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The Pupil and Stimulus Probability

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ABSTRACT

Three studies were conducted to examine the relationship of the task-evoked pupillary response (TEPR) to the probability of the eliciting stimuli in Bernoulli sequences. Subjects counted target tones in sequences containing two types of tones differing in pitch. For a given probability level, both targets and non-targets elicited pupillary dilations that were similar in amplitude. The dilation to both targets and non-targets was inversely related to probability at low probability levels. This relationship appeared to break down at high probability levels, at least for non-targets. When tone omissions were used as targets they elicited a larger dilation than tonal targets at very low target probability. The amplitude of dilations produced by omitted targets was also affected by probability. The data converge to indicate that the TEPR in random stimulus sequences is sensitive to the surprise value of events, whether involving a physical stimulus or not, and not to the target designation of these events.

DESCRIPTORS: Pupillary response, Probability, Autonomic nervous system.

Pupillary dilations to sensory stimuli in the absence of luminance changes occur in all species from amphibians through primates. In lower species, these dilations are often referred to as the pupillary psychosensory response (Lowenstein & Loewenfeld, 1969). Such responses may be elicited by cutaneous, visual, and auditory stimulation; they begin within .3 to .5 seconds after the stimulus and peak approximately one second later. Two mechanisms are known to mediate the psychosensory response, the inhibition of parasympathetic input and the excitation of sympathetic input to the iris musculature. Although the neurophysiological basis of this response is not fully understood, it is known to depend on input from forebrain structures (Lowenstein & Loewenfeld, 1969) and it is similar in many respects to the effect of low-level stimulation of the midbrain reticular formation which also produces cortical activation (Bonvallet & Zbrozyna, 1963). The dependence of the psychosensory response upon brain activation is indicated by the finding that the dilation is also much reduced during sleep and anesthesia (Lowenstein & Loewenfeld, 1969).

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The concept of the psychosensory response derives from physiological research with sub-human species. In these investigations, the response is frequently taken as an indication that a stimulus is perceived. However, the psychosensory response may also be relevant to human cognition. Cognitive tasks, including perceptual processing in all modalities, memory, problem solving, and linguistic processing, elicit task-evoked pupillary responses (TEPRs) which bear a close relationship to the aggregate processing demands involved in the performance of these tasks (see Beatty, 1982, for a review). Whether the psychosensory response indexes a reflexive stimulus processing operation in a variety of species remains a matter of conjecture. However, the pupillary response can reflect the amount of processing performed on sensory stimuli, since its amplitude predicts the probability of detection of weak acoustic signals employed in standard signal detection tasks (Beatty & Wagoner, 1983).

The present experiments were designed to examine the characteristics of the TEPR in a simple perceptual situation similar to that eliciting the psychosensory response in lower species. Specifically, the present investigations tested the effects of the probability and task-relevance of peripheral auditory stimuli on the TEPR in random stimulus sequences. Previous investigations of the relationship between pupillary dilations and probability have found an inverse monotonic relationship between pupillary amplitude and probability in guessing situations (Friedman, Hakerem, Sutton, & Fleiss, 1973). Other autonomic measures such as heart rate and the galvanic skin response also appear to vary with probability (Higgins, 1971; Lovibond, 1969).

Central responses such as the late positive complex (LPC) of the event-related potential show similar effects. The amplitude of the LPC is an inverse function of stimulus probability and it can even be invoked by low-probability stimulus omissions (Sutton, Tueting, Zubin, & John, 1967; Tueting, Sutton, & Zubin, 1970). However, the mechanisms underlying the peripheral and central probability effects appear to be somewhat different. Friedman et al. (1973) found a dissociation between the LPC and the pupil dilation in relation to probability in a guessing task; the pupillary response varied with probability only when the expected stimulus type was uncertain, whereas the LPC was sensitive to probability when the stimulus type was both certain and uncertain.

Method

Subjects

Ten college students aged 18–38 yrs (7 men, 3 women) served as subjects in all three experiments.

