented for immediate recall; (ii) a string of four high-frequency monosyllabic nouns presented for immediate recall; (iii) a string of four digits presented for transformation (the subject was to add one to each digit). The subject was informed of the task just before each trial began. Five pictures of the subject's eye were then taken at a rate of one per second. On the sixth click of the camera, the experimenter began the presentation of the string, calling out digits or words in time with the camera. The subject was instructed to wait for two clicks after the experimenter finished speaking before she began responding, again in time with the camera. Four additional pictures were taken after the completion of the subject's report. A synchronous record of the speech of both experimenter and subject and of the timing of the pictures was made on a Bausch and Lomb VOM-5 recorder. Errors of recall and errors of timing were both rare, and such trials were immediately replaced.

Photographs of the eye were taken through a half-mirror on Kodak Tri-X film with a Grass C4D camera (1/25 second; $f = 8$). During this part of the experiment, the subject looked through the mirror at a white card (luminance 220 lu/m^2), 6 inches (15 cm) from her eyes, which filled her field of view. A faint gray circle ¾ inch in diameter was drawn on the card for fixation. Additional illumination of the eye was provided by a fluorescent tube which could be seen in peripheral vision. Total illumination at the eye was 1980 lu/m^2. All photographs were taken of the right eye, with the left eye occluded.

The development of the pupillary response during the presentation and recall of strings of digits is shown in Fig. 1 (left), where each point is an average of 20 measurements (four each for five subjects). Although there are marked differences among subjects in the magnitude of the pupillary response, the general features of the response are quite consistent. Large spontaneous variations of pupil size are notable by their absence in this situation where subjects' thought processes are effectively controlled by the task. Two distinct phases are apparent in the pupillary response to this immediate memory task: a loading phase during which the pupil dilates with every digit heard, and an unloading phase during which the pupil constricts with every digit reported. The peak pupillary diameters obtained (typically in the latter part of the pause) are directly related to the number of digits in the string. This ordering of peaks was found with no inversions in the responses of four of the five subjects, and with a single inversion for the remaining subject ($p < 10^{-4}$ by chi-square test). An anticipation effect was also noted: when subjects are warned that a difficult trial is coming, their pupils tend to dilate slightly. This effect of length of string on pupil size during the early control pictures is significant by trend analysis ($F = 6.62$ 1/16 df, $p < .05$), but it is restricted in magnitude (as Fig. 1, left, indicates) and does not account for the main results.

Two additional tasks, recall of words and transformation of digits, were included in the experimental design to permit an investigation of the effect of task difficulty on the pupillary response. The two tasks are clearly more difficult than the recall of digits; for our subjects the mean span for recall of digits was 7.8, while the mean span was 5.7 for words and 4.5 for the transformation task. In Fig. 1 (right), the pupillary response during the presentation and recall of four digits is compared with the response for the recall of four words and for the transformation of four digits. The expectation that pupillary dilation will be related to task difficulty is strongly confirmed; the loading function is substantially steeper in the more difficult tasks than in the recall of digit series of all lengths ($t = 3.85$, 24 df, $p < .001$).

The comparison of the results for digit transformation with those for digit recall is of particular interest; the physical conditions of stimulation are precisely identical but the loading response is more pronounced when the subject is storing digits for transformation than when she is storing digits for recall. While physical conditions are identical, the process of storing information is probably different in the two tasks; for example, grouping is advantageous for recall, but obviously detrimental to transformation. Incidental evidence suggests that the difference in slope is not due to subjects' performing the transformation operation during the listening phase. Subjects characteristically report that they are con-

