Table 1. The NH_2-terminal and COOH-terminal sequences of *Catostomus clarkii* and *Catostomus insignis* hemoglobins.

	Catostomus (subgen. *Pantosteus*) *clarkii*		*Catostomus* (subgen. *Catostomus*) *insignis* hemoglobins
	Anodal hemoglobins	Cathodal hemoglobins	
		NH_2-termini	
α Chains	Ac-Ser-Leu-Ser-	Blocked*	Ac-Ser-Leu-Ser-
β Chains	Val-Glu-Trp-	Val-Glu-Trp-*	Val-Glu-Trp
		COOH-termini	
α Chains	-Lys-Tyr-Arg	Arg (CPB)	Lys-Tyr-Arg
β Chains	-Gln-Tyr-His	Tyr and Phe (CPA)	Ser-Tyr-His

*See (*11*).

C. (subgen. *P*) *clarkii* but neither hypothesis would alter the fact that His is not a COOH-terminus.

The α chains from both species had blocked NH_2-termini. However, there is a major difference between the cathodal and anodal hemoglobins. The anodal hemoglobins of both species had COOH-terminal His for the β chains, while the cathodal hemoglobins did not release His when hydrolyzed with CPA. Therefore, both the usual (*6–8*) participating Bohr groups were missing in the cathodal components, which could largely explain the absence of the Bohr effect.

These results indicate the cathodal hemoglobins of *C. clarkii* have structural modifications of the α and β chains which are manifest in their physiological function (that is, no Bohr effect). The physiological role of the cathodal hemoglobins in adaptation for a particular intrastream habitat is suggested by the primary ecological preferences of these sympatric subgenera. Fishes of the subgenus *Pantosteus* prefer fast-moving portions of the stream, while members of the subgenus *Catostomus* have a preference for the pools or sluggish water (*1*). For example, *C.* (subgen. *P.*) *clarkii* is predominantly active in the faster parts of a stream while *C.* (subgen. *C.*) *insignis* is found predominantly in the quieter pools.

Fish in fast water habitats generally have hemoglobins with low oxygen affinities and a large Bohr effect (*19*). Although a large Bohr effect is beneficial in releasing oxygen at the cellular level, it can suppress oxygen binding at the gills when the blood *p*H is sufficiently low. According to Black (*20*) the increase in lactic acid after violent exercise (for example, to escape a predator) can result in the death of hyperactive fish. Riggs (*19*) states, "The Bohr effect, deemed an advantage under normal circumstances, may thus prevent adequate oxygen from reaching the tissues." It would appear that the cathodal hemoglobins, without a Bohr effect, provide a backup system for *C.* (subgen. *P.*) *clarkii* so that swimming may be maintained after emergency exertions. If the interpretation is correct, one would predict a similar adaptation in hyperactive fishes. It is reassuring that both trout (*21*) and salmon (*22*) have been found to have some hemoglobin components devoid of a Bohr effect.

