

Visual Responses of Neurons in the Dorsolateral Amygdala of the Alert Monkey

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There is evidence that the inferotemporal visual cortex in the monkey projects to the amygdala, and evidence that damage to this region impairs the learning of associations between visual stimuli and reward or punishment. In recordings made in the amygdala to determine whether or not visual responses were found, and if so how they were affected by the significance of the visual stimuli, neurons were found in the dorsolateral part of the amygdala with visual responses which in most cases were sustained while the animal looked at effective visual stimuli. The latency of the responses was 100 to 140 ms or more. The majority (85%) of these neurons responded more strongly to some stimuli than to others, but physical factors which accounted for the responses of the neurons, such as shape, size, orientation, color, or texture, could not usually be identified. Although 22 (19.5%) of these neurons responded primarily to food objects, the responses were not uniquely food-related. Furthermore, although some neurons responded in a visual discrimination test to a visual stimulus which indicated reward, and not to a visual stimulus which indicated saline, only minor modifications of the magnitude of the neuronal responses to the stimuli were obtained when the reward-related significance of the stimuli was reversed. The visual responses of these amygdaloid neurons were thus intermediate in some respects between those of neurons in the inferotemporal cortex, which are not affected by the significance of visual stimuli, and those of neurons in a region to which the amygdala projects, the lateral hypothalamus and substantia innominata, where neurons respond to visual stimuli associated with food reward.

INTRODUCTION

There is anatomical evidence for a projection in the monkey from the inferotemporal cortex, a region of visual association cortex, to the

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amygdala (6, 9, 24, 27). We therefore investigated neurophysiologically whether or not neurons in the amygdala of the monkey respond to visual inputs, and if so how they respond. This investigation is described here.

It is of interest that damage to the temporal lobes produces the Klüver-Bucy syndrome, in which monkeys cannot react normally to the significance of visual stimuli, in that they tend, for example, to place both food and nonfood objects into the mouth (1, 9, 10), and that damage to the amygdala may be involved in the effect (25). Furthermore, animals with temporal lobe damage have a deficit in learning visual discriminations, which was ascribed to an impairment in the capacity to form associations between visual stimuli and reinforcement (8). Therefore, particular attention in the experiments described here was paid to whether or not the responses of amygdaloid neurons depended on the reinforcing value of the visual stimuli shown. This was investigated quantitatively in several ways. First, the responses of each amygdaloid neuron to rewarding visual stimuli such as food for the hungry animal, to aversive visual stimuli such as a syringe from which the animal was fed aversive hypertonic saline, and to relatively neutral visual stimuli such as cards with gratings and different geometrical shapes were compared. Second, the monkey performed a visual discrimination to obtain food as opposed to aversive hypertonic saline while recordings were made from the amygdaloid neurons. This allowed investigation of neuronal responses to stimuli which the monkey treated in the visual discrimination as rewarding or aversive, and also allowed measurement of the response latency of amygdaloid neurons, to clarify whether they could be crucial to the visual discrimination, as implied by the lesion evidence, or simply had long latency responses which reflected the animal's performance. Third, the significance of visual stimuli in terms of whether they were reward-associated or aversive was altered in reversal training while recordings were being made. This test shows whether the neuronal responses occur because of the association of a visual stimulus with reward or punishment, or because of the physical characteristics of the visual stimulus. These tests have been developed and evaluated in recordings made in the hypothalamus (3, 12, 18, 22) and inferotemporal cortex (20). It was found that neurons in the inferotemporal cortex respond independently of the significance of the visual stimuli shown (20), whereas a population of neurons in the lateral hypothalamus and substantia innominata responds to visual stimuli such as the sight of food on the basis of the significance of the stimuli (3, 12, 18, 22). In this context analysis of whether or not amygdaloid neurons show visual responses, and if so how they are affected by this type of learning, is of added interest, for the amygdala not only receives connections from the inferotemporal cortex, but is also known to have projections to the

hypothalamus (13). Furthermore, amygdaloid neurons are activated by electrical stimulation of the region of the hypothalamus and substantia innominata in which feeding and reward-related neurons are found (19).

