

THE EFFECT OF RESECTIONS OF THE INFEROTEMPORAL CORTEX OR THE AMYGDALA ON VISUAL ORIENTING AND HABITUATION

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Abstract—Visual orienting and its habituation were studied by means of an eye-camera technique in monkeys with bilateral inferotemporal or amygdala resections. The number of observing responses emitted was increased by inferotemporal lesions and drastically curtailed by amygdalectomy. By contrast, the change in the distribution of observing responses when the orienting stimulus was displayed was no different in inferotemporally lesioned monkeys and in the controls but orienting was abolished by amygdalectomy. These results are discussed in terms of an analysis of attention into a selective and an intensive component.

IN A RECENTLY published report we analyzed, by means of an eye camera, MACKWORTH [1], the observing responses of monkeys with bilateral inferotemporal cortex resections. These animals, who are severely impaired in visually guided instrumental behavior, PRIBRAM [2], were no different from unoperated controls in the proportion of eye fixations directed to stimulus figures rather than to background. However, selective observation of one figure out of two on the basis of differential reinforcement was absent in these brain-operated monkeys.

The present study reports an additional analysis of the observing responses of monkeys with partial ablations of the temporal lobe. With regard to lesions of the inferotemporal cortex the question is asked whether such ablations affect the visual selection of one of a group of figures when selection does not depend on differential reinforcement. A situation was chosen in which visual orienting and its habituation could be measured, MACKWORTH and OTTO [3]. Additionally, the opportunity was taken to include investigation of the effects of another temporal lobe lesion, bilateral resection of the amygdala, on visual orienting. This opportunity was welcome because in our laboratory amygdalectomy had been shown to interfere in a complex fashion with orienting and its habituation. GSR and cardiac orienting reactions are depressed, BAGSHAW, KIMBLE and PRIBRAM [4]; BAGSHAW and BENZIES [5] while behavioral indicators of orienting (and certain aspects of the EEG) while present, fail to habituate in the time course shown by control subjects, BAGSHAW and BENZIES [5].

METHOD

Subjects

Three groups of naive preadolescent rhesus monkeys were used. Group N ($N=5$) were unoperated controls. Group IT ($N=4$) sustained bilateral inferotemporal cortex ablations and Group AM ($N=4$) had bilateral resections of the amygdala. All training was given postoperatively.

Histology and surgery

The inferotemporal lobe lesions have been published previously, BAGSHAW, MACKWORTH and PRIBRAM, [6]. The amygdala lesions are shown in Fig. 1. Bilateral suction ablation in a single surgical procedure was the technique used and is described in detail in an already published article, BAGSHAW, KIMBLE and PRIBRAM [4].