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References and Notes

1. G. R. Smith, *Misc. Publ. Mus. Zool. Univ. Mich. No. 129* (1966), p. 5.
2. R. K. Koehn, *Copeia*, No. 1 (1969), p. 21.
3. O. Smithies, *Biochem. J.* **61**, 629 (1955).
4. ———, *ibid.* **71**, 585 (1959).
5. D. A. Yphantis, *Biochemistry* **3**, 297 (1967).
6. A. Riggs and R. A. Wolbach, *J. Gen. Physiol.* **39**, 585 (1956).
7. J. V. Kilmartin and J. F. Wooton, *Nature* **228**, 766 (1970).
8. M. F. Perutz, H. Muirhead, L. Mazzarella, R. A. Crowther, J. Greer, J. V. Kilmartin, *ibid.* **222**, 1240 (1969).
9. J. V. Kilmartin and L. Rossi-Bernardi, *ibid.*, p. 1243.
10. J. B. Clegg, M. A. Naughton, D. J. Weatherall, *J. Mol. Biol.* **19**, 91 (1966).
11. The chains from the cathodal components could not be separated; NH_2-terminal and COOH-terminal analyses were, therefore, performed on cathodal globins. From most whole globins, CPA releases the first two COOH-terminal residues from the β chains but cannot proceed past Arg or Lys. However, CPB is specific for Arg and Lys and would, therefore, release only the Arg from the α chain.
12. P. Edman and G. Bigg, *Eur. J. Biochem.* **1**, 80 (1967).
13. J. O. Jeppsson and J. Sjörquist, *J. Anal. Biochem.* **18**, 262 (1967).
14. J. J. Pisano and T. J. Bronzert, *J. Biol. Chem.* **244**, 5597 (1969).
15. A. B. Edmundson, N. B. Simonds, F. A. Sheber, T. Johnson, B. Bangs, *Arch. Biochem. Biophys.* **132**, 502 (1969).
16. R. P. Ambler, *Methods Enzymol.* **11**, 155 (1967).
17. D. Powers and A. B. Edmundson, *J. Biol. Chem.*, in press.
18. Abbreviations: Ac, acetyl; Ala, alanine; Arg, arginine; Asp, aspartic acid; Gln, glutamine; Glu, glutamic acid; Gly, glycine; His, histidine; Ile, isoleucine; Leu, leucine; Lys, lysine; Phe, phenylalanine; Ser, serine; Thr, threonine; Trp, tryptophan; Tyr, tyrosine; and Val, valine.
19. A. Riggs, in *Fish Physiology*, W. S. Hoar and D. J. Randall, Eds. (Academic Press, New York, 1970), vol. 4, pp. 209–252.
20. E. C. Black, *J. Fish. Res. Bd. Can.* **15**, 573 (1958).
21. I. Binotti, S. Giovenco, B. Giardina, E. Antoni, M. Brunori, J. Wyman, *Arch. Biochem. Biophys.* **142**, 274 (1971).
22. K. Hashimoto, Y. Yamaguchi, F. Matsuura, *Bull. Japan. Soc. Sci. Fish.* **26**, 827 (1960).

23. Supported by the U.S. Atomic Energy Commission and NSF postdoctoral fellowship 41053. I thank Dr. B. Sullivan.

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Evoked Potential Correlates of Response Criterion in Auditory Signal Detection

Abstract. *The amplitude of a late positive component of the average evoked potential recorded from the human scalp varied systematically as a function of the observer's response criterion as defined within the context of signal detection theory. With signal intensity invariant, the P_3 component of the evoked potential increased monotonically with increasing strictness of the criterion. The results are viewed as supporting the signal detection theory approach to the analysis of discrimination behavior as well as providing further evidence of the sensitivity of P_3 to the manipulation of psychological variables.*

Various degrees of correlation between average evoked potentials and psychophysical judgments have been reported, ranging from "complete isomorphism" (*1*) to complete lack of association under an anesthetic drug (*2*). Discrepancies or lack of correspondence between physiological and behavioral data have been attributed by Donchin and Sutton (*3*) to lack of methodological precision. They particularly stressed the importance of segregating average evoked potentials according to both stimulus conditions and perceptual responses. A systematic study by Hillyard *et al.* (*4*), which satisfies these conditions, demonstrates close correspondence between a late positive component (P_3) of the auditory potential and *d′*, a measure of the sensitivity of the observer to a particular signal, based on signal detection theory (*5*). Because differences in response bias, not sensitivity, often result in altered performance, a signal detection theory approach to behavioral measurement is often superior to the traditional methods of psychophysics (*6*). Since perception is not dependent exclusively on the physical parameters of stimulation, and since P_3 is sensitive to psychological variables (*7*), it is essential to assess these nonsensory factors when analyzing evoked responses obtained in psychophysical tasks. Hillyard *et al.* (*4*) took account of criterion factors when studying evoked potential correlates of intensity discrimination, but so far no data are available on the effects of manipulating a subject's response criterion while controlling stimulus-dependent measures of sensitivity.

We have examined average evoked potential data obtained in auditory signal detection with the physical parameters of stimulation invariant. Changes in the response criterion were manipulated by two methods: varying the a priori probability of a signal, and changing the relative payoffs attached to decision outcomes.

