A Role of Amygdala in Visual Perception and Cognition in Macaque Monkeys (*Macaca fuscata* and *Macaca mulatta*)

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Division of Clinical Neurology and *Department of Behavioral Physiology, Tokyo Metropolitan Institute for Neurosciences, Tokyo 183, and †Department of Ophthalmology, Kitasato University School of Medicine, Sagamihara 228

Iwai, E., Yukie, M., Watanabe, J., Hikosaka, K., Suyama, H. and Ishikawa, S. A Role of Amygdala in Visual Perception and Cognition in Macaque Monkeys (*Macaca fuscata* and *Macaca mulatta*). Tohoku J. Exp. Med., 1990, 161, Suppl., 95-120 — To elucidate the role of the amygdala in visual perception and cognition, the effects of ablations of the amygdala and inferotemporal cortex on several visual tasks were compared with each other, and also the distribution patterns of the projections between them were investigated. The findings indicate that the inferotemporal cortex plays a critical role in visual perception, cognition and memory, whereas the amygdala is involved fundamentally in controlling emotional and motivational behavior. However, the amygdala is concerned with vision in the following ways: It receives neutral visual information highly processed in the visual cortex, invests the information with emotional and motivational significance through interactions with the cortical and subcortical systems of emotion and motivation, and then it returns the information coded to the visual areas to be re-processed; to be consciously perceived in area TEO, and to be meaningfully cognized, recognized and memorized in areas TE and TEG. Therefore, two channel model regarding the mechanism of visual information processing in the inferotemporal cortex is proposed: A first channel is concerned with processing neutral information, while the second one, with processing meaning information coded emotionally and motivationally in the amygdala. In addition, the present studies demonstrate that area TEG, which is cytoarchitecturally a transitional area between areas TE and TG and whose functional significance has remained unclear, is involved significantly in visual cognition rather than visual perception — amygadaloid complex; inferotemporal cortex; amygadaloid projection; visual perception; visual cognition; monkeys

Recent cognitive neuropsychology has emphasized that the amygdala (amygdaloid complex) is involved closely in the cognitive and memory mechanisms
(Iwai 1982; Mishkin 1982; Squire and Zola-Morgan 1983). On the other hand, the finding of the dichotomy of cognitive and emotional mechanisms between the association cortex and the amygdala (Akert et al. 1961; Jones and Mishkin 1972; Horel et al. 1975) implies that the amygdala does not play a critical role in perception and cognition. Therefore, what role the amygdala plays in cognition and how it plays this role have proved to be extremely baffling questions.

Of all sensory systems, the visual system is at the best understood. In the visual system, it is well-known that there is a hierarchical caudorostral organization in the occipitotemporal cortex. In addition, the functional significance of each cytoarchitecturally defined cortical area in the occipitotemporal cortex has been clarified (Iwai 1982): Inferotemporal cortex is closely and modality-specifically involved in visual perception, cognition and memory (Mishkin 1972; Iwai 1982). Accordingly, the present studies were undertaken to the visual area of the inferotemporal cortex.

We have proposed that there are four fundamental systems in the central mechanisms of visual goal-directed behavior. These are the systems of form vision for objects, spatial vision for objects, emotional and motivational reinforcement for visual objects and performance to visual objects. The visual goal-directed behavior would be evoked though interactions among these systems. It is further surmised that the form vision system links closely with the reinforcement system, while the spatial vision system does not (Iwai 1982). Therefore, the main purpose of the present studies is to elucidate the interaction mechanism between the amygdala as a representative site in the reinforcement system and the inferotemporal cortex as a representative site in the form vision system.

For convenience of understanding the structures of amygdala and inferotemporal cortex, we present our anatomical findings on visual cortico-amygdaloid connections before describing the findings regarding their functional significance.

Amygdalopetal and amygdalofugal connections with inferotemporal cortex

The distributions of amygdalopetal projections (amygdaloid afferents) from the monkey cortex have been repeatedly investigated, using many different techniques, whereas there have not been so many studies for the amygdalofugal projections (amygdaloid efferents) to cortex as those for the amygdalopetal projections. The previous findings indicate that the amygdala has widespread amygdalopetal and amygdalofugal connections with all cortical sensory systems. Although these previous studies provide substantial evidence for the domain of visual cortico-amygdaloid interactions (Whitlock and Nauta 1956; Nauta 1961; Herzog and Van Hoesen 1976; Aggleton et al. 1980; Turner et al. 1980; Van Hoesen 1981; Amaral and Price 1984), the details still remain to be clarified. For example, there have been no studies in monkeys, which detail the origins of the amygdalofugal projections to inferotemporal cortex. The elucidation of amygdaloid efferents to cortex would be especially important in understanding the
feedback mechanism to the system of forward visual information processing.

Using the HRP method with the TMB treatment (Warr et al. 1981; Mesulam 1982; Yukie and Iwai 1981, 1985), we investigated systematically the characteristics of distributions of the terminations of amygdalopetal projections in nine amygdaloid nuclei and those of the origins of amygdalofugal ones, respectively, from and to areas TEG, TE and TEO in the inferotemporal cortex and area TG in the temporal polar cortex.