Material

Testing took place in a sound attenuated room with normal level incandescent illumination. The subject sat at a terminal keyboard with his head in the pupillometer chin rest and fixated a white screen at a 2 m distance. This situation ensured that the accommodation reflex was nearly relaxed, providing a stable baseline level to record the TEPR.

Vertical pupillary diameter was recorded at 40 samples/second using a Whittaker video pupillometer (model 1050S). Auditory prompts signalling the beginning and end of trials consisted of samples of digitized (8000 Hz) natural speech. All stimuli were presented through a loudspeaker. All aspects of stimulation and data acquisition were controlled by a DEC PDP-11/34 computer.

Procedure

Subjects listened to sequences of 50 tones of 50 ms each presented regularly at 1.5-s intervals. The sequences were arranged as Bernoulli series with one of two stimuli presented every 1.5 s. On each series, subjects heard the word 'READY' at which time they could initiate the series by pressing a key on the terminal. The subject's task was to count the number of events of a given type (targets) in the series. At the end of the sequence, the word 'RESPOND' prompted the subject to enter the total count on the terminal. Subjects were instructed to try to refrain from blinking or moving during the presentation of the tones. In all three experiments, the subjects were informed of the probability of targets in the series that followed and of all probability conditions in the experiment.

In all experiments, the pupillary records from each tone series were stored on disk as a sequence of 50 traces of 1.5-s duration beginning at the presentation of each tone. Individual traces were inspected for the presence of blinks, movements, or accommodation artifacts, and records containing such artifacts were rejected from the analysis. This editing procedure was blind as to the type of tone associated with a particular trace in the series. This procedure eliminated an average of 10% of the records obtained.

Average pupillary waveforms were then computed from the artifact-free records for each stimulus type in each probability condition within a particular experiment.

EXPERIMENT 1

The first experiment examined the effect of stimulus probability over a wide range of values. Series with target probabilities of .2, .5, and .8 were used. Tones of 1100 Hz and 1150 Hz were used in the series, each type of tone being designated as target for half the subjects. Subjects were given 9 series of tones with each probability condition repeated three times. The series were ordered in one of two Latin square designs so that the probability conditions were equated for order of presentation.

Results

Figure 1 shows the average TEPRs obtained in Experiment 1 for the entire subject sample. The pupillary response to the tones consisted of a regular dilation starting an average of 370 ms after the stimulus and peaking between 700 and 1000 ms after the stimulus. The peak of the TEPR for a probability of .2 has a larger amplitude and a longer

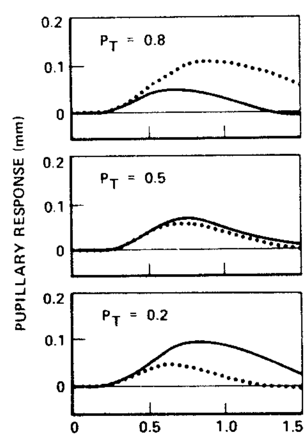

Figure 1. Average pupillary responses to target and non-target tones having probabilities of .2, .5, and .8. Target probability (P_T) is indicated for each condition. Continuous lines are responses obtained to targets and dotted lines are responses to non-targets.

latency than that in the other two probability conditions irrespective of stimulus type.

An analysis of variance was performed on peak TEPR amplitude measured relative to the first four points of the waveform and confirmed the presence of the probability effect ($F(2/9) = 71.84$, $p<.001$). Post-hoc comparisons showed that this effect was significant when probability varied between .2 and .5 ($Q(2/18) = 1.5$, $p<.05$ for non-targets, $Q(2/18) = 6.9$, $p<.05$ for targets). However, there was no significant effect of probability between .5 and .8 probability conditions ($Q(2/18) = 1.09$, NS for non-targets, $Q(2/18) = 2.0$, NS for targets). Stimulus type did not affect the amplitude of dilations ($F<1.0$).