The subject's task was to indicate, by a "yes-no" key-pressing response after each observation interval, whether or not, in his judgment, a signal had occurred. Each observation interval, or trial, was delineated by the onset and offset of a 1.95-second burst of white noise, and the signal (a 3-msec click) was presented on a probabilistic basis (50 percent of the trials) in the middle of this interval. For each subject, the intensity of the signal was chosen to yield a sensitivity index corresponding to 60 to 75 percent correct detection.

Evoked potentials were recorded from a scalp electrode at the vertex and an electrode under the eye to monitor eye movements, both referred to the right earlobe. For vertex electrical activity the bandpass of the amplifier was between 0.0165 and 20 hertz, and for eye movement electrical activity the bandpass was between 0.15 and 100 hertz. Evoked potentials were averaged separately according to the following stimulus-response contingencies: hits, misses, correct rejections, and false affirmatives. The evoked potential measure under study was NP_3, measured from the maximum negative deflection to the maximum positive deflection at about 400 msec.

In experiment A, the three levels of the independent variable (a priori probability of a signal) were .25, .50, and .75. These were designed to generate "cautious," "unbiased," and "liberal" criteria. The payoff matrix was symmetrical: a reward of 6 cents for correct responses and a penalty of 6 cents for incorrect responses. In experiment B, the probability of signal presentation was held at .50, and three different payoff matrices constituted the three levels of the independent variable. Each of these matrices was designed to yield optimum criterion cutoffs of the same value as the criteria generated by varying the a priori probability.

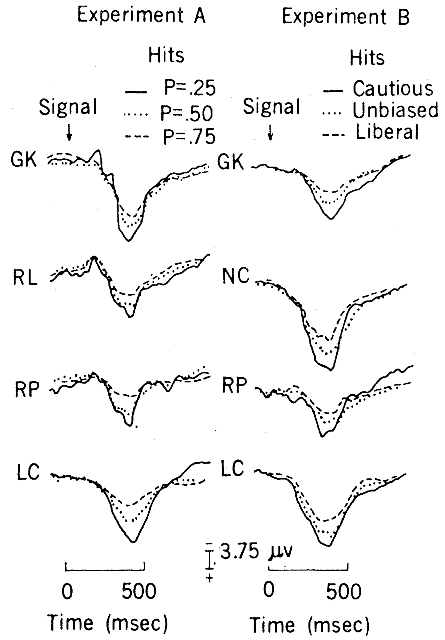

Fig. 1. Comparison between evoked responses for hit trials at each level of the independent variable—a priori signal probability (experiment A) and expected value of decision outcomes (experiment B). Wave forms for each of the three experimental conditions are shown superimposed, for each of four subjects. The arrow indicates occurrence of the signal, which was delivered in the middle of the interval designated as a trial. The abbrevations GK, RL, RP, LC, and NC refer to subjects.

For the cautious condition, the rewards were 3 cents for a hit and 9 cents for a correct rejection: the fines were 3 cents for misses and 9 cents for false affirmatives. For the unbiased condition, the matrix was symmetrical; 6 cents was gained for correct decisions and 6 cents lost for incorrect decisions. For the liberal condition, the rewards were 9 cents for a hit and 3 cents for a correct rejection; the fines were 9 cents for a miss and 3 cents for a false affirmative. Criterion conditions were presented in counterbalanced order, in blocks of 60 trials, for a total of 1440 trials per condition in each experiment. Information about the correctness of the performance was given to the subject orally after each block of trials.

Both experiments yielded essentially the same results, behaviorally and physiologically. Wave forms for hit trials, for each subject, are shown in Fig. 1 for experiment A, in which the a priori probability of a signal was varied with identical payoff matrices, and for experiment B, in which payoffs were manipulated with the signal probability constant at .50. Wave forms obtained at each of three levels of the independent variable are superimposed. Changes in NP_3 were the same under both experimental procedures: the late positive component was largest for the cautious condition, intermediate for the unbiased condition, and smallest for the liberal condition. In both experiments, the amplitude of NP_3 for hit trials increased monotonically (Fig. 2) with "percent bias," a nonparametric measure of the response criterion (*8*).