Fig. 1A shows the diagrammatic representations of the loci and extents of areas TG, TEG, TE and TEO examined in this study. The delineation of these cortical areas was based essentially on the cytoarchitectural charts of von Bonin and Bailey (1947), with reference to the functional and fibroarchitectural findings in our laboratory (Iwai 1980, 1982). Cytoarchitecturally, area TEG is a transitional area between areas TG and TE, and area TEO is also a transitional area between areas TE and OA (cf. color map of von Bonin and Bailey 1947). These TEG and TEO areas are considered long, respectively, to be parts of areas TG and OA. However, as it turns out in the present studies, these areas are anatomically and functionally separable areas from areas TG, TE and OA.

The positions of the nine amygdaloid nuclei are diagrammatically shown in Fig. 1B and C. The nomenclature of the amygdaloid nuclei adopted in this study is based mainly on the cytoarchitectural description of the primate amygdala by Crosby and Humphrey (1941) and in part on that by Price (1981). The amygdaloid complex is divided into nine nuclei in two groups. The deep group consists of six nuclei of the lateral (L), lateral basal (LB), medial basal (MB), accessory basal (AB) and central (Ce) nuclei and anterior area (AA). The superficial group consists of three nuclei of the medial (Me) and cortical (Co) nuclei and periamygdaloid cortex (PAM).

The distribution patterns of anterogradely HRP-labeled terminals and retrogradely labeled cells in the amygdaloid complex are diagrammatically shown in Fig. 1, and their relative densities, in Table 1. The results of a representative case with HRP injection into area TEG is presented in Fig. 2. The present findings in part confirm the previous anatomical ones and extend the domain of visual cortico-amygdaloid interactions.

**Amygdaloid connections with area TG.** The study demonstrated that area TG sent the amygdalopetal projections heavily to the PAM and the dorsal L, moderately to the lateral and dorsal AB and the rostral two-thirds of the MB, and lightly to the rostroventral LB, the Co and the Me. The major and important difference from the previous findings is the existence of the projection to the PAM. No studies have reported this projection. Turner et al. (1980) reported the projections to the anterior Co and a temporal part of the piriform cortex. However, they did not adopt the PAM in their classification of the amygdaloid nuclei of the superficial group, and thus their ventral Co might correspond to our PAM. It should be noted here that the PAM is not uniform in cytoarchitecture:
Fig. 1.
The caudal part is a transitional zone with the basal nuclei and entorhinal cortex. The projection to this cortical transition area was much less heavy than that to the proper PAM.

On the other hand, area TG received the amygdalofugal projections heavily from the PAM and the dorsal L, moderately from the AB and the MB, and lightly from the LB, the Co and the Me. Again, the projection from the cortical transition area was sparse. Amaral and Price (1984) suggested on the findings from the autoradiographic study that the heavy projections to area TG arose mainly from the L and the LB. However, our study demonstrated that the heavy projections arose from the PAM and the dorsal L: The LB projected lightly to area TG, whereas it did heavily to areas TEG and TE.

**Amygdaloid connections with area TEG.** Area TEG projected heavily to the L and the dorsal LB, moderately to the AB and lightly to the MB. Turner et al. (1980) reported the amygdalopetal projection from a region corresponding to area TEG. The present findings of the projections to the L, LB and MB from area TEG were in accord well with theirs. However, they did not describe the projection to the AB, whereas we could not convincingly identify labeled terminals in the AA, where they observed degenerating terminals in their study.

On the other hand, areas TEG receives the amygdalofugal projections heavily from the LB, moderately from the AB and lightly from the MB.

**Amygdaloid connections with area TE.** Area TE projected heavily to a dorsal half of the L and lightly to the dorsal LB. The former projection was reported in the previous studies (Herzog and Van Hoesen 1976; Turner et al. 1980; Van Hoesen 1981), while the latter one has not been reported. Although Herzog and Van Hoesen (1976) described light projection to the Ce from area TE
Fig. 2.
(perhaps, including area TEG), we could not convincingly identify labeling in the Ce.

On the other hand, area TE received the amygdalofugal projections heavily from the LB and lightly from the AB and MB.

*Amygdaloid connections with area TEO.* No HRP-labeled terminals were found in any amygdaloid nucleus. This negative finding confirms the previous ones (Nauta 1961; Aggleton et al. 1980; Turner et al. 1980).

On the other hand, areas TEO received the amygdalofugal projection moderately from the dorsal two-thirds of the LB and none from the ventral LB.

