LUMINANCE DISCRIMINATION PROBABILITIES DERIVED FROM THE FROG ELECTRORETINOGRAM

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Abstract

A method was developed and tested for reconstructing luminance discrimination probability functions from the electroretinographic responses of the frog to instantaneous changes in stimulus luminance. Historically, this seems to be the first systematic attempt to compute a psychometric function for sensory discrimination from electrophysiological data, opening new ways of quantifying and comparing sensory activity in various neurophysiological systems. To the extent discrimination probability functions can be used to compute Fechnerian metrics in stimulus spaces (in accordance with the theory developed by Dzhafarov and Colonius), the method described in this paper enables one to think of Fechnerian distances among stimuli "from the point of view" of a specific neurophysiological system (such as retina or cortical area).

One of the most basic facts about sensory perception is that any two stimuli presented to an organism, human or animal, is associated with a definite probability of being discriminated from each other, and that this discrimination probability is generally different for different pairs of stimuli. The function

$$P(x, y) = \Pr[\text{“}y \text{ is different from } x\text{”}]$$

defined on all ordered pairs of stimuli chosen from a stimulus space is referred to as a discrimination probability function. If the comparison of stimuli is made with respect to a single semantically unidimensional attribute, such as “subjective intensity”, then the same term can be used for the function

$$p(x, y) = \Pr[\text{“}y \text{ is greater than } x\text{”}].$$

Since the earliest years of psychophysical science discrimination probabilities have been estimated by behavioral means to characterize sensory perception in a wide variety of species, modalities, and observation contexts. The importance of discrimination probability functions, moreover, extends beyond the confines of readily confusable, physically very similar stimuli. Fechner’s pioneering proposal that laid the foundation for scientific psychology was to measure the “sensation magnitude” for a unidimensional stimulus by

integrating a local discriminability measure between the stimulus and the absolute detection threshold. This proposal acquires a solid mathematical basis and generalizes to multidimensional stimulus spaces if the local discriminability is derived from the discrimination probability functions $P(x, y)$ and the notion of "sensation magnitude" is replaced with the general notion of a Fechnerian distance (Dzhafarov & Colonius, 1999).

No work is known to us, however, aimed at reconstructing the discrimination probability functions from neurophysiological rather than behavioral responses, notwithstanding the fact that the functioning of many neurophysiological systems can be readily interpreted in terms of their reacting to stimulus differences. The frog electroretinogram (ERG) studied in the present work is an example of such a neurophysiological system (see Fig. 1): it quickly achieves and maintains a statistically standard level of background activity under a prolonged presentation of any stimulus, but changes the level of activity as soon as this stimulus changes.

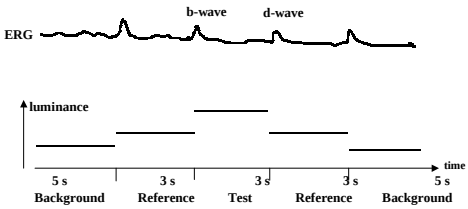

Figure 1. The temporal profile of the stimulus sequence in a single trial and the corresponding ERG record.

The reason why this phenomenology has not been previously utilized for computing discrimination probabilities lies in the extremely variable character of electrophysiological activity. To obtain a record like the one shown in Fig. 1, the activity has to be averaged across several trials using the same pair of stimuli. If no averaging is done, it is a formidable if not hopeless task to reliably determine whether the electric activity following a stimulus change contains or does not contain a reaction. The averaging, on the other hand, may seem to preclude the possibility of speaking of a stimulus pair being discriminated in some but confused in other trials, seemingly eroding thereby the logical basis for computing discrimination probabilities.

This quandary, however, has a simple solution, which consists in using just right amount of averaging: the number of replications per average should be sufficiently large to obtain reliable and readily analyzable records, yet it should be sufficiently small to allow one to obtain averages across many different blocks of trials, with the expectation that some of these averages will and some will not contain a reaction to stimulus change, in accordance with an appropriately chosen criterion.

Method

The ERG activity in the frog was recorded by means of a circular platinum electrode attached to the frog's cornea, with the reference electrode placed on the frog's head behind the eye. The electric output was amplified and converted into a digital code fed into a computer, each number of the digital code representing a 4 ms period of the analogue output. The synchronization of the temporal profile of the stimuli with the ERG recording was provided by the Conan system, which also provided a preliminary data analysis: filtration, averaging, and censoring out of the recording artefacts (for details see Zimachev et al., 1986).

The stimuli were 3 s flashes of a monitor screen homogeneously illuminating the frog's entire retina, with the temporal profile shown in Fig. 1: reference–test-reference triads separated by 5 s background illumination of 8 cd/m^2. The reference stimulus had the fixed luminance of 14 cd/m^2, while the luminance of test stimuli varied between 12.5 and 16 cd/m^2, with 0.5 cd/m^2 steps (3 values below, 4 above, and one equal to the reference value). The difference between the reference stimulus and the marginal test stimuli (12.5 and 16 cd/m^2) was, to a human eye, small but clearly noticeable.

