Cortical Mechanisms That Augment or Reduce Evoked Potentials in Cats

Abstract. *The augmenting or reducing of flash-evoked potentials in paralyzed cats was significantly correlated with their previously videotaped behaviors. Augmenting-reducing was due to alterations in cortical rather than subcortical responsiveness, and was duplicated by increasing cortical arousal by means of reticular stimulation while the animal was exposed to visual stimuli of constant intensity. Brainstem activation of cortical inhibition may underlie the behavioral results as well as the results obtained with the evoked potentials.*

Within the rubric of augmenting-reducing (*1, 2*), the relation between the nervous system and personality is currently under investigation. Augmenters are individuals whose peak evoked potential (EP) amplitudes recorded at the vertex increase with increasing flash intensity. Other individuals whose EP amplitudes show smaller increases or even decreases with increasing flash intensity are defined as reducers. Several neurophysiological mechanisms for EP reducing have been proposed, including a stimulus intensity control system (*1*) and a negative feedback loop inhibiting the ascending reticular activating system (*3*). However, human subjects cannot be used for invasive study of the nervous system. Recently, a relation between animal behavior and flash-evoked augmenting-reducing was reported (*4*). Cats that were augmenters rated high in exploration, activity, and aggression and low in withdrawal, whereas reducer cats had the opposite behavioral traits. However, since the EP data were collected from partially restrained cats, peripheral visual mechanisms such as pupillary diameter and position of eyelids or differences in attending to the flashes could have altered the retinal flux and hence the EP amplitude.

In the current experiment, EP data in response to flash stimuli were collected from paralyzed cats in which the pupils were completely dilated and the nictitating membranes were retracted. This technique assured stability of the visual system with respect to the light flashes, and provided us with an opportunity to explore the neural basis for augmenting-reducing. Based on the effects of reticular stimulation on the responsiveness of the visual system (*5*) and a recently proposed negative feedback loop which inhibits the ascending reticular activating system and thereby produces the EP reductions (*3*), we tested the effects of arousal produced by stimulation of the mesencephalic reticular formation (MRF) on the responsiveness of the visual system. Stimulation of the optic tract (OT) was used to assess alterations in lateral geniculate (LGN) responsiveness with

changes in arousal, while stimulation of the optic radiation (OR) fibers, which bypasses thalamic processing, offered a direct test of cortical responsiveness (*6*). Our results show that EP reducing is caused by alterations in cortical functioning rather than secondary manifestations of subcortical changes. In EP reducers we were able to produce EP reductions by using visual stimuli of constant intensity while increasing the animal's arousal. The same procedure in augmenter cats increased the EP amplitude. These results indicate that differences in cortical functioning with changes in arousal may produce both the individual behavioral traits and augmenting-reducing in response to flash stimuli.

Adult female cats (*N* = 15) were videotaped individually in a sound-attenuated chamber. Each cat was allowed 4 minutes in which to explore the chamber, and was then presented with five noxious stimuli patterned after the previous research (*7*). At the conclusion of the study, a videotape of an animal from

a pilot study was shown to four judges, and the criteria for rating each of the following seven behaviors were discussed: exploration, activity, aggression, withdrawal, visual contact, emotionality, and responsiveness (*8*). The judges, without knowledge of the EP results, independently rated each animal using a behavioral rating form and explicit scoring criteria.

Electrodes were placed while the cats were under Fluothane anesthesia; the cats were then immobilized with Flaxedil and artificially respirated. Care was given to ensure each animal's comfort and to maintain its vital signs within normal limits (*9*). Data were collected only when the animal remained responsive, as indicated by spontaneous and induced shifts from EEG synchrony to desynchrony. The EEG activity recorded from stainless steel screws located over the primary visual cortex (area 17) was amplified and recorded on a polygraph and FM tape (half-amplitude settings at 1 and 3 khz). A flashtube that was sound-attenuated with fiberglass and enclosed in a box sealed with a Plexiglas front was centered 15 cm in front of the cat's eyes. Mydriacyl and Neo-Synephrine were applied to the eyes to ensure complete pupillary dilation and retraction of the nictitating membranes.