*Characteristics of amygdaloid connections with inferotemporal cortex and temporal polar cortex.*

Our study indicates that the characteristics of the amygdaloid connections with the visual areas in the temporal cortex significantly differ from each other (Fig. 1 and Table 1). As many investigators have reported, it is observed, as a whole, that area TG has much heavier and more extensive amygdaloid connections than any areas with areas TEG, TE and TEO. However, this observation is mainly attributed to the existence of the connections with the PAM, L (for retrograde one only), Co and Me, which have no projections with the inferotemporal cortex. The innervations between the amygdaloid nuclei and area TG are reciprocal, whereas those between the amygdaloid nuclei and the visual areas are not. More important, there is clear dissociation between the distribution patterns of these projections. For the amygdalopetal connections, the projection to the PAM from area TG is heavy, whereas those from the inferotemporal cortex are absent; on the other hand, the projections to the L and the LB from area TG are less heavy than those from areas TEG and TE. For the amygdalofugal ones, the projections from the L and the PAM to area TG are heavy, whereas those to the inferotemporal cortex are absent; on the other hand, the projection from the LB to area TG is light, whereas those to the inferotemporal cortex are heavy. These findings indicated that the characteristics of the amygdaloid connections with area TG is significantly different from those with the inferotemporal cortex.

The characteristic of the amygdaloid connections with area TEG is also...

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Fig. 2. Results from a representative case with HRP injection into area TEG. A: Locus and extent of injection site shown by shading on lateral view of standard left hemisphere and coronal brain sections. Marks of x and y above sections, section numbers. B: Distribution of anterogradely HRP-labeled terminals shown at four different rostrocaudal levels of amygdala. Section intervals, 1000 \( \mu \text{m} \). Dots represent labeled terminal distributions of projections. Numbers below sections, section numbers. C: Distribution of retrogradely HRP-labeled cells shows at eight different levels of amygdala. Section intervals, 500 \( \mu \text{m} \). Each dot represents one labeled cell.

In this case, slight diffusion of HRP into area TG was observed, and this resulted in light labeling in lateral nucleus (L) of amygdala.
TABLE 1. Distributions and relative densities of amygdaloid connections with temporal cortical areas

A. Amygdalopetal projections

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Relative densities of amygdalopetal projections were estimated on the basis of observation on relative intensities and extents of labeled terminals. Relative densities for amygdalofugal projections were determined by numerical evaluation; #, for more than about 500 labeled cells throughout the sections treated in the present study; #, for more than about 100 cells; +, for less than about 100 cells.

B. Amygdalofugal projection

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<thead>
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<th>Sources</th>
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different from those with areas TE and TEO. Both amygdalopetal and amygdalofugal connections with area TEG is heavier and more extensive than those with areas TE and TEO. The amygdalopetal projection to the LB from area TEG is heavier than that from area TE. Both terminal and origin sites of the densest amygdaloid projections with area TEG locate rostrally to those with area
There are light amygdalopetal projections to the AB and MB, whereas there are no projections from areas TE and TEO.

The distribution pattern of the amygdaloid connections with area TEO is also different from that with the other temporal areas. There is no amygdalopetal projection from area TEO. The amygdalofugal projection to area TEO arises from the LB only, and this projection is less heavy and less extensive than those to areas TE and TEG; no projection arises from the ventral LB. The origin of the densest amygdalofugal projection to area TEO locates dorsocaudally to that to area TE. There is no amygdaloid connection with the contralateral TEO, whereas there are both amygdalopetal and amygdalofugal projections with the contralateral TE, TEG and TG.

Area TEG is cytoarchitecturally a transitional area between areas TG and TE, and is considered long to belong area TG (Jones and Mishkin 1972). However, the above findings indicate that the characteristic of the amygdaloid connections with area TEG is significantly different from those with both TG and TE areas. Accordingly, area TEG is significantly different from those with both TG and TE areas. Accordingly, area TEG is an independent area, as area TEO is (for its functional significance, see Section 6). Also, area TEO is cytoarchitecturally a transitional area between areas TE and OA; previously, this area was considered to belong to area OA, but now is established anatomically and functionally as an independent area of both areas TE and OA (Iwai and Mishkin 1968, 1969; Umitsu and Iwai 1980).

Anatomical organization between amygdala and inferior temporal cortex

As mentioned above, while the amygdaloid projections to the respective inferotemporal areas are quantitatively different from each other, their distribution patterns appear qualitatively to be similar to each other; Three TEG, TE and TEO areas in common receive the amygdalofugal projections from the LB and send the amygdalopetal ones to the L, although there is no amygdalopetal projection from area TEO. Comparison of the findings indicates that there are two apparent trends concerning the caudorostral organization of the amygdaloid connections with the inferotemporal cortex (Fig. 1).

First, there is a clear gradient that the projections become progressively heavier and more extensive through the sequence of the projections to the caudal to rostral visual areas (from area TEO to area TEG). For the amygdalopetal connections, the respective projections to the L and the LB from area TEG are heavier and more extensive than those from area TE. For the amygdalofugal connections, the projections to the more rostral areas become successively heavier and wider by adding those from the more ventral and rostral segments of the LB to those from the more dorsal segments of the LB projecting to the more caudal areas. In addition, the connections with areas TEG and TE become extensive and heavy by adding the amygdalopetal projections to the LB, MB and AB and
Fig. 3. The summary of effects of various cortical lesions on discrimination learning on the same patterns (a plus sign pattern vs. an outline square pattern) tested in a modified WGTA (Wisconsin General Testing Apparatus). Lesion sites are indicated in black in each small brain chart below abscissa.