The trials (i.e., the reference–test-reference triads) containing the same test stimulus were blocked into long runs from 100 to 300 trials each (about 35-40 min per 100 trials, not counting occasional interruptions for a variety of technical reasons). The length of a run was determined by the number of censored artefacts and by whether the discrimination probability in the run was clearly very close to 100% (in which case the run was abridged). The runs were then partitioned into successive 10-trial pieces and the records within each piece were averaged. The length of the piece (10 trials) was determined from a preliminary experiment, described next.

Determining the number of trials per average

We conducted a run of 100 trials using 14 cd/m^2 as the reference luminance and 16.5 cd/m^2 as the test one (higher than the highest test value used in the main experiment). After censoring out recording artefacts we were left with 90 trials. We then averaged the records across the first *N* trials, the value of *N* being 10, 20, 30, 50, 60, or all 90 trials. For every *N*, we computed the following four quantities from the averaged record:

X1 = the mean activity within the 44 ms interval ending 10 ms prior to the first stimulus change (reference–test);

Y1 = the mean activity within the 44 ms interval beginning 40 ms after the first stimulus change (reference–test);

X2 = the mean activity within the 44 ms interval ending 10 ms prior to the second stimulus change (test-reference);

Y2 = the mean activity within the 44 ms interval beginning 40 ms after the first stimulus change (test-reference).

The values of X1 and X2 reflect the pre-test and post-test background levels, respectively, while Y1 and Y2 characterize the magnitudes of the two response waves shown in Fig. 1.

The data presented in Fig. 2 show that the increase from 10 trials per average to 90 trials per average produces little if any change in the values of X1, Y1, X2, and Y2. As a result, if the criterion of a response to stimulus change is based on these values (see below), one can set the number of trials per average equal to 10.

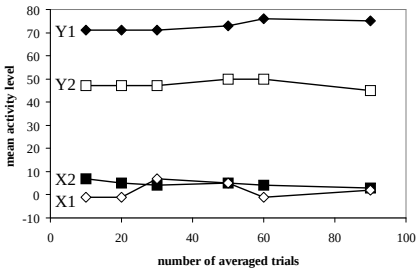

Figure 2. Dependence of the mean electric activity (X1, Y1, X2, Y2) on the number of averaged trials.

Response criterion

It is natural to classify an ERG record as containing a response to the change reference–test (or test-reference) if the value of T1=|Y1-X1| (respectively, T2=|Y2-X2|) exceeds a preset criterion t_{crit}. The analogue-to-digital conversion used in our study maps any 44 ms interval of electric activity into 11 numbers, whose averages are referred to in the definitions of X1, Y1, X2, and Y2 above. We can, therefore, compute standard deviations SX1, SY1, SX2, SY2 corresponding to X1, Y1, X2, and Y2, and use the conventional Student test (df = 11-1 = 10) to test the hypotheses T1>0 and T2>0 against the respective null-hypotheses T1=0 and T2=0. The value of t_{crit}, with this approach, becomes the critical Student distribution value at a particular level of significance. The analysis was conducted with four significance levels: 0.001 (the most conservative criterion of a response), 0.01, 0.02, and 0.05 (the most relaxed criterion). Arguably, a change in the significance level may be thought to mimic the change in the predisposition to using the category “different” in a behavioral experiment.

Results

Figs. 3 and 4 show the percentage of the 10-trial averages containing a response to the stimulus change as a function of test stimulus luminance at different response criteria. The results are presented separately for the first change (reference-test) and the second change (test-reference).

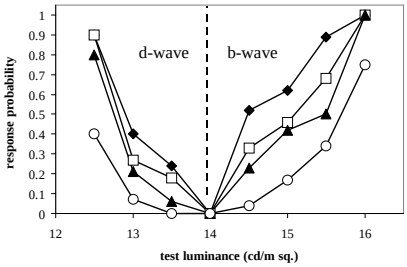

Figure 3. Response probability as a function of test luminance in the sequence reference – test. Different symbols represent different response criteria: filled diamonds (alpha=0.05), open squares (alpha=0.02), filled rectangles (alpha=0.01), open circles (alpha=0.001).

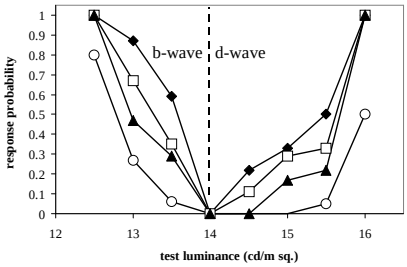

Figure 4. Response probability as a function of test luminance in the sequence test – reference. The rest as in Fig. 3

Conclusion

The most obvious and also most important outcome of the present work, as its aim was to develop a method for reconstructing probability discriminations from ERG responses, is that the method produces reliable and plausible psychometric functions, comparable to those obtained by psychophysical means (e.g., Indow et al., 1992). The probability of the discrimination response monotonically increases with increasing difference between the reference and test stimuli, in both directions, for both types of changes (the reference first and the reference second), and for all levels of the response criterion. Note that in the above-the-

reference half in Fig 3 and in the below-the-reference half of Fig. 4 the probabilities are based on the b-wave, while the other halves of the figures are based on the d-wave. The d-wave probabilities are clearly lower than the b-wave ones for one and the same absolute value of the difference between the reference and the test stimuli. This should be related to the well-known fact (Zimachev et al., 1991) that the amplitudes of the d-waves in the frog ERG is smaller than the corresponding amplitudes of the b-waves.

Acknowledgement

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