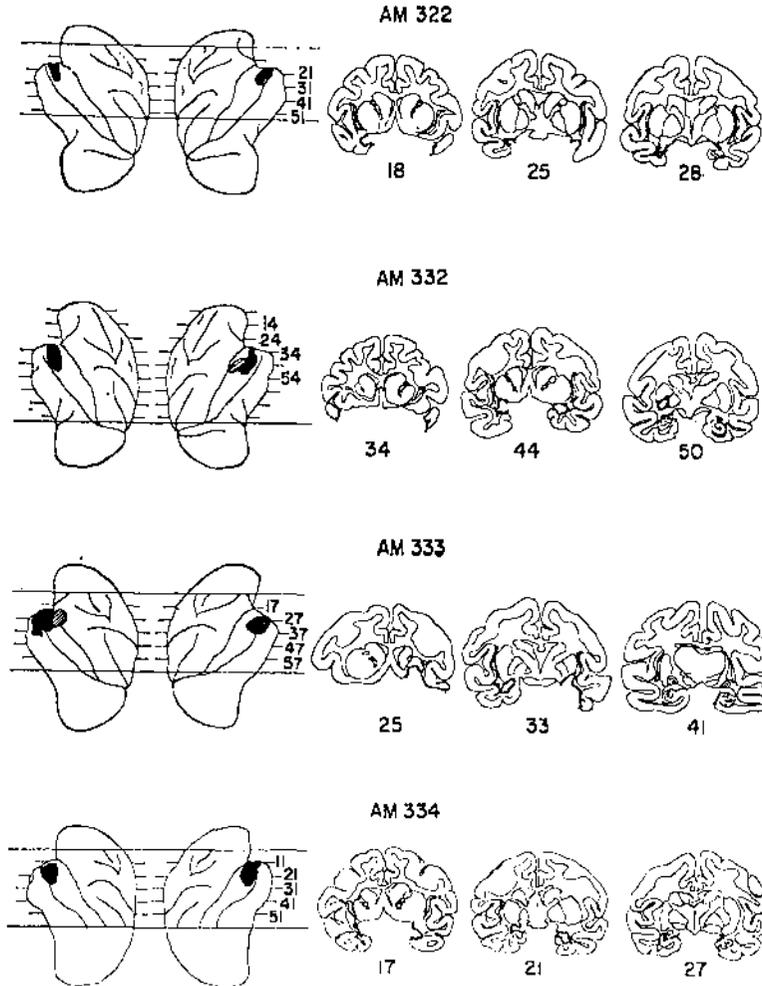


Fig. 1. Reconstruction of bilateral lesions of the amygdala projected onto the lateral surface of the temporal lobes. Cross-hatched areas denote extension of the lesion into the putamen.

Apparatus

Details of the adaptation of the reflection eye camera apparatus for animal work have been reported, BAGSHAW, MACKWORTH and PRIBRAM [7]. It consists of an animal chamber which contains the unrestrained monkey and allows him access to view outside only through an opening slightly larger than the eye, in the right eye region of a face mask fitted into one wall. This chamber is attached to the camera and display chamber so that the eye area of the mask is $16\frac{1}{2}$ in. from a backlighted 10 in. \times 10 in. transparency (Fig. 3). Appropriate optics, using a half-silvered mirror, allows the image of the right eye (with the reflection of the display upon it) to be photographed with a top-mounted Beaulieu 16 mm movie camera at a speed of 5 frames per sec. using Kodak film # 2475. Fiber optic cables aimed at the inner and outer canthi of the right eye cutout of the mask provide incident light. A rotating disc with two quadrants cut out serves as a shutter to start and stop the trials by alternately covering and opening the eye peephole.

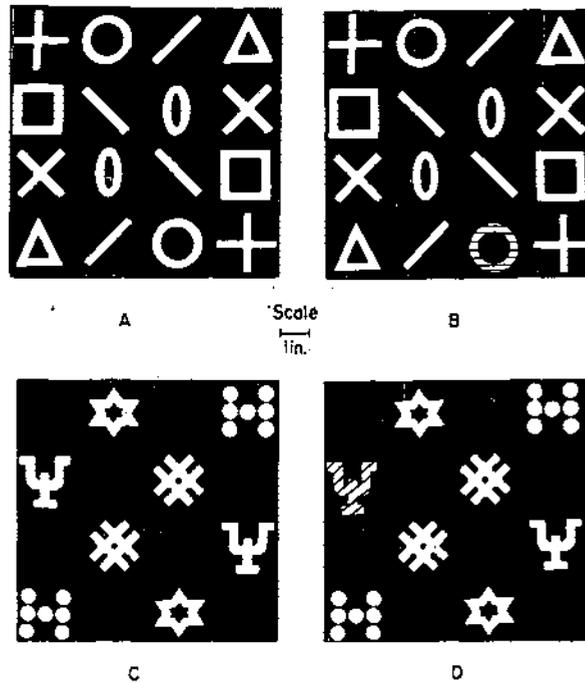


FIG. 2. Stimulus arrays used in the present experiments. (A and B) in experiments I and 11, and (C and D) in experiment III. Horizontal lines in B denote a red filter, slanted lines in D denote a green filter.

Stimuli

Control condition—10 in. x 10 in. transparencies of arrays of clear geometric figures (each 2 inches high) on a black opaque background were prepared. When backlighted in the camera chamber the figures appeared bright white. One array consisted of simple geometric figures (A in Fig. 2), and a second of more complex figures (C in Fig. 2) symmetrically placed over 16 possible locations.