In a middle figure, findings on concurrent object discrimination learning by open circles with dashed line and serial object learning by open triangle with dotted line are shown. Notice double dissociation of deficits for pattern discrimination and concurrent object learning following ablations of areas TEO and TE. Pattern discrimination task is considered to be a kind of perceptual task, while concurrent learning task, an associative memory task; serial object learning task was employed as a control task for above two tasks.

Abbreviation: AIT; anterior inferotemporal, CeOA; central OA, CeOB; central OB, CePS; central prestriate, DEPS; dorsal extracentral prestriate, FEF; frontal eye field; FoSt; foveal striate, FPH; fusiform-parahippocampal-lingual, IC; inferior convexity, IP; inferior parietal, MaSt; macular striate, PIT; posterior inferotemporal, Pr; principal, SP; superior parietal, ST; Superior temporal, TP; temporal pole, VEPS; ventral extracentral prestriate.
the amygdalofugal projections from the AB and MB.

Second, there is an apparent trend that the terminations and origins of the densest amygdaloid projections shift successively from the caudal to the rostral segments of the amygdala through the sequence of the projections with the caudal to the rostral visual areas: The more rostral inferotemporal areas connect densely with the more rostral LB and L, and the more caudal visual areas, with the more caudal LB and L.

Role of inferotemporal cortex and amygdala in pattern discrimination learning

The above finding that there is the apparent caudorostral organization between the amygdala and inferotemporal cortex implies that the amygdala is involved closely in the cognitive mechanism. Also, the finding suggests that it is the terminal station in the cognitive system, as Rolls (1978) surmised. Before discussing the interaction mechanism between these two sites, we present our several findings regarding their functional significance obtained from the studies undertaken to examine the above inference.

It is well-known that bilateral ablations of inferotemporal cortex result in marked deficit on pattern discrimination (cf. Iwai 1980, 1982, 1985). A question is whether or not ablations of cortical areas and subcortical areas other than the inferotemporal cortex produce visual impairment as severely as that of the inferotemporal cortex does. Therefore, the effects of various lesions on the same pattern discrimination (a plus sign vs. an outline square) with the same procedure (go-left, go-right testing procedure) in a Wisconsin General Testing Apparatus (WGTA) were compared with each other.

The results from more than one hundred monkeys studied for these two decades are summarized in Fig. 3. As seen, the only lesions made for inferotemporal cortex produce marked deficit on pattern discrimination, whereas no lesions for the other areas and nuclei produce significant impairment. More important, even small lesions made within the inferotemporal cortex and even small encroachment of lesions into it result in significant impairment of pattern vision. The results indicate that among the cortical areas and subcortical nuclei, the inferotemporal cortex is involved most predominantly in pattern vision among the brain structures. It is mentioned, therefore, that the inferotemporal cortex is a critical or focal area for pattern vision.

Involvement of area TE and TEO in visual cognition

The above finding indicates that two areas, TEO and TE, in the inferotemporal cortex are concerned closely with pattern vision, whereas area TEG is not. More important, ablations of area TEO result in severer deficit on pattern discrimination than that of area TE does. This findings suggests that two areas, TEO and TE, are involved in vision in two different ways. We have succeeded in several studies to yield a double dissociation of deficits following ablations of these two
areas. For example, Fig. 4 shows the finding from a stimulus equivalence test for patterns. In the study, for the standard or training task was the discrimination of a plus sign vs. an outline square, and response to the plus pattern was rewarded (the positive, as in the studies shown in Fig. 3). The equivalence test employed in this study was a preference test to the upper and lower halves of the positive and negative standard patterns, and both responses to partial patterns were rewarded.

The results are presented in Fig. 4. As seen, in the first half stage of five test sessions, the subjects of the unoperated normal control group showed a consistent preference to the positive partial patterns, whereas in the second half stage, they extinguished this meaningless preference and responded to the positive and negative partial patterns at random. Monkeys with TEO lesions failed to show preference to the positive partial patterns through the whole test sessions. The subjects with TE lesions chose the positive partial patterns through the sessions, and they failed to extinguish this useless selection through the period of the equivalence test. From this finding and our other ones as well, it is mentioned that Area TEO is concerned closely with visual form perception of the objects, whereas area TE, with visual cognition and memory of the objects.
Response properties of inferotemporal neurons to patterns

A question is whether the above behavioral finding is supported from the neuron level. Therefore, we investigated the response properties of inferotemporal neurons to four standard patterns and to the components and variant patterns of the standard ones in relation to areas TE and TEO. The four standard patterns were a plus sign, an outline triangle, an outline square and an outline circle, which are employed in the behavioral studies in our laboratory.