We know of only one previous study of the activity of amygdaloid neurons in the alert monkey. Fuster and Uyeda (5) recorded from neurons in brain regions which included the basolateral complex of the amygdala in the monkey during a visual discrimination between visual stimuli (horizontal vs. vertical rows of lights or red vs. green) which indicated either that food would be obtained if the right lever was pressed or that shock would be obtained if the left lever was pressed. Although some amygdaloid neurons differentiated between the stimuli in this test, the neuronal responses were measured during a 6-s period in which the stimuli were shown, so that factors other than visual responsiveness, for example, movements or arousal elicited by the stimuli, could have contributed to or accounted for the neuronal responses, and no reversal series were carried out to assess the effect of the significance of the visual stimuli on the responses obtained. In the alert cat, there are reports of responses of amygdaloid neurons to complex stimuli such as a black mouse, a bird call, and a meow (7, 14), but the exact nature of the responses, and in particular the role of stimulus-reinforcement association learning in the responses, was not investigated.

METHODS

To investigate possible visual responses of amygdaloid neurons, and how these were influenced by learning, and to allow the activity of neurons in the amygdala to be compared directly with the activity of neurons in the inferotemporal cortex, lateral hypothalamus, and substantia innominata, the methods used were similar to those described elsewhere (18, 20, 22).

Recording Method. Five juvenile rhesus monkeys (*Macaca mulatta*), weighing 2.5 to 3.5 kg, were implanted under thiopentone sodium anesthesia with stainless-steel holders on which a Trent-Wells adaptor for chronic single-unit recording could be placed during recording sessions. Stimulation electrodes (for a related investigation) were implanted during the same operation. After a recovery period of 2 weeks or more, daily recording sessions started. Single-unit activity was recorded using glass-coated tungsten microelectrodes [after Merrill and Ainsworth (11), but without platinum plating] while the monkey sat in a primate chair with head restraint to provide recording stability. The electrodes were lowered into the brain through a stainless-steel guide tube whose tip was 3 to 4 mm below the dorsal surface of the dura. At the end of each track, X-rays were taken of the frontal and lateral aspects of the head to determine (to

within ± 0.5 mm) the position of the tip of the recording electrode relative to the permanently implanted stimulating electrodes.

The signal from the microelectrode was passed through the FET buffer amplifier mounted on the microdrive, amplified by conventional band-pass filtered amplifiers, displayed on an oscilloscope, and stored on magnetic tape. Data were analyzed using an on-line PDP-11 computer, which was programmed to perform peristimulus time histograms with the additional presentation of every trial individually as a dot display, or to compute the mean firing rate (and its SE) of the neurons during stimulus presentation or control periods.

Presentation of Stimuli. Stimuli were presented to the animal against a uniform background, in a circular aperture 15° in diameter (at a distance of 30 cm) in a screen which otherwise filled the animal's field of view. The stimuli used were real foods (such as peanuts and pieces of orange or banana), card or Plexiglas cut into shapes such as bars, squares, and triangles, or common laboratory objects, as these had been found useful in recordings in the inferotemporal cortex (4, 20). When a unit with a visual response was found, different food and nonfood stimuli were presented to determine whether or not physical factors such as the outline shape, size, orientation, color, and surface texture of the stimuli could account for the responses of the neurons. The animal's fixation was usually observed via a peephole, and the response to each stimulus was measured while the monkey looked at the stimulus. The latency and magnitude of the neuronal responses to different visual stimuli were measured by presenting the stimuli immediately behind a 6-cm-diameter electromagnetically controlled shutter positioned in the circular aperture of the screen. The shutter was opened to reveal the visual stimulus when the monkey was looking at the shutter, usually at the termination of a tone (usually 0.5 s long) which signalled the opening of the shutter. The magnitude of the response on each trial was calculated as the number of action potentials in the period 100 to 780 ms after the shutter opened, and was available on-line to guide further testing. Repeated trials were run to estimate the standard error of the response. The shortest latency of the response was measured from the sum buffer for 15 trials. All latencies were measured relative to the time of the shutter opening, the exact opening time of which was confirmed with a phototransistor circuit. To assess the significance of the changes in firing rate found in the peristimulus time histograms, Mann-Whitney *U* tests or tests appropriate to the Poisson distribution of the spikes in the bins of the sum buffer were used to compare the firing rate in 18 bins of 10 ms each in a 180-ms peristimulus period with the firing rate in any set of post stimulus bins. Similar tests were also used to compare poststimulus activity to

different stimuli, and to test the shortest poststimulus time at which a significant change in the firing rate occurred from the prestimulus period.