After 10 minutes of dark adaptation each cat was presented with three series of light flashes. The first two series were identical in intensity and approximately 1 log unit lower in overall intensity than
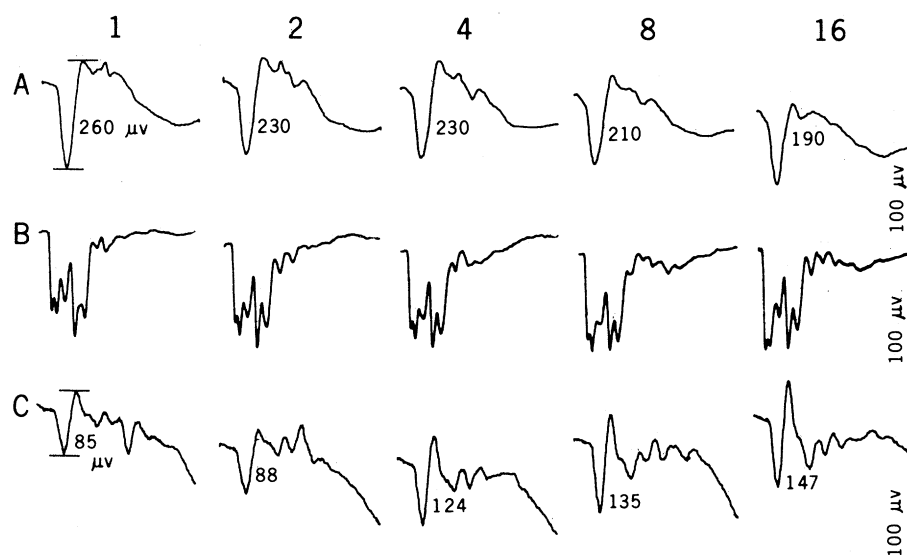

Fig. 1. Evoked potential averages consisting of 50 sweeps to five intensities of light flashes from a Grass PS1 Photo Stimulator (1 = .5, 2 = 17, 4 = 55, 8 = 155, and 16 = 370 footcandles). Sweep duration is 125 msec and positivity is down. (A) Marked amplitude reduction-recorded from the primary visual cortex (area 17, posterior 1, lateral 3) from cat 27, the least behaviorally responsive animal. This animal was rated as having no exploration, activity, aggression, and any signs of emotionality in response to the noxious stimuli. (B) Evoked potentials recorded from the OR fibers in cat 27. None of the EP components decrease in amplitude with increasing flash intensity. (C) Cat 20, a clear augmenter, was judged as one of the most behaviorally responsive animals. Recordings are from the same cortical area as in (A).

the third series. Five intensities were presented in each series in random blocks of ten flashes at a rate of one per second with an interblock interval of 7 seconds. Upon completion of the flash procedures, the OT and OR electrodes were lowered until cortical EP's of maximum amplitude were produced when these electrodes were stimulated. Throughout the remainder of the experiment, the OT and OR electrodes were stimulated alternately with 0.1 msec constant current pulses at a rate of one pulse per second. The MRF electrode was then lowered until maximum increases in the OT-produced EP occurred after stimulation of the MRF (10). Seven intensities of MRF stimulation (11) were presented in an ascending order (10, 30, 50, 70, 90, 120, and 150 μa) in each of two runs. The first run was with a 30-second intertrial interval (ITI) between intensities and the second run consisted of a 90-second ITI to allow the animals more time to return to EEG synchrony between trials. At the conclusion of the experiment, lesions were produced at the electrode sites so that electrode placements could be verified histologically (12).

Cat 27 was the least behaviorally responsive animal and was clearly an EP reducer, producing the largest EP with the dimmest flash intensity (see Fig. 1A). No EP reductions were evident in the recordings taken simultaneously from the OR fibers (Fig. 1B), indicating that EP reducing is a cortical phenomenon. Cat 20, one of the most behaviorally responsive animals, showed a typical augmenting pattern (Fig. 1C). Slopes for the peak-to-peak amplitude of the largest positive–negative component (peak 3 to peak 4) of the cortical EP for the five flash intensities were computed by the least-squares method and expressed as microvolts per log footcandle (13). All 15 animals had positive slopes for the low-intensity series of flashes; however, the high-intensity series produced negative slopes in seven animals (reducers) and positive slopes in the remaining eight animals (augmenters).