The growth of NP_3 with increased strictness of the criterion does not seem related to the attention or arousal level, at least in the preparatory period between the trial onset and the time of signal presentation. This is supported by the fact that no differences were found between contingent negative variations (CNV's) for correct as opposed to in-

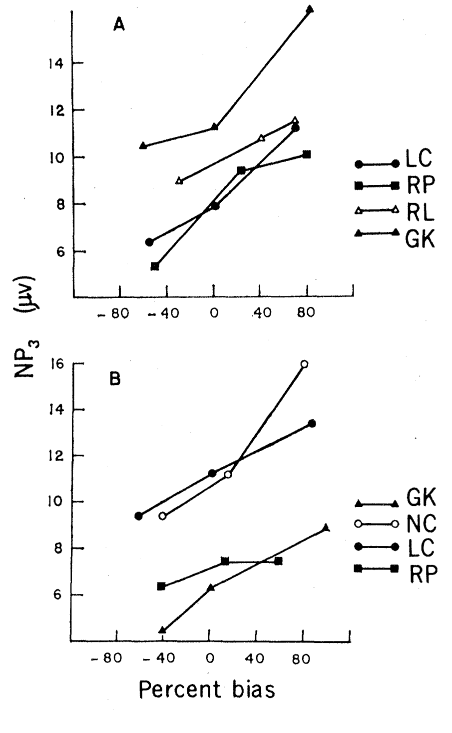

Fig. 2. Relationship between percent bias and amplitude of NP_3 for hits. This relationship is shown in (A) for each of four subjects when the independent variable was a priori probability of signal occurrence, and in (B) for each of four subjects when the values and costs of decision outcomes were varied. The abbreviations LC, RP, RL, GK, and NC refer to subjects.

correct responses, nor between CNV's for hits as compared to misses.

In this study, the evoked potential data are reported in terms of peak-to-peak measurements. However, since most of the literature on evoked potentials deals with specific components, the data were reanalyzed with N and P_3 measured separately from the baseline at signal onset. The same relationships were found between P_3 and percent bias as between NP_3 and percent bias, whereas the N component was barely, if at all, related to the criterion measure.

Although the average signal-to-noise ratio was constant in our experimental conditions, it might be argued that increased sensitivity, and not the response criterion, was responsible for the changes in P_3. This was not the case, as evidenced by the sensitivity index *A'* (*9*), which did not vary significantly in our experimental conditions. Nor could criterion effects be attributed to changes in incentive, since the combined total value of the rewards and penalties was equivalent in all conditions: the overall value of each payoff matrix was the same in all cases, 12 cents gained for correct decisions (hits plus correct rejections) and 12 cents lost for incorrect decisions (misses plus false affirmatives).

An interpretation proposed by Hillyard *et al.* (*4*) for low-detectability signals provides a consistent way of viewing both the sensitivity relation to P_3 and the criterion relation to P_3 reported here. They suggested that for difficult discriminations the increase in the amplitude of P_3 with sensitivity might reflect the degree of confidence felt by the subject in his decisions with respect to the signals. As the intensity is increased, the subject becomes increasingly confident in the accuracy of his decision that the signal was presented. Similarly, in our study, the P_3 amplitude for hit trials may be said to grow with the subject's increased confidence that a signal did occur. However, it is important to point out that the growth of P_3 is not necessarily a result of increased amplitude in individual trials. It may be due to the segregation of trials according to different levels of confidence: for example, in the cautious condition where P_3 is large, the evoked potential wave form for hits is the average for trials in which the subject was highly confident that he heard the signal. On the other hand, in the liberal condition where P_3 is small, the wave form for hits is an average for many trials in which the subject said "yes" in spite of a relatively low degree of confidence in his judgment.