Effects of the Significance of the Visual Stimuli. Three methods were used to assess whether or not the significance which visual stimuli had for the animal affected the magnitude of the responses of neurons in the amygdala. First, the magnitude of the responses of the neurons was measured when a wide range of objects was shown to the animal. This was done in both the "clinical" test situation described above and with the stimuli shown with the shutter procedure. It was then possible to determine whether the amygdaloid neurons responded to, for example, all food objects [banana, mash (i.e., laboratory chow), peanut, raisin, a 2-ml syringe from which the monkey was fed 5% glucose solution, when these were shown to the monkey], to all aversive objects (e.g., a 1-ml syringe from which the monkey was fed 5% saline, a squeeze bulb from which air was gently blown on the monkey's face, a face making a threat gesture, etc.), or to objects independently of whether they were rewarding or aversive.

Second, the activity of the amygdaloid neurons was measured while the monkey performed a visual discrimination. After a signal tone (usually 0.5 s) the shutter opened to reveal a visual stimulus. If the reward-associated visual stimulus (S^D) was shown (usually a 2-ml syringe containing black currant juice and mounted on a white plaque), then the monkey, which was 18-h food-deprived during these experiments, could obtain fruit juice from a tube fixed in front of its mouth if it licked the tube during the shutter-open period of 1.0 s. (The lick activated a pump which delivered 0.3 ml fruit juice for the monkey to drink.) If the shutter opened to reveal the aversive visual stimulus (S^A) (usually a 1-ml translucent syringe containing 5% saline mounted on a black plaque), then the monkey obtained aversive hypertonic (5%) saline if he licked the tube. So that the animal could not predict the type of the next trial, trials were presented in a Gellerman series. Trial spacing was approximately 15 s, and the usual level of performance was 90% correct. Further details of this visual discrimination task were described elsewhere (16, 22), including the point that neuronal responses shorter in latency than 250 to 300 ms relative to the shutter opening precede and therefore do not simply reflect the initiation of the monkey's lick response.

Third, the response of the neurons was measured while the significance of the visual stimuli for the monkey was changed. This procedure shows whether any difference in response to the reward-associated and aversive visual stimuli is due to the different physical characteristics of the stimuli, or to the significance of the stimuli. This was sometimes done in the visual

discrimination situation described above by reversing the significance of the visual stimuli during a series of trials. (Thus if the monkey licked when he was shown the previously rewarded black currant juice stimulus he obtained saline and vice versa.) Although the monkeys quickly learned not to lick to the previously rewarded stimulus, it often took 50 or more trials for licks to become established to the previously aversive visual stimulus. An alternative procedure was to introduce a neutral visual stimulus on some trials, and after determining the neuronal responses to this stimulus, to use the stimulus as a reward-associated stimulus which predicted fruit juice, to determine whether or not the alteration of significance altered the responses of the neuron to the visual stimulus. Another procedure was to alter or reverse the significance of the visual stimuli used in the clinical test situation by, for example, filling the 1-ml syringe which normally contained saline with glucose [see (12, 20)].

Localization of Recording Sites. The recording sites of the neurons described in the paper were determined in two ways. First, from the frontal and lateral X-ray photographs of the electrode at the end of its track, the position of each unit could be determined relative to the tips of the chronically implanted stimulation electrodes, the sites of which were histologically verified. Second, at the end of the recording period, lesions were made through the recording microelectrode to mark typical units. This was done by passing either anodal or cathodal current of 60 to 100 μ A for 60 to 100 s. After a lethal i.p. dose of pentobarbital sodium, the animal was perfused with 0.9% saline followed by formal-saline. After equilibration in sucrose-formalin, serial frozen 50- μ m brain sections were cut and stained with thionin.

RESULTS

Microelectrode tracks were made in five rhesus monkeys, and the activity of a sample of more than 1754 neurons in different parts of the amygdala was analyzed. In this sample, 113 neurons were found in a lateral part of the amygdala which were classified as receiving a visual input on the basis of the experiments described below.

Visual Responses of the Amygdaloid Neurons. One hundred and thirteen neurons in the lateral amygdala altered their firing rates to the presentation of visual stimuli and were classified as showing visual responses because of the following characteristics. First, the responses of this population of neurons were locked to the time of presentation of effective visual stimuli. For example, the responses of the amygdaloid neuron illustrated in Fig. 1 occurred with a latency of 120 to 150 ms after the wide-aperture shutter