As shown in Table 1, five of the behavioral traits were significantly correlated with the EP slopes for the high-intensity series of flashes. Augmenter cats responded in overt emotional and aggressive ways in reaction to the noxious stimuli and maintained a strong visual contact with their environment. In addition, they tended to rate high in exploration and activity. Reducers had the opposite constellation of behaviors, and were quite unresponsive to the same

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Table 1. Rater reliability and Pearson correlation coefficients of evoked potential slopes with the behavioral ratings. Slopes were calculated from the peak-to-peak amplitude (peak 3 to peak 4) of the evoked potentials to the higher intensity series of flashes and were expressed as microvolts per log footcandle. Behavioral ratings were the sum of the four judges' scores.

Behavior	Rater reliability	Correlation with slopes*
Exploration	.55	.445
Activity	.88	.298
Aggression	.99	.589†
Withdrawal	.84	.704‡§
Visual contact	.78	.702‡
Emotionality	.87	.790‡
Responsiveness	.95	.793‡

*Data from one animal were statistical outliers (21) on all behavioral scores ($P < .01$) and were excluded from this analysis. Including this animal's data affected only the significance of aggression ($r = .326$, $P > .10$)   †$P < .05$.   ‡$P < .01$.   §See (22).

stimuli. These data indicate that slope differences between augmenter and reducer cats are not due to peripheral visual mechanisms or selective avoidance of the more intense flashes. Further, the fact that the EP's were collected from immobilized animals that were undoubtedly under stress attests to the robust nature of the phenomenon. In the second part of this study, we present data suggesting that brainstem arousal mechanisms
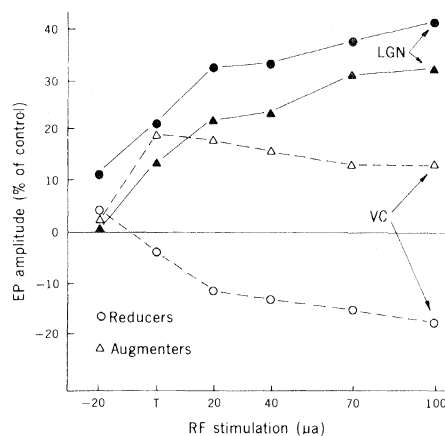

Fig. 2. The effects of reticular stimulation on lateral geniculate (LGN) and visual cortex (VC) responsiveness in augmenter-reducer cats. The abscissa values represent the absolute amount of current above and below the threshold for producing desynchronization as determined by computer frequency analysis of the EEG. For LGN responsiveness, changes in baseline to peak 1 amplitude of the EP produced by OT stimulation are expressed as a percentage change from the averages collected immediately preceding the onset of reticular stimulation (control data). For VC responsiveness, changes in peak 4 to peak 5 of the EP produced by OR stimulation are expressed as a percentage change from the control data.

nisms modulating cortical responsiveness may produce both the individual differences in behavioral responsiveness and EP augmenting-reducing.

As shown in Fig. 2, reticular stimulation above the threshold for producing EEG desynchronization (as determined by computer frequency analysis of the EEG) increased LGN responsiveness for both groups of animals (14). These results in conjunction with previous studies of single units (15) and EP's (16) indicate that increased arousal from sleep to waking and higher states of arousal, whether occurring naturally or following reticular stimulation, increase thalamic responsiveness. In contrast to the lack of differences in thalamic responsiveness for the augmenters and reducers, cortical responsiveness differed dramatically (Fig. 2). The reducers' cortical responsiveness decreased after all intensities of reticular stimulation above the threshold for EEG desynchronization, whereas cortical responsiveness in the augmenters was elevated above control levels (17). Hence, the phenomenon of augmenting-reducing was duplicated by holding the visual stimuli constant and increasing the animal's cortical arousal.

These results demonstrate that EP augmenting-reducing does not depend on peripheral visual mechanisms or differences in thalamic responsiveness. The phenomenon occurs cortically following the interaction of ascending visual stimuli with brainstem arousal mechanisms. The EP reductions may involve the activation of cortical inhibition. There is ample evidence that inhibition occurs at the cortex (18), and it is known that intense light flashes (19) or ascending reticular influences (20) are capable of activating cortical inhibition. Reducers either have a lower threshold for initiation of cortical inhibition or, alternatively, have higher levels of arousal which would summate with lower intensities of light flashes to activate the inhibitory system. Whatever the mechanism, individual differences in the degree of cortical inhibition may have profound behavioral effects. Future animal research may provide a model system for understanding the relations between cortical functioning, augmenting-reducing, and individual differences in personality.