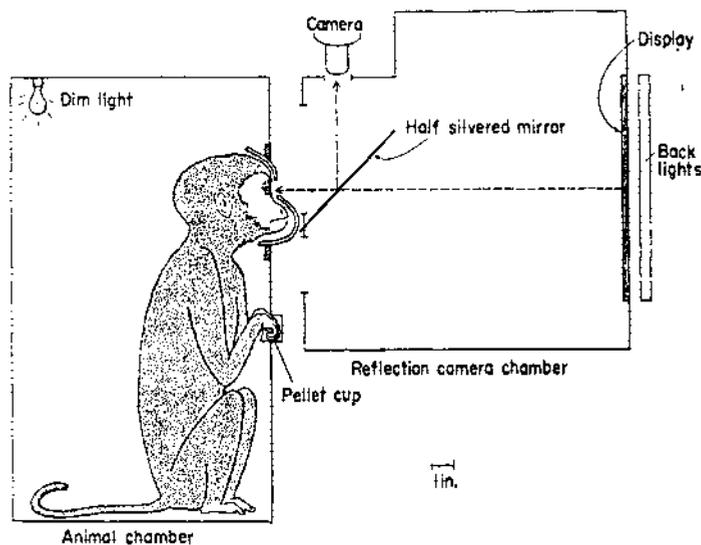


FIG. 3. Diagram of the recording apparatus and animal chamber.

Novel condition—One figure, a circle (either upper or lower) was colored with a red filter in Experiment 1, lower, (B in Fig. 2) and Experiment 2, upper. The upper psi was similarly treated using a green filter in Experiment 2 (D in Fig. 2).

Procedure

To shape viewing through the eye port, all Ss were trained to observe a 10 in. \times 10 in. photograph of an adult rhesus monkey with a reward for viewing at least 3 sec of a 5 sec trial period.

Then the experimental stimuli were presented, one session for each experiment session consisted of 40 trials, each trial was 5 sec in duration. On the first ten and last ten trials of each session, the uncolored (control) stimulus array was used; on Trials 11-30 the corresponding stimulus array with one item colored was presented.

Data analysis

Film negatives were read frame by frame. The film was enlarged with a Visopan microscope and the frame was recorded if the eye was recognizable, even if out of focus. The location of the center of the pupil was recorded according to its position on the display (in one of 16 locations in a 4 \times 4 matrix of the original 10 in. \times 10 in. display). If the pupil was not centered somewhere on the display it was called either "off display" or "not readable" (if out of focus). These data were tabulated with the aid of a PDP-8 computer. Print-out consisted of raw totals and proportions of the above categories tabulated for single trials and for five trial blocks. A separate tabulation of runs of frames in each of the 16 locations "on display" was also printed out.

The data were then analyzed, in-5 or 10 trial blocks, first for the overall number and distribution of the fixations off and on the stimuli, and secondly, for the specific distribution among the stimuli of the fixation on the display.

All analysis of fixations on specific stimuli were done on a standard sample, i.e. the first five fixations in each trial. For Ss with fewer than 200 appropriate fixations per session only those with at least 100 frames were included.

RESULTS

The two types of measures, overall distribution of total eye positions and distribution of fixations on specific stimuli are presented separately.

1. *Overall distribution*

Group IT had 50 per cent more *total frames* than the controls throughout the three experiments, but the proportion of "unreadable", "off display" and "on display" fixations was always the same as for the controls. Group AM, on the other hand, accumulated the same number of total frames as controls, but they had markedly higher proportions of frames "unreadable", in the sense of out-of-focus eye pictures. These findings are shown in Fig. 4 where the total number of frames recorded are shown for each of the three groups for the three experiments. The clear portion of each bar represents out of focus, "unreadable" frames; the shaded portion, fixations "off display"; and the black portion fixations "on display". Each bar represents one 10-trial block. Note that Group AM still consistently shows fewer fixations "on display" compared to the control group, even in the third experiment, whereas Group IT shows consistently more. Two tailed U tests bear out these differences (Table 1).

2. *Distribution of fixations on specific stimuli*

Figure 5 illustrates the shift in gaze towards the stimulus to which color was added (Trial Block 3) in the three experiments. This orienting to novelty was present for all Ss in both the control and inferotemporal groups. The novel stimulus gathered 30 per cent (24 per cent above chance level) of the fixations in the first five novelty trials in Experiments 1 and 2. Habituation occurred at varying rates but was clearcut in all Ss by Trial Block 5. By contrast, none of the amygdallectomized group showed any orienting to the novel stimulus. In Experiments 1 and 2 there were insufficient Group AM fixations to demonstrate this quantitatively; however, available data gave results qualitatively similar to those shown for Group AM in Experiment 3.