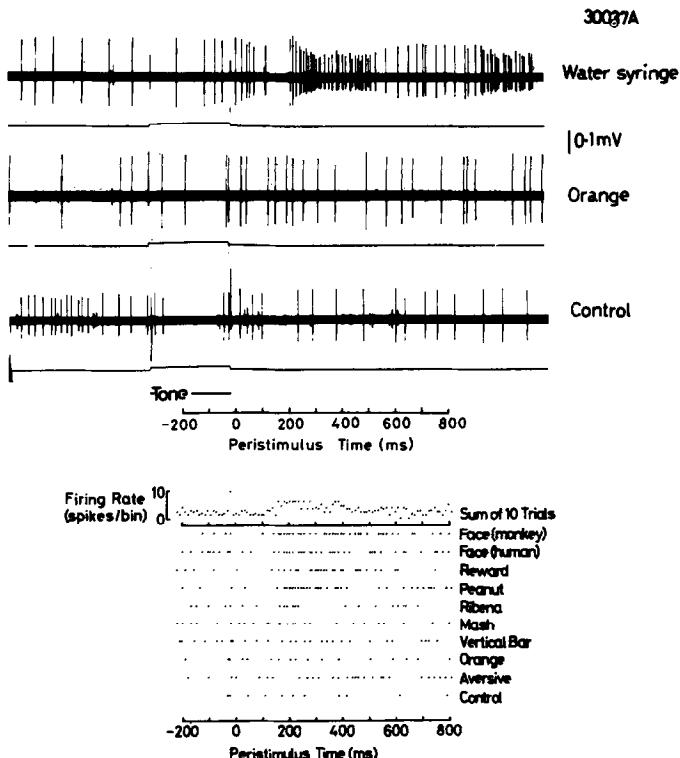


FIG. 1. Response of a unit in the dorsolateral amygdala to different visual stimuli. Above—photographs of the unit activity after an effective visual stimulus (10-ml syringe containing water), a relatively ineffective stimulus (an orange segment), and a trial on which the shutter opened to reveal the blank back-screen. Below—dot displays of unit activity after different visual stimuli to show the latency of the response and the different magnitude of the responses found to different visual stimuli. The histogram shows the sum of the unit activity on these 10 trials to provide an indication of the latency of the neuronal responses. The shutter opened at time 0, and is preceded by a signal tone. Bin width: 10 ms.

opened to reveal certain visual stimuli (e.g., for this unit, see the top four trials of the dot display which are presented only in this order for clarity). Further examples of the way in which the neuronal responses were related to the presentation of effective visual stimuli are shown in Fig. 2. For the different neurons the shortest latencies to the responses following the presentation of effective visual stimuli were in the range 100 to 180 ms, with the majority of the units having latencies of 110 to 130 ms. Second, if the shutter was opened but the monkey was prevented from seeing the shutter by a screen, no response occurred in these units (see e.g., Fig. 1, trial 10), so that the responses of the units were not due to the noise of the shutter

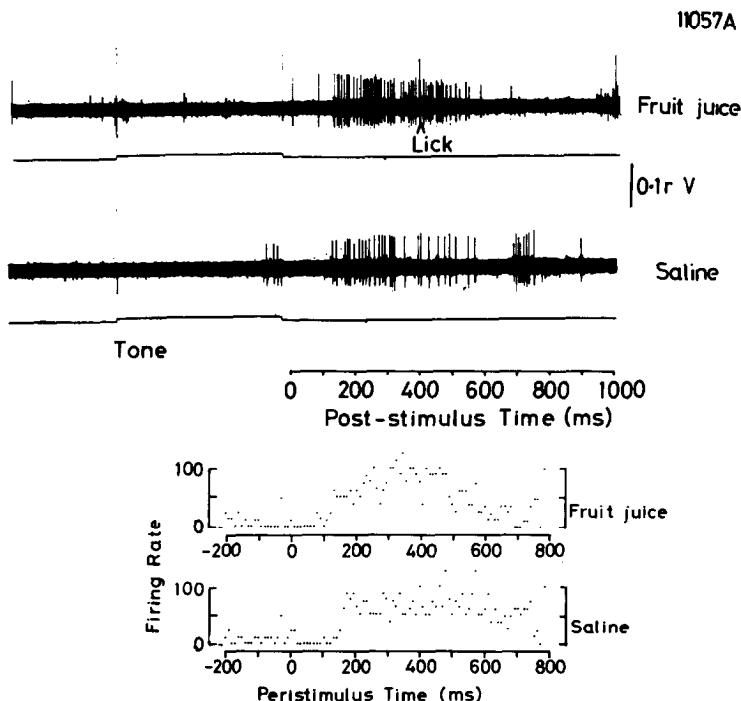


FIG. 2. Activity of a unit in the lateral amygdala during visual discrimination. Above, top trace, reward trial—at the end of the signal tone the shutter opened at time 0 to reveal a 2-ml syringe filled with red fruit juice, the unit responded to the stimulus with a latency of approximately 140 ms, and the monkey licked the tube in front of its mouth at approximately 400 ms to obtain fruit juice. Lower trace, saline trial—the shutter opened to reveal a 1-ml syringe containing clear saline, the unit again responded to the stimulus, and correctly the monkey did not lick the tube, or he would have obtained hypertonic saline. Below—histograms, with 10-ms bins, of the average peristimulus activity for this unit on 10 reward trials and 10 saline trials. The number of spikes/10-ms bin is expressed as the mean firing rate for a trial (spikes/s).