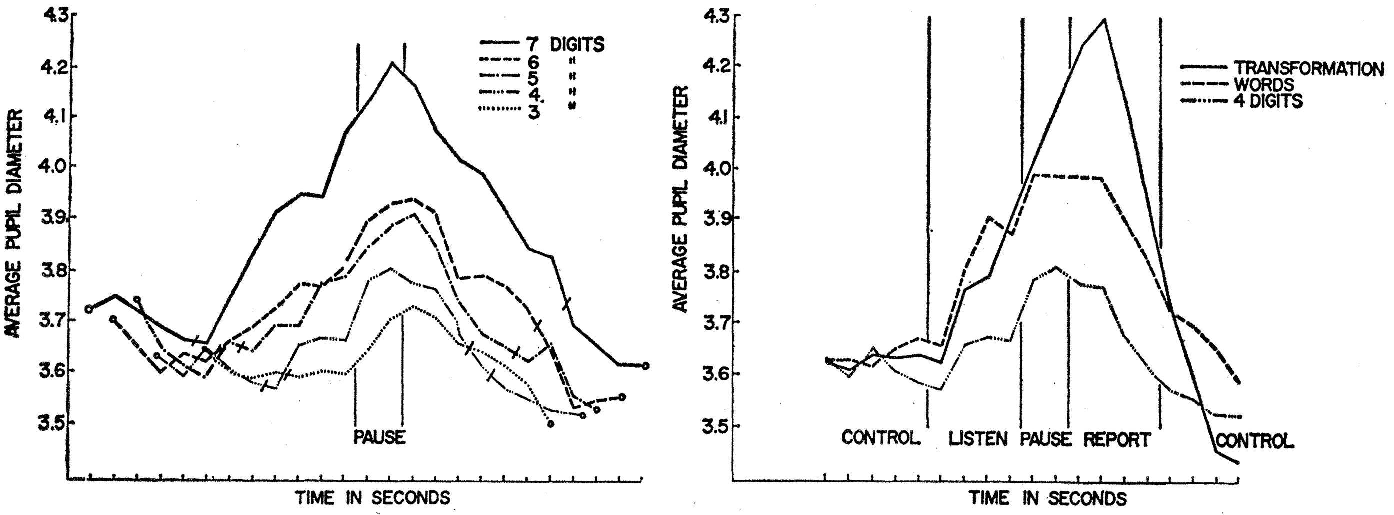

Fig. 1. (Left) Average pupil diameter (in millimeters) for five subjects during presentation and recall of digit strings of varying lengths. Time axes have been shifted so that the 2-second pause between presentation and recall falls within the central division of the graph for all string-lengths. Slash marks are placed on each curve just before the first digit presented and just after the last digit reported. (Right) Average pupil diameter during presentation and recall of four digits, four words, and transformation of a string of four digits.

scious of computing only during the pause and report phases. On the basis of these reports, we would expect the load on the subject to be maximal during the report phase; this is also the time at which the pupillary dilation reaches its peak (for three of the subjects, on the second digit reported). The difference in timing of maximal dilation between the transformation task and the recall of four words or four digits is significant ($t = 2.44$, 8 df, $p < .05$).

The results reported above indicate that pupillary diameter provides a very effective index of the momentary load on a subject as he performs a mental task. We interpret the pupillary changes shown in Fig. 1 as indicating variations in the number of items which are rehearsed, or "recirculated," during the course of the trial (*4*). At the relatively slow rate of presentation and report used in the present study, this number certainly increases during the presentation of the string, and subsequently decreases as items are successively dropped from rehearsal during the report phase. The interpretation that major pupillary dilations are closely related to rehearsal and other active modes of information-processing derives from the following observation: when complex sentences are auditorily presented at fairly rapid rates, which effectively prevent rehearsal as well as concurrent comprehension, no dilations occur during the listening phase, although this may last for several seconds. A very large dilation occurs at the termination of the sentence. Subjects report that this is the time at which they actively rehearse the sentence in an effort to make sense of it. Recent descriptions have appeared (*5*) of the different patterns of autonomic response which accompany the direction of attention to inner activity or to the outside environment; the absence of dilations when subjects' attention is entirely directed to the reception of a message is probably related to these results. Another sequence of pupillary responses which conforms to this interpretation is observed when subjects are required to repeat a string of digits twice in immediate succession. Subjective descriptions indicate that preparations for the second repetition of the string are initiated during the first repetition. Correspondingly, a partial constriction occurs at the beginning of the first report, which is soon followed by a second dilation.