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7. Stimuli were presented three times at 20-second intervals in the following order: (i) 100-db (A scale) noise bursts; (ii) intense light flashes (370 footcandles); (iii) high-pressure oxygen was emitted from a hose causing it to hiss and flail about; (iv) low-pressure oxygen was emitted producing a mild hiss; and (v) a mechanical, battery-operated ape approached the animal swinging its arms and producing a loud, mechanical noise.
8. The results and behavioral descriptions from the study of Hall *et al.* (*4*) suggest that these behaviors in cats are related to the augmenting-reducing phenomenon.
9. The use of Flaxedil presents two interrelated problems: the animal when conscious can perceive pain, and Flaxedil when used in high dosages for a prolonged time can produce a comatose state [R. Hodes, *Electroencephalogr. Clin. Neurophysiol.* **14**, 220 (1962)]. Therefore, Flaxedil was continuously infused (intravenously) at the lowest rate and concentration necessary to produce paralysis and was discontinued whenever the animal failed to desynchronize to natural stimuli. Periodically all wounds were treated with local anesthetics, the eyes and tongue were moistened, and the animal was rotated and its legs flexed. The EEG, electrocardiogram, expired CO_2, and body temperature were continuously monitored and maintained within normal limits.
10. Concentric stimulation electrodes were formed from an insulated wire extending 0.5 mm from within a 24-gauge tube. The final 0.25 mm of the tip and 0.5 mm of the barrel were stripped of their insulation. Reticular coordinates were anterior 2.0, lateral 2.5, and horizontal -1 to -2.5. This region was shown to be most effective for producing long-lasting EEG desynchronization [M. Bonvallet and A. Newman-Taylor, *Electroencephalogr. Clin. Neurophysiol.* **22**, 54 (1967)].
11. Reticular stimulation consisted of 0.5-second trains of 0.1-msec pulses delivered at a rate of 150 pulses per second. Each train terminated 25 msec prior to presentation of the visual stimulus, with 30 trains given at each intensity. Three averages each consisting of five EP's for both OT and OR stimulation were collected during each intensity of MRF stimulation. In addition, the five potentials recorded immediately preceding each MRF stimulation run were averaged and served as baseline data.
12. J. Siegel, *Physiol. Behav.* **3**, 203 (1968).
13. One footcandle is equivalent to 10.76 lumen/m².
14. A three-factor analysis of variance for unequal number of subjects per group indicated that the main effects for groups (augmenter-reducer) and ITI were not significant. Suprathreshold MRF stimulation significantly increased thalamic responsiveness for both groups, $F (5, 60) = 21.75$, $P < .001$.
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17. The groups differed significantly, $F (1, 10) = 5.34$, $P < .05$, as did the groups by RF stimulation interaction, $F (5, 50) = 3.05$, $P < .05$.
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22. Previous results indicated a negative correlation between EP augmenting and withdrawal (*4*). We defined withdrawal as the degree of movement away from the noxious stimuli. Augmenters reacted more to the stimuli than did the reducers and part of their initial reaction was a definite withdrawal. We have the impression that the reducers withdrew more to the back of their home cages when approached than did the augmenters. The discrepancy, therefore, may be in the definition of withdrawal.
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Imitation of Facial and Manual Gestures by Human Neonates

Abstract. *Infants between 12 and 21 days of age can imitate both facial and manual gestures; this behavior cannot be explained in terms of either conditioning or innate releasing mechanisms. Such imitation implies that human neonates can equate their own unseen behaviors with gestures they see others perform.*

Piaget and other students of developmental psychology consider the imitation of facial gestures to be a landmark achievement in infant development. Infants are thought to pass this milestone at approximately 8 to 12 months of age. Infants younger than this have been postulated to lack the perceptual-cognitive sophistication necessary to match a gesture they see with a gesture of their own which they cannot see (*1*). The experiments we report show that the infant's imitative competence has been underestimated. We find that 12- to 21-day-old infants can imitate both facial and manual gestures (Fig. 1). This result has implications for our conception of innate human abilities and for theories of social and cognitive development.

An experimental evaluation of the neonate's imitative competence raises several methodological difficulties. One consists of distinguishing true imitation from a global arousal response. For example, one can conclude nothing about imitation if an infant produces more tongue protrusions in response to a tongue protrusion demonstration than he does to

Fig. 1. Sample photographs from videotape recordings of 2- to 3-week-old infants imitating (a) tongue protrusion, (b) mouth opening, and (c) lip protrusion demonstrated by an adult experimenter.