opening. Third, the responses of most (see below) of these amygdaloid units depended on the visual stimulus which appeared behind the shutter. For example, the unit shown in Fig. 1 did not respond to a segment of orange or to the white background against which visual stimuli were presented. Fourth, these neuronal responses were visual and were not due to arousal, or to motor movements, in that they did not occur when the monkey was aroused by pinching the skin or by puffing air lightly onto the face, during general body movements, during feeding, or for many neurons, when noneffective visual stimuli which aroused the monkey (e.g., the sight of a face or of a syringe containing hypertonic saline) were shown.

Fifth, these neurons did not respond when the shutter opened in the dark. Sixth, the responses were not olfactory in that glass separated the visual stimuli behind the shutter from the monkey. Seventh, in the clinical test situation, the responses of these neurons occurred when the monkey looked at effective visual stimuli and were not related to auditory or olfactory stimuli or to movement or arousal. Because of these characteristics, this population of neurons in the lateral amygdala was classified as showing visual responses.

Response Characteristics: Selectivity. The responses of some of the differentially responding units could not be related to obvious differences in the physical properties of the visual stimuli. Figure 1 illustrates the responses found for one amygdaloid neuron when the shutter opened to reveal different visual stimuli. The upper unit trace shows a response to the display of a syringe containing water. In contrast, there was little or no visual response to a piece of orange or a blank control when the shutter opened to show a blank field. The dot histogram shows further differential responses of the same unit on different trials with different stimuli. Even though edges, bars, and gratings were shown systematically, and the color, size, and shape of the visual stimuli were varied, physical dimensions of the stimuli which accounted for the neuronal responses of this and other differentially responding amygdaloid neurons could not usually be identified. Of the 113 amygdaloid units classified as responding to visual stimuli, testing with a wide range of visual stimuli was completed for 102 of them. Of these, 87 (85%) responded differentially to different visual stimuli (69 were excited, 15 were inhibited, 2 were inhibited or excited by different visual stimuli, and 1 had a biphasic response), and 15 (15%) responded similarly to different visual stimuli (12 were excited and 3 were inhibited). The responses of the majority of these neurons were sustained in that as long as the animal fixated an effective visual stimulus, the neuronal response continued. Thus in the clinical test situation, if the animal was shown a syringe which contained glucose and this happened to be one of the effective visual stimuli for the neuron, then the neuronal response started when the monkey was shown the syringe, and continued for the whole period in which the syringe was brought toward the monkey's mouth for feeding. If the same neuron happened to respond to a syringe of a different size which contained hypertonic saline, then the same sustained neuronal response was obtained in the test situation, although the animal refused to drink the saline. The responses of a minority of the neurons (14 of the sample of 113 neurons, or 12.4%) showed only transient responses to effective visual stimuli, with the responses starting usually at 110 to 120 ms and continuing only for 30 to 100 ms.

As physical dimensions of the stimuli which accounted for the neuronal responses could not usually be identified, the possibility that the significance of the visual stimuli for the animal accounted for the responses of these amygdaloid neurons was investigated as described below.

Response Characteristics: Effects of the Significance of the Visual Stimulus. The first way in which the effects of the significance of the visual stimuli were analyzed was by comparing the responses of the amygdaloid neurons to different visual stimuli. No units were found which responded uniquely to food-related visual stimuli (e.g., the sight of the monkey's regular foods, and of visual stimuli which the monkey had learned in a visual discrimination test indicated that food reward would be delivered if the monkey licked). Furthermore, no units were found which responded only to aversive visual stimuli (e.g., the sight of a face which caused the monkey to make a threat response, of a squeeze bulb used to puff air onto the monkey's face, and of a visual stimulus which the monkey had learned indicated that hypertonic saline would be delivered). Thus these amygdaloid neurons did not respond on the basis of the food-related or aversive significance of visual stimuli. Although this was the case for all neurons, 22 amygdaloid neurons did respond mainly to rewarding objects, such as different types of food, and visual stimuli which the animal had learned indicated that he would receive food. But all these neurons responded to one or more visual stimuli in a way inconsistent with a characterization of food reward-related responsiveness by, for example, responding to one or more neutral or aversive stimuli or failing to respond to one or more types of highly preferred food. Comparably, three neurons responded mainly to aversive visual stimuli. Thus these amygdaloid neurons did not respond on the basis of, but could perhaps have been influenced by, the food-related or aversive significance of visual stimuli.