Inferotemporal neurons have different response and receptive field properties from each other, as if they would play in different role in visual perception and cognition (Iwai 1980, 1985). About 10% of inferotemporal neurons are responsive to one particular pattern only (Type I neurons) and neither to the other patterns nor to the components. Here, the response properties of Type I neurons are described. More important, the responsiveness of Type I neurons in areas TE and TEO differs from each other. Fig. 5A and B present the response properties of neurons in areas TE and TEO, respectively, as representative cases. The responsiveness of the neurons in both areas is not affected by changing the physical factors of the response-eliciting pattern such as size, color and luminance etc. The properties of TE neurons appear to be relatively uniform: As seen in Fig. 5A, almost all are responsive to tilted patterns and partial patterns of the response-eliciting standard one. The finding suggests that these neurons concerned with the mechanism of stimulus categorization and thus memory.

On the other hand, the response properties of Type I neurons in area TEO are not necessarily uniform. Many of them are not responsive to variant patterns, as seen in Fig. 5B. Some neurons respond differentially to different sizes of the response-eliciting standard patterns. In addition, there are small number of neurons, which appear to concerned with a synthetic process of the components to a specific pattern. Although sufficient data have not been accumulated to discuss the neural mechanism of pattern vision from the neuron level, these findings indicate at least that the neurons in areas TE and TEO contribute differently to attaining pattern vision from each other: Perhaps, as found in behavioral studies, the latter neurons are concerned predominantly with achieving pattern perception, and the former one, with accomplishing pattern cognition and memory.

Involvement of area TEG in visual cognition

The finding that the distribution pattern of the amygdaloid connections with area TEG is entirely different from that with area TG, while it has common features, though only in part, with that with area TE (Table 1) implies that area TEG may belong to the visual cognitive system. On the other hand, as seen in Fig. 3, the finding that bilateral ablations of area TEG does not affect pattern discrimination learning (Fig. 3) suggests that area TEG is not directly involved in the visual cognitive mechanism.
Fig. 5. Representative PSTHs (peristimulus time histograms) of neurons responding to one particular pattern only (Type I neurons) and not to other patterns. 

A: Representative PSTHs of Type I neuron in area TE. This unit was responsive to standard, or training, “plus sign” pattern only. Notice that this neuron was responsive to plus patterns of enlarged and reduced sizes and variant pattern stimuli such as tilted (X) and partial ( and ) pattern stimuli of standard plus pattern, whereas unresponsive to components ( and ) of standard pattern.

B: Representative PSTHs of Type I neuron in area TEO. This neuron was responsive to standard outline triangle pattern only and unresponsive to the others. Notice that this neuron was unresponsive to variant patterns and components, but responsive to triangle patterns changed in size and luminance.
Pohl (1973) reported that monkeys with lesions of inferotemporal cortex showed significant impairment in object reversal learning. Jones and Mishkin (1972) demonstrated that large ablations of temporal polar cortex, which appear to include areas TG, TEG and amygdala, did not affect the retention of visual discrimination learning on a pair of objects, but significantly affected the reversal learning of prior learned habit. To investigate the contradiction between the behavioral and anatomical implications regarding the functional significance of area TEG, therefore, the effect of small lesion made within area TEG on the retention of preoperatively learned pattern discrimination and its reversal learning was compared with those of small lesions made within areas TE, TEO and OA.

The results are shown in Fig. 6. As seen, the subjects with lesions of area TEG did not show significant impairment in the retention of preoperatively learned pattern discrimination, confirming our previous finding. However, they showed significant impairment in reversal learning of the pattern discrimination as severely as the subjects with TE and TEO lesions did. More important, as seen in the figure, the ratio value of reversal learning score to relearning score of Group TEG was remarkably larger than those of Groups TE, TEO and OA, which were almost the same across the groups. Therefore, the finding by Jones and Mishkin may be attributed largely to lesion of area TEG.

The finding implies that area TEG is not concerned with pattern perception itself. Our anatomical finding demonstrates that among three inferotemporal areas, area TEG has the densest connections with the amygdala. These behavioral and anatomical findings indicate that area TEG is closely involved in visual cognition, particularly, in the mechanism of stimulus-reward association. Although we have not succeeded in demonstration of functional dissociation
across area TEG, TE and TEO, these three areas in the inferotemporal cortex may be concerned with vision in three different ways.

*Involvement of area TG in emotion and motivation*

The findings that the characteristics of the amygdaloid connections with area TG are significantly different from those with the inferotemporal areas suggest that the functional significance of the temporal polar cortex differs from that of the inferotemporal cortex: The temporal polar cortex does not belong to the visual cognitive system. This notion is supported by the present behavioral findings: Lesions, even small ones, of inferotemporal cortex produce marked impairment in pattern discrimination learning, whereas large ablations of temporal polar cortex result in no deficits of visual discriminations.

It is known that some aspects of the Klüver-Bucy syndrome occur after removal of any of these structures, and the effect is greater when more than one of these areas are damaged (Butter and Snyder 1972; Horel et al. 1975; Kling and Steklis 1976). Area TG connects preferentially with orbitofrontal and medial frontal cortices (Pandya and Kuypers 1969; our unpublished data), which connect with amygdala, and these cortices are closely involved in the cortical mechanism of emotional, motivational and social behavior (Butter and Snyder 1972; Kling and Steklis 1976; Thorpe et al. 1983).