A similar analysis performed on the latencies of the peaks also showed an effect of probability ($F(2/9) = 35.02$, $p<.001$) and no effect of stimulus type ($F<1.0$). The effect of probability on latency-to-peak was significant for all comparisons (all $Qs(2/18)>3.24$, $p<.05$) except for non-targets at probabilities of .5 and .8 ($Q(2/18) = 1.13$, NS).

Since three sets of pupillary waveforms were obtained for each probability condition, the possible presence of habituation effects on the pupillary response was examined. The amplitudes and latencies of peaks in the TEPRs of the first, second, and third series presented for each probability condition were compared. No significant differences were found whether in amplitude or latency measures among the three series for any of the probability conditions (all $Fs(2/18)<2.7$, NS).

EXPERIMENT 2

Experiment 1 showed that the TEPRs to targets and non-targets behaved similarly in relation to large changes in probability, showing a decrease in amplitude when probability increased from .2 to .5 and showing no change in amplitude when probability was further increased to .8. Moreover, for a given level of probability, TEPRs elicited by targets were quite similar to those elicited by non-targets. These effects suggest a dramatic dissociation between the behavior of the TEPR and that of the central LPC measure which is virtually insensitive to non-targets (see Pritchard, 1981).

Since the results of Experiment 1 were obtained with large variations in probability, a second experiment was designed to confirm these results with smaller variations in probability comparable to that used in the existing LPC literature.

In Experiment 2, the same procedure was used as in Experiment 1 to examine the probability effect in tone sequences with target probabilities of .1, .2, and .3.

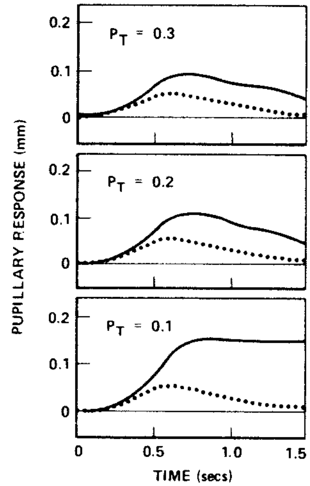

Figure 2. Average pupillary responses in tone sequences in which target probability (P_T) was .1, .2, and .3. Continuous lines represent dilations evoked by targets, dotted lines represent dilations evoked by non-targets.

Results

Figure 2 shows the group waveforms obtained in Experiment 2. The TEPR was affected by target probability from .1 to .3 but was unaffected by the complementary probabilities of non-targets ranging from .9 to .7. These results were reflected in the ANOVA procedure on peak amplitude by significant effects of probability for targets ($F(2/9) = 30.7$, $p<.001$) but not for non-targets ($F(2/9) = 2.5$, NS). Post-hoc comparisons showed that the probability effect on targets was significant for both the difference between the .1 and .2 conditions ($Q(2/18) = 7.8$, $p<.05$) and the difference between the .2 and .3 conditions ($Q(2/18) = 3.17$, $p<.05$).

An analysis of the peak latencies of the waveforms showed that the TEPR of targets peaked significantly later than that of non-targets ($F(1/19) = 47.2$, $p<.001$) but there was no effect of probability on the latency of peaks ($F(2/29) = 2.8$, NS).

EXPERIMENT 3

Experiment 3 examined the possibility that the probability effect was related to the frequency of events irrespective of the effects of stimulation by looking at the TEPR to low-probability omissions of tones. Target probabilities of .1 and .3 were used in series in which the targets were either tones as in Experiments 1 and 2 or omitted signals. Eight series of tones were presented in one of four orders, providing two series for each of the four conditions. For each subject, the two probability conditions were equated in terms of their order of presentation. Also, half the subjects were given the four series containing omitted targets first, followed by the series containing tonal targets, and the reverse was true for the other subjects.

Results

In Experiment 3, the variable of target type (omitted versus tonal) was added to that of probability and stimulus type in the analysis. The data for one subject had to be left out in this experiment because of the large number of artifacts in his pupillary records.