A second way in which this was tested was by measuring the change in neuronal activity of amygdaloid neurons when the shutter opened to show a stimulus which the animal had been taught was associated with food reward, as opposed to a stimulus which was aversive to the animal, in the visual discrimination test. Figure 2 shows the responses obtained from one such neuron in the lateral amygdala. The tone indicated to the animal that the shutter was about to open to reveal a visual stimulus. When the shutter opened to reveal the fruit-juice syringe (reward stimulus), a visual neuronal response occurred at a latency of 120 to 150 ms, and the animal made a lick to obtain fruit juice at a latency of approximately 430 ms. All latencies are relative to the time of the shutter opening, time zero. When the shutter opened to reveal the aversive, saline-associated, visual stimulus, there was a similar visual response at a latency of 120 to 150 ms, and correctly the

animal made no lick. The similarity of the magnitude of the responses to the reward-associated and aversive visual stimuli is further shown in the lower histograms of the firing rate in a sum of 10 reward trials and in a sum of 10 aversive trials. Thus in a visual discrimination, this neuron did not differentiate in its response to a stimulus which indicated food and a stimulus which indicated saline. Of the 19 neurons investigated fully in this visual discrimination, nine did give differential responses. Of these, five were excited and two were inhibited by the reward stimulus, one was excited by the aversive stimulus, and one was both excited by the reward and inhibited by the aversive stimulus. The remaining 10 neurons gave similar responses to both of the stimuli, as illustrated in Fig. 2. Even though nine of the units did not show responses which were different to the reward and aversive visual stimuli, the significance of the stimulus did not account for the responsiveness of these neurons because they did not respond uniquely to rewarding or aversive visual stimuli (see above), and when this was tested, their responses were not modified during the reversal of a visual discrimination (see below).

As a further test to determine whether or not the significance of the visual stimulus could account for the visual responses obtained, the significance of the stimulus was altered while recordings were made from some neurons in reversal tests, as described under Methods. In eight of nine experiments of this type on nine different neurons, there was no modification of the neuronal responses when the significance of the visual stimulus was changed. In the ninth case there was a possible minor enhancement of neuronal responsiveness to an initially neutral 1° grating when it became associated with reward, but the effect was small, and the responses to this stimulus did not approach in magnitude the responses seen to the usual reward stimulus (mean \pm SE spontaneous firing rate, 23.5 ± 1.0 spikes per second; rate to grating when neutral, 21.3 ± 1.8 ; rate to grating when associated with reward, 29.2 ± 0.9 ; and for comparison, response to the usual reward stimulus, 51.6 ± 4.6 ; and to the aversive stimulus, 20.1 ± 0.8).

Location of Rewarding Sites. The sites at which neurons with the visual responses described here were recorded are shown in Fig. 3 and were mainly in the dorsolateral region of the amygdala.

Characteristics of Other Neurons Recorded in the Amygdala. Of the total sample of 1754 neurons recorded throughout the amygdala, the characteristics of 113 neurons, which were mainly in the dorsolateral amygdala and had visual characteristics, have been described above. Of the other neurons, 104 also had some visual characteristics but were not investigated sufficiently to be included with the main sample of visually