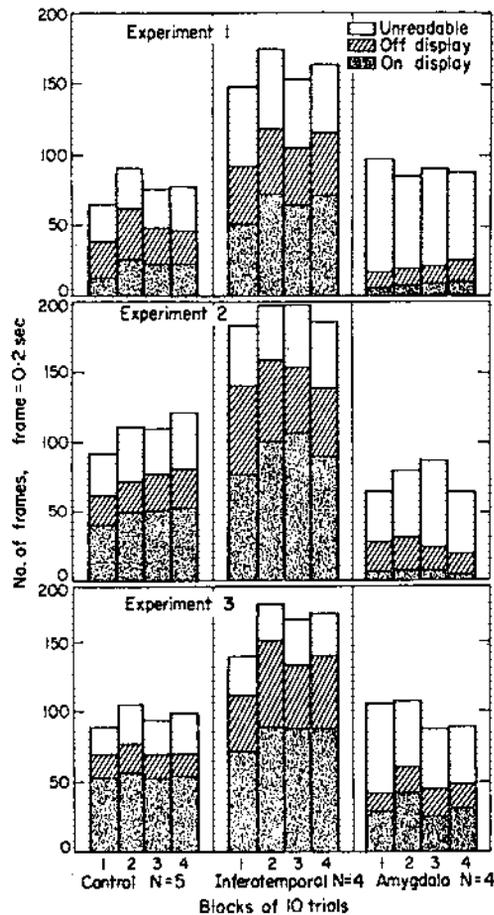


FIG. 4. Overall distribution of visual fixations for control, IT, and AM Groups in the three experiments. The addition of a colored filter occurred in trial blocks 2 and 3. Note that the novel condition does not change the characteristic scanning patterns of any group.

In addition to the number of fixations, the *duration* of fixations on the "novel" figure increased for all Ss in the control and IT groups, but was unchanged in Group AM. Similarly for the control and IT groups the proportion of fixations on preferred stimuli dropped markedly with the introduction of the color and returned as habituation occurred. Again Group AM did not show this effect.

DISCUSSION

The two temporal lobe lesions studied in this experiment produce two opposite effects on visual orienting behavior. The inferotemporal cortex lesion (which so dramatically disrupts discrimination learning dependent on reinforcement) does not disrupt visual

Table 1. Overall distribution of eye positions

Expt. 1		Expt. 2		Expt. 3	
		Total frames			
<i>(p value compared to Grp. N; 2 tailed U test)</i>					
N	301	437		386	
IT	660 (0.016)	768 (0.024)		653 (0.024)	
AM	362	295		391	
<i>Frames on display</i>					
N	92	194		214	
IT	261 (0.036)	372 (0.036)		334 (0.036)	
AM	34 (0.072)	28 *(0.036)		124 (0.072)	
<i>Per cent total frames unreadable</i>					
N	37%	31%		25%	
IT	31%	25%		19%	
AM	77% (0.036)	63% (0.072)		57% (0.072)	
<i>Per cent readable frames on display</i>					
N	51%	59%		72%	
IT	58%	63%		65%	
AM	35% (0.072)	27% (0.072)		56%	

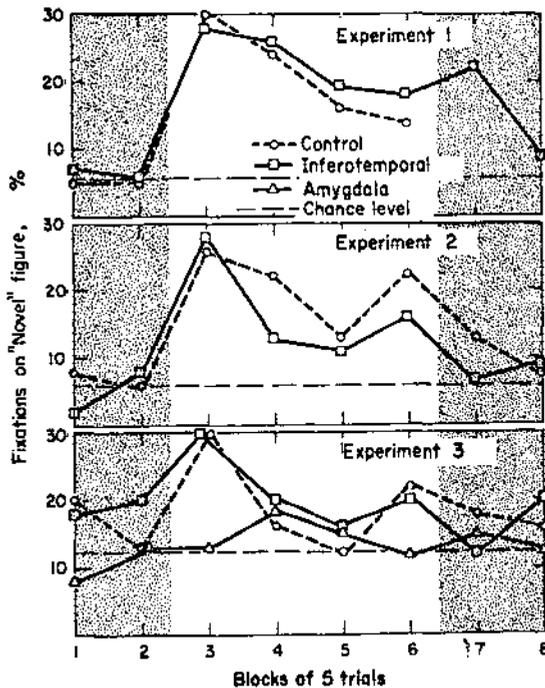


FIG. 5. Proportion of fixations "on display" which were located on one stimulus before, during and after addition of color to that stimulus in each of three experiments.

orienting to one of a group of stimuli. However, the total amount of observing time spent by these monkeys at the eyepoint is increased. By contrast, the amygdala lesion (which minimally affects discrimination performance) interferes dramatically with visual orienting. Performance in this "free choice" situation appears to be diffuse and aimless, with most of the time spent in rapid shifts of eyes or head, resulting in virtually no observing behavior directed to the stimuli.