Our findings and the previous reports mentioned above indicate, therefore, that the temporal polar cortex belongs to the system of emotion and motivation rather than to the cognitive system. On the other hand, area TG connects with inferotemporal cortex, too (Turner et al. 1980; our unpublished data). The temporal polar cortex or Area TG may be involved in emotional and motivational modulation for visual behavior through the interaction with the subcortical and cortical system of emotion and motivation.

*Role of inferotemporal cortex and amygdala in food discrimination*

The Klüver-Bucy syndrome produced by temporal lobectomy of macaques is well-established (Klüver and Bucy 1937, 1939), and it is seen regardless of animal species. The syndrome is a complex set of symptoms, and the amygdala is considered to be a critical site for the syndrome (Gloor 1960; Goddard 1964). The most fundamental behavioral change associated with the Klüver-Bucy syndrome is the psychic blindness. As seen in Fig. 3, however, damage to the amygdala does not result in deficit of pattern discrimination. This raises a question whether the amygdala is a site responsible for the psychic blindness.

The most drastic documentation regarding the psychic blindness is a so-called K-B sign, which is failure in discriminating foods from non-foods (inedible objects). The K-B sign test itself is a simple task, and even naive normal monkeys attain this task quickly without any training. Nevertheless, it is striking that monkeys with temporal lobectomy can not accomplish this task: They
touch, take and smell even the non-food, put them into their mouths and then discard them, as if they could only discriminate between edibles and inedibles orally by means of olfactory, gustatory and tactile sensation. The food itself involves a high incentive value, emotionally and motivationally, to evoke feeding behavior. Therefore, the negative finding on pattern discrimination following damage to the amygdala would be attributed to that the patterns themselves are not invested with a high incentive value. On the other hand, although there were some reports demonstrating that lesions of inferotemporal cortex did not result in the K-B sign (Akert et al. 1961), the effect of total inferotemporal cortex on the K-B sign test has not been studied yet. Accordingly, the effects of ablations of the total inferotemporal cortex and amygdala were compared with each other.

The results are shown in Fig. 7 by the curves of group mean percent choices of foods in the first five responses of test sessions. Monkeys with the amydaloid lesion selected foods and nonfoods at random during first several test sessions, but their choice of food improved through the testing, showing recovery from the sign. The subjects with total lesions of inferotemporal cortex also chose foods at the chance level, but little improvement was seen throughout the test sessions; more important, they still showed a significant K-B sign even three years after the surgery, suggesting that the sign must have been nearly permanent. On the other hand, neither lesion of an anterior inferotemporal cortex nor a posterior one, which

![Fig. 7. Curves of group mean percent choices of edibles (foods) in a K-B sign test. Curves denote lesion sites: (○—○), area TEO; (●—●), area TE; IT (▲—▲), total inferotemporal cortex; (▲—▲), amygdala; (×—×), unoperated normal control. For a test trial, five pieces of different foods and five small and different junk objects were arranged at random on test board of a WGTA. Subjects were tested in four trials in one day (a session) per week. Score in a trial was number of food selections in the first five responses to stimuli (foods and nonfoods), and a session score was mean percentage from the sum of four trial scores in a session test. They were tested until attaining the criterion of 90% food choices in a session. For failure, testing was conducted for seven weeks.](image_url)
was a partial lesion of inferotemporal cortex, did produce a significant sign.

The findings indicate that although the amygdala is involved significantly in
the cognitive mechanism, it is not the critical site responsible even for the
cognition of foods, and it may play a cognitive role subordinate to the infer-
otemporal cortex. The previous negative findings on K-B sign test following
inferotemporal lesions are attributed to partial lesions of the inferotemporal
cortex: The lesion of Akert et al. appears to be made for an anterior temporal
neocortex, including areas TG, TEG and TE.

Roles of inferotemporal cortex and amygdala in emotional and motivational
behavior

The above findings imply a possibility that the inferotemporal cortex is a
critical site responsible for the Klüver-Bucy syndrome instead of the amygdala,
because the lesions in the previous studies were not made for total inferotemporal
cortex. Therefore, we carefully investigated the presence and absence of the
Klüver-Bucy symptoms after total inferotemporal and amygdaloid lesions.