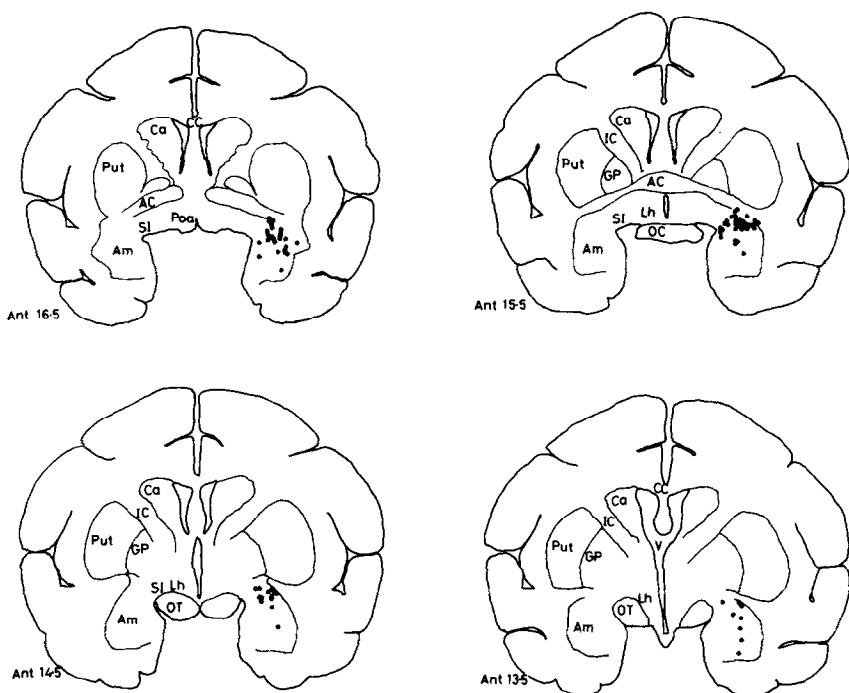


FIG. 3. Sites, mainly in the lateral and dorsal amygdala, from which the units with response to visual stimuli as described here were found. The sections are at different distances anterior to the ear bars. Coordinates from (23). AC—anterior commissure; Am—amygdala; Ca—caudate nucleus; CC—corpus callosum; Gp—globus pallidus; IC—internal capsule; Lh—lateral hypothalamus; OC—optic chiasma; OT—optic tract; Poa—pre-optic area; Put—putamen; SI—substantia innominata.

responsive neurons. In the course of this study tracks were made through much of the amygdala, and the following other types of response were noted. Many amygdaloid neurons (167 in the sample of 1754, or 9.5%) altered their activity in relation to movements made by the monkey, for example during reaching, or during mouth movements, e.g., chewing, protrusion of the tongue, swallowing, or lip movements. Although some of these neurons were active when the monkeys worked for food, the activity could be shown to be related to the movements made by the monkeys, both because of its characteristics, and because of its relatively long latency which did not precede the electromyogram associated with the initiation of the lick response [see (22)] significantly. With these neurons it was not usually possible to determine in the test situation whether the activity of the neurons was related to motor or sensory aspects of the control of the

movements, but in 12 additional neurons the activity was classed as related to somatosensory stimulation, because the neurons were activated by light touch to the hair or fur in the absence of movements made by the monkey. Nine neurons altered their activity only when certain tastes were present in the mouth, and did not respond because of mouth movements. Although this was not routinely tested, three neurons showed clear auditory responses, and three of the neurons with responses to visual stimuli described above did alter their activity when the tone which signaled a trial sounded. Also, it was noted that the activity of one neuron was related to olfactory stimulation. The activity of 13 neurons was related to arousal. The remaining 1332 neurons did not show clear responses in the test situations described above.

DISCUSSION

These results show that there is a visual input to neurons in the lateral part of the amygdala in the monkey. The neuronal responses were visual in that they occurred with a consistent latency to effective visual stimuli, usually occurred to only some visual stimuli and not when the shutter opened to reveal a blank visual field, and were not associated with arousal or with movements made by the animal. These findings are in line with the anatomical evidence obtained mainly with anterograde degeneration techniques that there are connections from the inferotemporal cortex, which is a region of visual association cortex, to the lateral amygdala (6, 9, 24, 27). The part of the amygdala in which visual responses were found was the dorsal part of the lateral region, as shown in Fig. 3. This corresponds with the anatomical finding that terminals from the inferotemporal cortex reach the dorsal part of the lateral amygdala, whereas terminals from the superior temporal (auditory association) cortex reach the more ventral part of the lateral amygdala (6). Although microelectrode tracks were made throughout the amygdala this dorsolateral region was where the majority of the visual neurons described above were recorded (see Fig. 3). In other parts of the amygdala, some neurons with auditory responses (occurring to e.g., clicks) were found, and many other amygdaloid neurons had activity related to somatosensory input or to movements made by the animal.