Perhaps the simplest interpretation of these results is in terms of attention. BERLYNE [8] for instance, distinguishes between (1) "the *intensive* aspects [of attentive behavior] which are a matter of how much attention the organism is giving to the stimulus field as a whole" and (2) "*selective phenomena*, which are a matter of how attention is distributed among elements of the stimulus field". The monkeys with IT lesions appear to have no difficulty with the *intensive* aspects, i.e. they attend to the stimulus array and to novelty: in fact, these monkeys are almost compulsively persistent in viewing the stimuli through the viewing port and their manner of viewing is (except for the increased amount) indistinguishable from that of the normal monkey. Amygdalectomy, on the other hand, practically abolishes the intensive aspect of observing behavior.

These results stand in sharp contrast to those obtained when reinforcement guides visual behavior. Stimulus *selection* through reinforcement is drastically impaired by inferotemporal lesions not by amygdalectomy: this holds for both instrumental, PRIBRAM [1] and observing, BAGSHAW, MACKWORTH and PRIBRAM [6] responses.

These results may provide an explanation for a set of apparently discrepant data obtained on monkeys with inferotemporal resections. PRIBRAM [2] and BUTTER [9] found that monkeys with such lesions sampled fewer of an array of stimulus objects and of features characterizing any particular display to be discriminated. OSCAR-BERMAN, HEYWOOD and GROSS [10] and GROSS, COWEY and MANNING [11] on the other hand, suggested on the basis of their experiments, that inferotemporal lesions increased sampling behavior. This suggestion appears to be supported by the results of the current study using the eye camera. The discrepancy is resolved by making a distinction between a general increase in randomly distributed sampling (an increase in vigilance, in the intensive aspects of attention) and the selective sampling on the basis of reinforcement of cues and features that is necessary to making a discriminative choice. Only this selective aspect of attention is disturbed by inferotemporal lesions.

Using evoked potential techniques, other studies from our laboratories have demonstrated the involvement of the inferotemporal cortex in attentional processes, GERBRANDT, SPINELLI and PRIBRAM [12]; ROTHBLAT and PRIBRAM [13]. Taken together with the results of the present experiments, the conclusion can be reached that two forms of attention have been dissociated. One form, served by the inferotemporal cortex, is selective of stimulus features, and is fundamental to discrimination learning. The other form of attention is intensive, is akin to vigilance, MACKWORTH [14], is based on the ability to process novelty and is served by the amygdala and related structures (e.g. the anterior frontal cortex, LURIA, PRIBRAM and HOMSKAYA [15]; KIMBLE, BAGSHAW and PRIBRAM [16]).

In an earlier series of experiments we had in a similar manner "doubly dissociated" by the same temporal lobe lesions, the behavioral processes of stimulus generalization (subserved by IT cortex) and transfer of training (subserved by amygdala), BAGSHAW and PRIBRAM [17]; HEARST and PRIBRAM [18]; HEARST and PRIBRAM [19]. The current studies show evidence that these same structures dissociate the selective and intensive aspects of attention and suggest that there may in fact be a relationship between these two forms of