Table 2 indicates the summary of behavioral changes following ablations of
the amygdala and inferotemporal cortex. Against the expectation, the monkeys

| Table 2. Summary of Findings: Presence or absence of Klüver-Bucy syndrome following ablations of inferotemporal cortex and amygdala |
|----------------------------------|------------------|------------------|------------------|--------------------|
| Lesion sites                     | Amygdala         | Inferotemporal (IT) cortex |                 |                    |
|                                  |                  | Total IT | Area TE | Area TEO          |                    |
| On Klüver-Bucy symptoms          |                  |          |        |                  |                    |
| Psychic blindness (K-B sign)     |                  | #        | #      | ±                 | –                  |
| Oral tendency                    |                  | #        | #      | –                 | –                  |
| Hypermetamorphosis               |                  | +        | –      | –                 | –                  |
| Fear-loss, tameness and docility |                  | #        | –      | –                 | –                  |
| Hypersexuality                   |                  | +        | –      | –                 | –                  |
| Changes in dietary habits        |                  | +        | –      | –                 | –                  |
| Analgesia                        |                  | +        | –      | –                 | –                  |
| On deficit of discrimination learning |                |          |        |                  |                    |
| Deficit on a pair of objects     |                  | ±        | ±      | ±                 | –                  |
| Deficit on a pair of patterns    |                  | ±        | #      | #                 | #                  |

#, #, +, ±: presence of severe, moderate, mild, and slight or temporal symp-
toms, respectively. –: absence of symptom.

Findings on Klüver-Bucy symptoms other than K-B sign were based on informal
daily observation.
Role of Amygdala in Visual Cognition in Macaques

with total inferotemporal lesions never showed Klüver-Bucy symptoms other than
the psychic blindness and oral tendency. On the other hand, the subjects with
amygdaloid lesions showed more or less all symptoms. Therefore, the results from
the lesions made for the two sites confirm the previous reports: The present
findings show the dichotomy of emotional and cognitive mechanisms in relation
to the amygdala and inferotemporal cortex. Therefore, the findings support the
notion that the inferotemporal cortex is not a critical site for the emotional and
motivational mechanism, but for the cognitive one.

Role of amygdala in Matatabi-response in cats

The fundamental function of the amygdala remains still unclear. The most
prevailing view for this is that it is involved closely in the mechanism of control-
ling emotional and motivational behaviors rather than directly in that of the
innate behaviors by themselves (Gloor 1960; Gloor et al. 1981). However, there
has been no direct evidence in support of this notion yet. Although we have
undertaken to provide supporting evidence for this view and obtained several
interesting findings in understanding the function of the monkey amygdala, any
finding appears still to be too circumstantial to support the notion directly. More
direct evidence was obtained from the study on the cat amygdala.

It is well-known that the Matatabi substance (Actinidia polygama, Japanese
plant) is very attractive and potent for cats, and is considered as a so-called
aphrodisiac one for this animal. When the Matatabi is presented, cats respond to
it quickly and are fascinated by it (Matatabi response), as if they were in an
ecstatic status (Sakan 1967). Therefore, the Matatabi response is an adequate and
sensitive index for studying emotional and motivational behavior in cats.

It is observed that a small number (about 5%) of cats hardly show Matatabi
response, although they show manifest response to the Matatabi during the mating
season. Therefore, the lack of this response appears to be due to a strong inhibi-
tory control for the evocation of their Matatabi response behavior. Unilateral
lesion of the animal amygdala does never produce the Klüver-Bucy syndrome
(Klüver and Bucy 1937, 1939; Gloor 1960). If the amygdala is concerned closely
with the inhibitory control of emotional and motivational behaviors, even unilat-
eral lesion for the amygdala of the cats showing no Matatabi response would make
their Matatabi response manifest, whereas it would evince no clear Klüver-Bucy
syndrome.

In the study, a branch of Matatabi was displayed about 15 to 20 cm in front
of cats. The presence of Matatabi response was determined when cats approached
quickly to and bit a Matatabi branch within a several minutes after its presenta-
tion and showed fascinating behavior. If cats failed to show the response in eight
out of 10 consecutive trials of Matatabi presentations in a day, they were designat-
ed to the cats with no Matatabi-response. On this behavioral criterion, we have
found three cats showing no Matatabi-response.
The results from the study on the effect of unilateral lesion of the cat amygdala on the Matatabi response is shown in Fig. 7B. After unilateral amygdalectomy (Fig. 7A), all three cats showed manifest Matatabi response as manifestly as normal cats did. On the other hand, unilateral lesion for the amygdala of the cats with Matatabi response did neither affected nor changed their response.

Fig. 8. The effect of unilateral amygdalectomy on Matatabi response in cats. A: Representative brain reconstructions with lateral view of right hemisphere and their cross sections. Loci and extents of lesions are indicated in black. Preoperatively, NR-cat 3 did show an unmanifested Matatabi response (see Fig. B), while R-cat 1 showed a manifest response. B: Individual preoperative and postoperative response charts to Matatabi in cats with no Matatabi response. Response and No response denote appearance and absence of Matatabi behavior in behavioral criterion, respectively (for criterion, see text). Abscissae show time courses by days from first testing in preoperative stage and from surgery in postoperative stage. Preoperatively, NR-cat 1 was tested for long series with longer intervals, to examine a question whether effect of amygdalectomy on Matatabi response was influenced by learning experience and different preoperative testing schedule.
Both cats with and without Matatabi response showed no Klüver-Bucy symptoms after unilateral lesions of the amygdala, whereas both of them evinced clear Klüver-Bucy syndrome after the contralateral amygdalectomy made in second stage of operation. The findings indicate that the cat amygdala is involved in the inhibitory control for the evocation of emotional and motivational behaviors.