The group waveforms for each condition are presented in Figure 3. The amplitude of the TEPR was higher for a target probability of .1 than .3 ($F(1/8) = 50.95$, $p<.001$). This effect of probability interacted with that of stimulus type ($F(1/8) = 18.5$, $p<.01$), showing that the effect was significant for targets ($F(1/8) = 42.6$, $p<.01$) but not for non-targets ($F(1/8) = 3.6$, NS). Amplitude was also affected by target type, being larger for omitted targets than for real targets ($F(1/8) = 6.94$, $p<.05$). This effect of target type also interacted with probability ($F(1/8) = 11.5$, $p<.01$), revealing that dilations obtained when targets were omitted were larger than when they were tonal at a probability of .1 ($F(1/8) = 79.8$, $p<.001$), but that this difference was much reduced at a probability of .3 ($F(1/8) = 8.7$, $p<.05$). Furthermore, post-hoc comparisons on the effect of target type (omitted vs. tonal) showed that it was only significant for targets at a probability of .1 ($Q(2/18) = 5.11$, $p<.05$) and not in any other condition (all $Qs(2/8)<1.59$, NS).

The latencies-to-peak of dilations in this experiment were longer for targets than for non-targets ($F(1/8) = 76.25$, $p<.001$) and this effect interacted marginally with probability ($F(1/8) = 6.2$, $p<.05$).

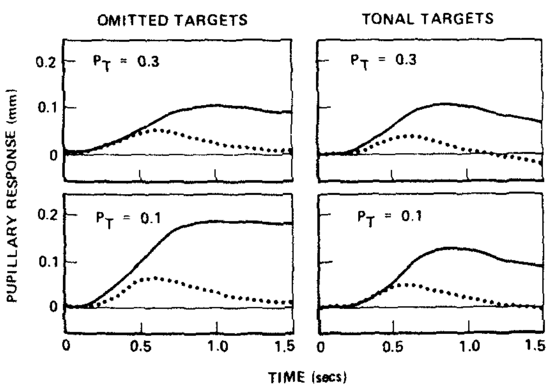

Figure 3. Average pupillary responses to targets (continuous) and non-targets (dotted) in tone sequences in which targets were either omissions or real tones. Target probability (P_T) was either .1 or .3.

DISCUSSION

The data from all three experiments confirm the existence of a stimulus probability effect on the TEPR as previously observed in a different task (Friedman et al., 1973). In addition, the present data indicate that the TEPR is not sensitive to the target designation of the stimulus and suggest, at least for non-targets, that the probability effect on the TEPR is restricted to low-probability levels. The strong similarity between the TEPRs to targets and non-targets at all probability levels suggests that the range restriction of the probability effect may also apply to targets, but this should be tested empirically. If generalizable, both the range restriction and the insensitivity to target designation represent strong differences between the TEPR and the central LPC measure.

The finding that stimulus omissions produced significant dilations sensitive to stimulus probability indicates that the pupillary response does not have to be stimulus driven; it appears to be endogenous rather than exogenous in nature. This result suggests a significant central influence on the response analogous to the one affecting the LPC. Such a central process could be involved in the regulation of the access of input to higher information processing centers in terms of their novelty. Both the probability data and the omitted stimulus data are consistent with an interpretation of the underlying process in terms of an orienting response or expectation mismatch (Sokolov, 1960). At the level indexed by the TEPR, this process seems to override the target designation (task-relevance) of the stimulus. However, at the level indexed by the LPC measure, the process becomes very sensitive to target designation (see Pritchard, 1981).

The dissociations between the LPC and the TEPR in their sensitivity to both probability and target designation suggest that pupillary and central measures probably index complementary aspects of orienting to task-relevant stimuli. However, it is difficult without neurophysiological data, to properly address the question of whether processing-related dilations are closely linked to the pervasive pupillary psychosensory reflex or if the additional sources of activation are significantly different.

The present data indicate that the pupillary response to sensory stimuli is sensitive to the relative probability of the eliciting stimulus over a limited range. This sensitivity of the TEPR appears to generalize to all experimentally defined events and is relatively independent of the occurrence of physical stimuli as well as of such task-related factors as target designation.

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