attention and the two behavioral processes. The relationship is fairly obvious in the case of selective attention: discrimination and generalization involve stimulus selection. In the case of the intensive aspects of attention, however, the relationship appears, at first, counter-intuitive: the suggestion is that transfer of training is based on the intensive properties of attention. When examined in detail, this suggestion is not as far fetched as it initially seems. Amygdectomized monkeys fail to transfer because of their abnormal processing of novelty, SCHWARTZBAUM and PRIBRAM [20]; DOUGLAS [21]. The problem in vigilance is to counter habituation, MACKWORTH [22]. Orienting to novelty and habituation to the familiar are recorded by the same psychophysiological indicators as is arousal (GSR, heart and respiratory rate changes, plethysmography and EEG activation). Thus the relationship between arousal and orienting stems from the very measures used to determine their occurrence. This common rooting in data led to the suggestion, PRIBRAM [23, 24] that the intensive (arousal) aspects of attention were not based on some general formless neural facilitatory process but resulted from a mismatch between structured neural configurations (the familiar memory trace and the current input) to produce orienting to novelty. Thus, the term "directive" attention ("interest") is more appropriate than the ordinarily used "intensive". The results of the current experiment reported here, on the basis of entirely different procedures, support this suggestion.

In what crucial way then do selective and intensive/directive attention differ? The results of the experiment reported earlier found monkeys with inferotemporal cortex resections deficient in selectively observing one of two reinforced cues. In the current experiment such subjects were found unimpaired in their observing responses to novelty. Selective attention is thus shown independent of novelty and familiarity but dependent on the salience (reinforcement history, in this case) of cues, a result that has repeatedly puzzled attention theorists (e.g. see discussion by TRABASSO and BOWER [25]).

Conversely, amygdectomy does not seriously interfere with discrimination learning, SCHWARTZBAUM and PRIBRAM [20] but does alter observing and other responses to novelty and familiarity. The results of the current experiment suggest that this difficulty is due to a failure to emit a sufficient number (intensive) of focused (directive) observing responses. It is as if these monkeys fail to take the decision to make observing responses, and suggests the possibility of recourse to decision theory for clarification of the distinction between selective and intensive/directive attention. JANE MACKWORTH [22, 26] has thoroughly reviewed the relationship between vigilance, (intensive/directive) attention and decision theory (see especially MACKWORTH, 1970, p. 85). In a set of studies, PRIBRAM, DOUGLAS and PRIBRAM [27]; SPEVACK and PRIBRAM [28, 29] an analysis was made of the effects on attention of partial temporal lobe lesions (similar to those used in the current study) in terms of hypothesis testing and Receiver Operating Characteristics (ROC curves). These studies showed that limbic lesions such as amygdectomy influenced response bias (setting a criterion for attempting responses) while inferotemporal cortex resections influenced the discriminability (detectability) of cues. From these results the conclusion can be broached that selective aspects of attention deal with cue distinctiveness, LAWRENCE [30] while the intensive/directive aspects deal with response bias, the setting of criteria for performance.

In summary then, resections of the inferotemporal cortex are believed to affect the selective attention necessary to discrimination and stimulus generalization by influencing the organism's ability to choose among cues. Resections of the amygdala, on the other hand, affect the intensive/directive aspects of attention necessary to the reactions to novelty and familiarity involved in orienting, habituation and transfer of training. This effect of

amygdalectomy apparently comes about by altering response bias, the criterion which the organism sets for his responsiveness in the situation.

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Résumé—L'orientation visuelle et son habitude ont été étudiées au moyen d'une caméra oculaire chez des singes ayant subi des résections bilatérales inférotemporales ou amygdaliennes. Le nombre des réponses d'observation augmentait après lésion inférotemporale et était réduit de façon très marquée par l'amygdalectomie. En contraste, la modification de distribution des réponses d'observation lors de la présentation du stimulus d'orientation, ne montrait pas de différence entre les singes avec lésion inférotemporale et les contrôles mais l'orientation était abolie par l'amygdalectomie. On discute ces résultats en fonction d'une analyse de l'attention selon ses composantes de sélection et d'intensité.

Zusammenfassung—Die optische Orientierung und Anpassung wurde bei Affen mit Hilfe einer Augenkamera untersucht. Bei den Tieren waren entweder temporobasale Bereiche oder die Amygdala reseziert worden. Die Zahl beobachteter Antworten stieg bei temporobasalen Läsionen an und war bei amygdalaektomierten Tieren erheblich verringert. Im Gegensatz dazu war der Wechsel der beobachteten Antworten bei temporobasalen und Kontrollgruppen nicht verschieden, wenn der Orientierungsreiz betont wurde. Die Orientierung an sich war bei Amygdalageschädigten aufgehoben. Die Resultate wurden unter dem Gesichtspunkt diskutiert, daß die Aufmerksamkeit in eine distraktive und konzentrierte Komponente zerfällt.