The notion that the monkey amygdala is concerned with the control of emotion and motivation is consistent with the anatomical evidence. The amygdala has strong reciprocal innervations with the hypothalamus, substantia innominata and brainstem (Aggleton et al. 1980; Price and Amaral 1981; Russchen et al. 1985), which are concerned with the subcortical mechanisms of emotion and motivation, and also reciprocal connections with the temporal polar, insular, orbitofrontal and medial frontal cortices (Aggleton et al. 1980; Turner et al. 1980; Mufson et al. 1981; Porrino et al. 1981; Amaral and Price 1984), which are concerned with the cortical mechanisms of emotion and motivation (Butter and Snyder 1972).

Consideration on mechanisms of visual amygdalo-cortical interactions

The present finding indicates that the inferotemporal cortex and the amygdala interact each other in multiple ways: There would be at least more than three interaction mechanisms. The major amygdaloid input nucleus from the inferotemporal cortex is the L and the major output nucleus to it is the LB. The intrinsic connections across the amygdaloid nuclei of monkeys have not been detailed yet. According to a recent report of Aggleton (1985; refer to Fig. 9B), there is no direct intrinsic connection between the L and the LB: The L sends intrinsic output widely to the amygdaloid nuclei other than the LB and MB, whereas it receives no intrinsic input from any amygdaloid nucleus; on the other hand, the LB receives input mainly from the Ce, which receives intrinsic input from almost all amygdaloid nuclei. Thus, the present finding of the separation of the major amygdaloid input and output nuclei suggests that the input to the L from the inferotemporal cortex arrives at the LB after extensive communication across the amygdaloid nuclei. As mentioned before (refer to Sections 8 and 12), the amygdala has strong connections with the cortical and subcortical systems of emotion and motivation. Therefore, the incoming visual information to the L evokes emotional and motivational mechanisms, and the LB returns the information coded in the amygdala to the visual areas.

The present anatomical study also demonstrates that there are minor amygdalopetal projections from areas TEG and TE to the dorsal LB and minor amygdalfugal one from the AB to these areas of TEG and TE. In addition to the above major interaction mechanism, therefore, there would be at least two more interaction mechanisms through shorter circuits than that for the above major one. One of them depends on the circuit that the information reaching the L is sent to the AB (Aggleton 1985), from which the information is returned to areas TEG and
TE. A third interaction depends on the reciprocal innervations between the LB and areas TEG and TE. Although the third one implies direct interaction, it is unlikely that the only LB among the amygdaloid nuclei is involved in the interaction mechanism with the inferotemporal cortex, because the projection from the inferotemporal cortex to the LB is a minor one and terminates at the dorsal LB only.

As mentioned before, the effect of damage to the amygdala depends on prior learning experience: Lesions of the amygdala affect little the retention of previously learned habits, but significantly affect the acquisition of learning (Iwai 1982; Mishkin 1982; Iwai et al. 1986) Therefore, the three different interaction mechanisms mentioned above may act differentially according to prior learning experience.
Two-channel model of visual information processing in inferotemporal cortex

There is a model regarding the cortical system of visual information processing (Mishkin 1972; Rolls 1978; Turner et al. 1980; Iwai 1982; Squire and Zole-Morgan 1983). The visual information arriving at striate cortex is transmitted serially to the amygdala via prestriate cortex and inferotemporal cortex: the amygdala appreciates the information as a meaningful one. The present study demonstrates that the distributions of the origin cells of amygdalofugal projections to the inferotemporal cortex are much heavier, more widespread and more complex than those of the terminals of amygdalopetal ones from the inferotemporal cortex. Our recent studies demonstrated that while there are no amygdalopetal projections from visual cortical areas of TEO, OA, OB and OC (Turner et al. 1980), there are the amygdalofugal ones to these areas (Mizuno et al. 1981; Tigges et al. 1982; Amaral and Price 1984). These findings indicate that the feedback mechanism from the amygdala to the visual areas plays an important role in the visual cognitive system of information processing. Thus, the amygdala is no longer the terminal station in the cognitive system.

On the basis of the above findings, it is proposed that there are two channels in the inferotemporal cortex for processing of visual information: A first channel is concerned with processing neutral visual information; the second one, with processing emotionally and motivationally meaningful information coded in the amygdala (refer to two rows shown by arrows in the visual cortical areas in Fig. 9A). The neutral visual information received at the retina is sent to the striate cortex, and it is sequentially processed through transmission of it from the striate cortex to areas TE and TEG via prestriate cortex (areas OB and OA) and area TEO. This neutral information highly processed in the visual cortex reaches the L of amygdala from the inferotemporal cortex. Then, it is sent to the other amygdaloid nuclei to be attached with emotional and motivational significance through the interaction with the cortical and subcortical systems of emotion and motivation. Finally, the meaningful information coded in the amygdala is returned from the LB to the visual cortical areas to be re-processed through the second channel. On this way, the visual information received at the retina as neutral one is consciously perceived in area TEO and cognized, recognized and memorized in areas TE and TEG (Iwai 1982).

References


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