A more general interpretation, of which confidence might be seen as a special case, is that the P_3 amplitude is increased whenever the "salience" of a stimulus is enhanced (*10*). In our experiment, it is reasonable to assume that whenever a cautious criterion is adopted which results in the correct detection of a signal, that particular signal is more salient for the subject—salience varying as a result of changing the probability of signal occurrence or changing the payoff contingencies. However, at this point all interpretations must remain tentative in the absence of a strong theoretical structure capable of encompassing the data accumulated in the last decade (*11*). Nor is it possible to assume that P_3 represents coding by the nervous system of the psychological variables inferred in our study. Nevertheless, the empirical findings reported here support an approach in terms of signal detection theory to the analysis of discrimination behavior and add to the growing evidence that P_3 is remarkably sensitive to subtle psychological changes.

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References and Notes

1. O. Franzen and K. Offenloch, *Exp. Brain Res. Berlin* **8**, 1 (1969).
2. D. Clark, R. Butler, B. Rosner, *J. Comp. Physiol. Psychol.* **68**, 315 (1969).
3. E. Donchin and S. Sutton, *Commun. Behav. Biol.* **5**, 111 (1970).
4. S. Hillyard, C. Squires, J. Bauer, P. Lindsay, *Science* **172**, 1357 (1971).
5. Signal detection procedures make it possible to obtain two independent measures of performance: a detectability index *d'*, affected primarily by physical changes in stimulus parameters, and a criterion measure L_x, determined by nonsensory variables which influence decision-making rather than detection. See J. A. Swets, Ed., *Signal Detection and Recognition by Human Observers* (Wiley, New York, 1964).
6. W. C. Clark, J. Brown, J. Rutschmann, *J. Abnorm. Psychol.* **72**, 35 (1967); W. C. Clark, L. Mehl, E. Rutter, *Proc. Amer. Psychol. Ass.* **5**, 35 (1970).
7. S. Sutton, in *Average Evoked Potentials: Methods, Results, Evaluation*, E. Donchin and D. Lindsley, Eds. (NASA SP-191, National Aeronautics and Space Administration, Washington, D.C., 1969), pp. 237–262.
8. Percent bias is a nonparametric analog of L_x. See H. Hodos, *Psychol. Bull.* **74**, 351 (1970).
9. Since *d'* is only appropriate when the distributions for signal plus noise and noise alone have equal variances, a nonparametric analog, *A'*, was preferred. See I. Pollack and D. Norman, *Psychonom. Sci.* **1**, 125 (1964).
10. D. Jenness, *J. Comp. Physiol. Psychol.*, in press.
11. P. Tueting and S. Sutton, in *Attention and Performance*, S. Kornblum, Ed. (Academic Press, New York, in press), vol. 4.
12. Supported in part by grants MH 14580 and MH 07997 from the National Institute of Mental Health, U.S. Public Health Service. We thank Crawford Clark, Marion Hartung, David Jenness, Robert Laupheimer, Ray Simon, and Joseph Zubin for assistance and suggestions and Dr. Morton B. Wallach, director of Brooklyn State Hospital, for providing the facilities for carrying out this research.

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Biting Attack Elicited by Stimulation of the Ventral Midbrain Tegmentum of Cats

Abstract. *An area in the ventral midbrain tegmentum has been discovered in which electrical stimulation elicits biting attack. The midbrain sites from which attack was elicited correspond well with the zone in the midbrain tegmentum where degeneration was previously observed after lesions were made in lateral hypothalamic attack sites.*

Although the hypothalamus is a center for the integration of the visceral and somatic components of aggressive behavior (*1–3*), the neural pathways by which the hypothalamus mediates these components have usually been surmised only indirectly through the results of stimulation and ablation (*1, 4, 5*). However, Chi and Flynn (*6, 7*), using modifications of the Nauta method for staining degenerating axons with reduced silver, have visualized directly the neural pathways associated with attack behavior elicited by hypothalamic stimulation in the cat. Most of the degeneration associated with biting attack followed the course of the medial forebrain bundle, the descending component of which could be traced into the ventral midbrain tegmentum. Since a role for the ventral midbrain tegmentum in the mediation of attack behavior had not been suggested before these degeneration experiments (*6, 7*), we have examined the effects of electrical stimulation of this area. It is important to verify whether the ventral tegmental area is involved in mediation of