The responses of these neurons in the dorsolateral amygdala did not appear to be related to the significance of the visual stimuli shown. For example, the neurons did not both respond to food objects and fail to respond to nonfood objects as was found for neurons in the substantia innominata and lateral hypothalamus in the same test situation (18), nor did they respond only to rewarding and/or aversive visual stimuli, nor was any strong evidence of modification of responsiveness obtained when the

significance of the visual stimulus was changed from neutral or aversive to rewarding or vice versa, or in three of three experiments when the animal was fed to satiety. [The only case of modification found in nine experiments was small compared to the almost complete reversal of responsiveness found in comparable situations in neurons in the substantia innominata (12).] Even if an amygdaloid neuron did differentiate in its responsiveness between a stimulus which indicated food and a different stimulus which indicated saline, then this differentiation did not appear to be due to the significance of the stimulus because the responses of these neurons to other stimuli were independent of whether or not the stimuli were rewarding, and reversal of responsiveness of these amygdaloid neurons when the significance of the visual stimuli in the visual discrimination tasks were reversed could not be demonstrated. Although this was the case, 22 amygdaloid neurons did respond primarily (but not uniquely) to stimuli which were rewarding, and three neurons showed preferential responses to aversive stimulus objects.

It is an interesting finding that amygdaloid neurons did not show clear reward-related visual responses, in the context of the lesion evidence which suggests that temporal lobe damage, perhaps particularly to the amygdala, disrupts the learning of associations between visual stimuli and reward or punishment (8, 25). [Neuronal responses related to reward can be found in the brain: for example, food reward-related responses are found in the hypothalamus—see (15, 16, 18, 22).] A number of possibilities follow. First, the amygdaloid neuronal responses which were partly, but not uniquely, related to rewarding or aversive visual stimuli could reflect activity at an early stage in the formation of connections between visual stimuli and reinforcement. Second, and not exclusively, the amygdaloid visual neurons found could be afferent to neurons which show reward-related responses. We note that neurons in the lateral hypothalamus and substantia innominata are activated in the same test situation by visual stimuli associated with reward and have latencies just longer than those of the amygdaloid neurons (100 to 140 vs. 150 to 200 ms) (16, 18, 22). Third, and also not exclusively, damage to the temporal lobe which produces the Klüver-Bucy syndrome including the visual discrimination deficit (8), may be effective because of deafferentation of, or perhaps even damage directly to, other neurons. One such population of neurons is that in the hypothalamus and substantia innominata with visual responses related to rewarding stimuli such as food (18, 22). Another neuronal population, in the same region, responds to aversive visual stimuli (22). These neurons lie in a horizontal band which extends out laterally above and toward the dorsolateral part of the amygdala (22).

These findings do not exclude the possibility that amygdaloid neurons form one link in a pathway related to the function of stimulus-reinforcement associations. Neurons in the inferotemporal cortex, which anatomically projects to the region of the amygdala in which visual responses were found (6), are activated with a comparable or just shorter latency in the same test situation, and have activity which is not related to the reward-associated significance of visual stimuli (20). As shown here, neurons in the dorsolateral amygdala do have visual responses, and although their activity could be partly reward-related, it is not uniquely so. A population of neurons in the lateral hypothalamus and substantia innominata is activated after the amygdaloid neurons in the same test situation, and the activity of these neurons is related to visual stimuli which include food reward (18, 22). Consistently, there are connections from the amygdala to the hypothalamus in the monkey (13), and these deserve further study. Also consistently, electrical stimulation in the region of the hypothalamus and substantia innominata which contains food reward-related neurons activates neurons in the amygdala (19), and indeed such stimulation is itself rewarding [see (16, 19)]. Whether or not this is part of an important pathway, there is a provocative gap in our knowledge of what happens after inferotemporal and amygdaloid neurons start to fire to visual stimuli at 100 to 130 ms, before hypothalamic neurons start to fire to reward-related visual stimuli at 150 to 200 ms after the visual stimulus is shown.

Neurons with movement-related activity were found in other regions of the amygdala. It is important to note that although the activity of such neurons might follow the presentation of a rewarding stimulus, it is related to movements made by the animal, and not to the significance of the visual stimulus. This is clear not only from the movement-related firing of these neurons, but also from their relatively long latency of activation, which did not precede the latency of approximately 250 to 300 ms with which movements were initiated to the visual stimuli [see (16, 22)]. It should also perhaps be noted that nine of the amygdaloid neurons with visual responses were found to respond primarily to faces or photographs of faces, and two more to respond to all stimuli except these. It is possible that innate or learned factors contributed to the responses of these neurons, as well as to the responses of a comparable group of neurons from which we have recorded in the anterior inferotemporal cortex. We finally note that when investigating temporal lobe mechanisms it may be important to use, as we have, stimuli more complex than just flashes or clicks [cf. (2)], as there is evidence that such stimuli can be processed independently of the temporal cortex (4, 26).

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