The final phase of the experimental session was devoted to a test of the hypothesis that pupillary changes dur-

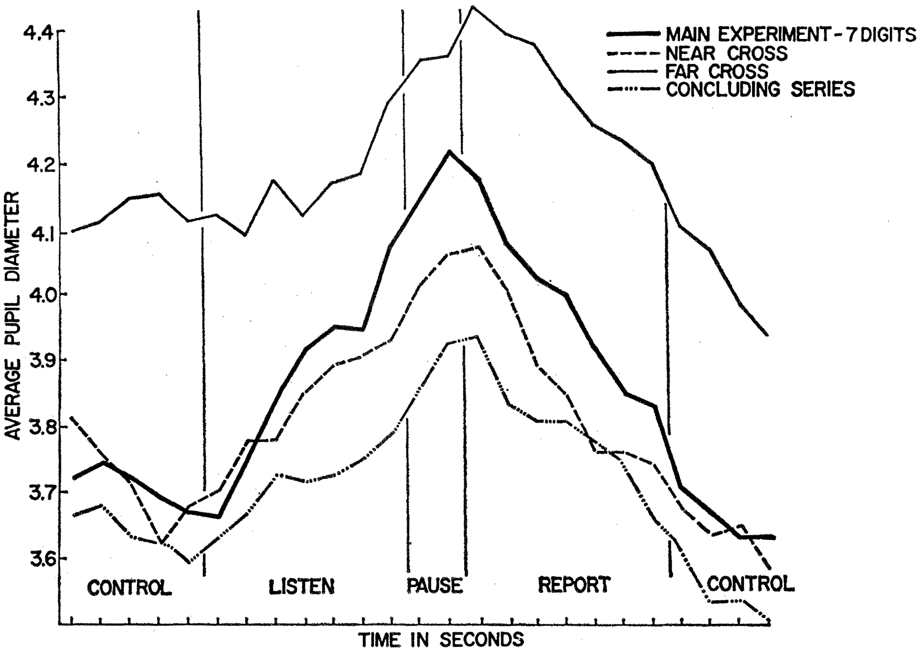

Fig. 2. Average pupil diameter (in millimeters) during presentation and recall of strings of seven digits under various conditions of fixation.

ing these tasks are due to changes in accommodative convergence. Hess and Polt (*3*) had concluded that changes of accommodation do not account for the effects of mental activity on the pupil. However, we were impressed by the subjective feeling reported by many subjects that the visual field apparently becomes blurred during those stages of memory tasks where pupillary diameter is at its maximum. These reports appeared to justify a further study of the role of accommodation.

It may be observed that the fixation conditions of the main experiment were such as to induce a high level of accommodation. If the pupillary response in fact depends on loss of accommodation, initial fixation to a near object should produce very large responses, which would be expected to disappear under different fixation conditions. Immediately after completion of the main experiment, the fixation card containing the faint gray fixation circle was replaced by another card, on which a 1-inch (2.5 cm) black cardboard cross was pasted, providing a high degree of figure-ground contrast for the fixation target. Four recall trials were run with strings of seven digits. The fixation card was then removed, and a white surface was exposed at a distance of 6 feet (about 2 m), with a 12-inch black fixation cross upon it. The two fixation surfaces were matched in both luminance and the visual angle subtended by the fixation distance. Four additional trials were run at this greater fixation distance. Finally, the original fixation card was replaced, and four trials were run under conditions identical to those of the main experiment. The data for these three conditions are shown in Fig. 2, which also includes the results for strings of seven digits in the main experiment. A strong effect of accommodation distance is evident in Fig. 2, where the pupils average 10 percent larger when the subject fixates at 6 feet than when she fixates at 6 inches. However, the experimental effect is clearly present even at the largest distance, which approximates the limit of accommodation effects (*6*). Finally, a further control experiment was conducted, in which the conditions of the initial study were replicated in full, except that the fixation target was now presented at a distance of 6 feet during the entire session. The results for two subjects were very similar to those of the initial experiment. These results confirm Hess's conclusion that pupillary changes in mental activity are not mediated by changes of accommodation.

Another conclusion which may be drawn from Fig. 2 concerns the effects of repeated performance of the same task. In the last block of trials, which was performed under fixation conditions identical to those of the main experiment, the pupillary response appears to be markedly reduced. One of our subjects, initially the least responsive, failed to show this reduction in the slope of the loading function, which is only of marginal significance in these data ($t = 2.28$, 4 df, $p < .10$). We draw attention to this effect after having observed it on several other occasions in which a single procedure was repeated for several trials, as was the case in Fig. 2. On the other hand, we observed no habituation effect over the successive blocks of the main experiment, where several different procedures were interspersed in each block. The data suggest that the adoption by subject of a consistent performance set will tend to reduce both the subjective difficulty of the task and the pupillary response to it. The appearance of such practice effects in the pupillary response appears to provide additional evidence for the validity of this response as an indicator of processing load.

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References and Notes

1. E. Hess and J. Polt, *Science* **132**, 349 (1960).
2. E. Hess, *Sci. Am.* **212**, 46 (1965).
3. ——— and J. Polt, *Science* **140**, 1190 (1964).
4. D. E. Broadbent, *Perception and Communication* (Pergamon, New York, 1958); I. Pollack, *Can. J. Psychol.* **17**, 380 (1963).
5. J. I. Lacey, in *Research in Psychotherapy*, E. A. Rubenstein and M. B. Parloff, Eds. (National Publishing Co., Washington, D.C., 1959); J. I. Lacey, J. Kagan, B. Lacey, H. Moss, in *Expressions of the Emotions of Man*, P. H. Knapp, Ed. (International Univ. Press, New York, 1963); P. A. Obrist, *Psychosomat. Med.* **25**, 450 (1963); J. Kagan and M. Lewis, *Merrill-Palmer Quart. Behavior Develop.* **11**, 95 (1965).
6. M. Alpern, G. L. Mason, R. E. Jardinico, *Am. J. Ophthalmol.* **52**, 330 (1961).
7. This research was supported by grant NIMH 08847-02 to G. S. Blum. It was conducted while the senior author (D.K.) was Visiting Scientist at the University of Michigan under the auspices of the Institute of Science and Technology. We thank M. Alpern, G. S. Blum, and I. Pollack for suggestions and assistance.

19 Septmber 1966

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Tryptophan Operon of Escherichia coli: Regulatory Behavior in Salmonella typhimurium Cytoplasm

Abstract. *Hybrids hemizygous for the tryptophan genes were prepared by episomal transfer of an* Escherichia coli *element into* Salmonella typhimurium. *Regulation of enzyme production by hybrids carrying wild-type* E. coli *genes in response to changes in the growth medium occurs in precisely the same manner as in haploid* E. coli *wild type. Mutant alleles of the anthranilate synthetase gene of* E. coli *which prevent derepression in* E. coli *function identically in* S. typhimurium. *At least one* Salmonella *tryptophan regulatory gene unlinked to the structural genes is known. Any differences which may exist between the tryptophan regulatory genes of* E. coli *and* Salmonella *have little effect on the regulation of enzyme formation in hybrids.*

There is a high degree of gross homology in both genetic structure and function between *Salmonella typhimurium* and *Escherichia coli* (*1*). Nevertheless, considerable divergence in the molecular architecture of analogous genes has been revealed by fine structure analysis with transduction techniques (*2*). These genetic results complement earlier experiments of nucleic acid hybridization in vitro (*3*) which showed poor homology between the two genera, despite close similarities in guanine and cytosine content (*4*).

The cluster of tryptophan structural genes has been studied in both *Salmonella* and *E. coli* (*5*). In both organisms the tryptophan genes are localized within a short segment of the chromosome in an order which corresponds to the biosynthetic sequence. However, the fine structures of corresponding genes vary considerably, as indicated by the low recombination frequencies observed in transduction crosses between the two genera (*2*). Fine structure differences between *E. coli* and *Salmonella* have also been inferred from comparisons of the peptide patterns after treatment by trypsin