Coding of visual patterns and textures in monkey inferior temporal cortex

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Neural coding for texture features of visual objects was investigated in monkey inferior temporal cortex by inactivating intrinsic GABAergic inhibition. The inactivation enabled a substantial number of cells to respond to originally ineffective texture pattern that had a particular feature distinct from the originally effective pattern, or to ineffective texture and non-texture stimuli that possessed a component feature of the originally effective texture. Cells that showed selectivity changes related to a texture feature were often met along a vertical recording track. We suggest that a texture feature is coded by a group of cells which signal different aspects of the texture. The coding occurs at different processing levels, from extracting a particular feature within patterns to detecting complex texture features combined with color and shape of natural objects. *NeuroReport* 14:453–457 © 2003 Lippincott Williams & Wilkins.

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INTRODUCTION

Texture is a surface property of an object characterized by the regular occurrence of a pattern (granular structure) over a region of its surface [1,2]. Natural scenes contain ample textures that provide rich information about visual objects and the environment. Texture patterns, such as the gratings on a fence, and complex texture features, such as the granularity and arrangement of grains on the surface of a melon, convey visual information regarding the important aspects of object surfaces. Discrimination, recognition and memory of visual objects can be greatly facilitated by texture cues [1,2]. The inferior temporal cortex of the primate brain is important for object discrimination, recognition and memory [3–6]. A population of cells in the cortex selectively responds to texture or a combination of texture with shape and/or color [7]. The property of texture responses, however, was investigated in detail only with the simple pattern stimuli [8,9]. The mechanism responsible for generating this complex selectivity remains unknown. We have recently shown that blockade of GABA-mediated inhibition by microiontophoretically applying a $GABA_A$ receptor antagonist, bicuculline methiodide (Bic), is a powerful tool in dissection of the machinery underlying object feature selectivity [10,11]. We applied this technique to functionally characterized texture-selective cells in area TE of macaque inferior temporal cortex and investigated the mechanisms responsible for constructing texture selectivity of the cells.

MATERIALS AND METHODS

Animal preparation: The general experimental procedures were described elsewhere [11]. All surgical and animal care procedures complied with the guidelines of the National Institutes of Health (1996), and were approved and monitored by the animal experiment committee of Osaka University Medical School. Recordings were made in the dorsal part of area TE (A5–18) lateral to the anterior middle temporal sulcus in three monkeys (*Macaca fuscata*). The monkeys were initially anesthetized with ketamine (10 mg/kg, i.m.) and atropine (0.25 mg, i.m.). During the recording, the monkeys were immobilized with pancuronium bromide (0.02–0.04 mg/kg/h, i.v.) and anesthesia was maintained with a mixture of N_2O and O_2 (7:3) and 0.5–1.0% isoflurane. The electrocardiogram and expired CO_2 level (4.0–4.5%) were monitored throughout the duration of the experiment. Body temperature was maintained at 37–38°C.

Visual stimuli: We first searched for stimuli that activated cells at local regions (1–1.5 × 1–1.5 mm) in area TE using a

single metal electrode. We made a set of stimuli (25–45) for the regions by choosing the effective and ineffective stimuli. Texture stimuli included simple patterns, such as straight gratings, a line or an array of dots; composite patterns, such as a grid, concentric squares or circles; and complex natural textures, such as photographs of a pineapple, a melon, and a zebra. By component features of a composite texture pattern, we meant that, for example, the component features of a grid are straight vertical, horizontal gratings and an array of dots. For a complex natural stimulus such as a pineapple, its component features are an array of dots, a grid, colors, and the ellipse-like shape with protrusions in the top. Stimuli ($4 \times 4^{\circ}$) were presented to the contralateral eye for 1 s at 0.5–0.67 Hz on a CRT monitor.

Microiontophoresis: Triple-barreled glass-coated tungsten microelectrodes were used for unit recording and iontophoretic application of Bic [10,12]. One of the two glass barrels was filled with 2.5 or 5 mM Bic in saline (pH 3.5), and the other with 0.9% NaCl (vehicle, pH 3.5) to act as a control and provide a balancing current. Bic was ejected with a low-intensity current (+1–5 nA). When Bic was not administered, a retaining current of −15 to −30 nA was used to prevent leakage. Usually, the effects of Bic on visual responses of a cell were tested after Bic had been applied for 5 min, and recovery data were obtained ≥ 5–10 min after Bic delivery was stopped.

Data analyses: Net visual responses were obtained by subtracting the spontaneous firing rate measured 0.5 s before stimulus presentation from the firing rate during stimulus presentation (1 s) averaged over 10 repetitions. Two-way ANOVA (visual stimulus condition *vs* drug condition) was applied to the net responses evoked by one stimulus set before and during Bic application to detect the effects of Bic, or to those before and after Bic application to assess the recovery from the effects.

RESULTS

We recorded 215 TE neurons. Visual responses of 168 cells of them were examined successfully before, during and after Bic application. All 168 cells showed selective responses (ANOVA, stimulus factor, $p < 0.05$) to some stimuli in a set that was determined in pilot experiments on the recording regions. Of the 168 cells, 29% (48) responded to at least one texture stimulus under normal conditions (*t*-test, $p < 0.05$). Among these, 79% (38/48) displayed significantly increased responses to some texture stimuli during Bic application (*t*-test, $p < 0.05$) relative to before Bic application. Bic induced 84% of this group of cells (32/38) to respond ($p < 0.05$) to ineffective texture stimuli, or ineffective non-texture stimuli that had a feature related to an originally effective texture. Ten of the 168 cells (6%) responded to texture stimuli only upon Bic application ($p < 0.05$). Application of a pH-matched vehicle did not affect firing in any of the tested cells. Responses returned to baseline when Bic application was stopped (both drug factor and drug × stimulus interaction, $p > 0.05$). The effects can thus be attributed to the blockade of GABAergic synapses.

The disinhibitory effects of Bic application occurred often in some particular feature domains: Of 29 cells selective for the luminance polarity of a pattern, 8 (27%) showed stimulus-specific changes in their selectivity for the feature. A cell (Fig. 1a), for example, responded to a white grid (*t*-test, $p < 0.01$), but not to a black one ($p > 0.05$). It was induced by Bic to respond to the black grid ($p < 0.01$) and significantly increased its responses to the white one. The cell exhibited a similar but opposite luminance-contrast

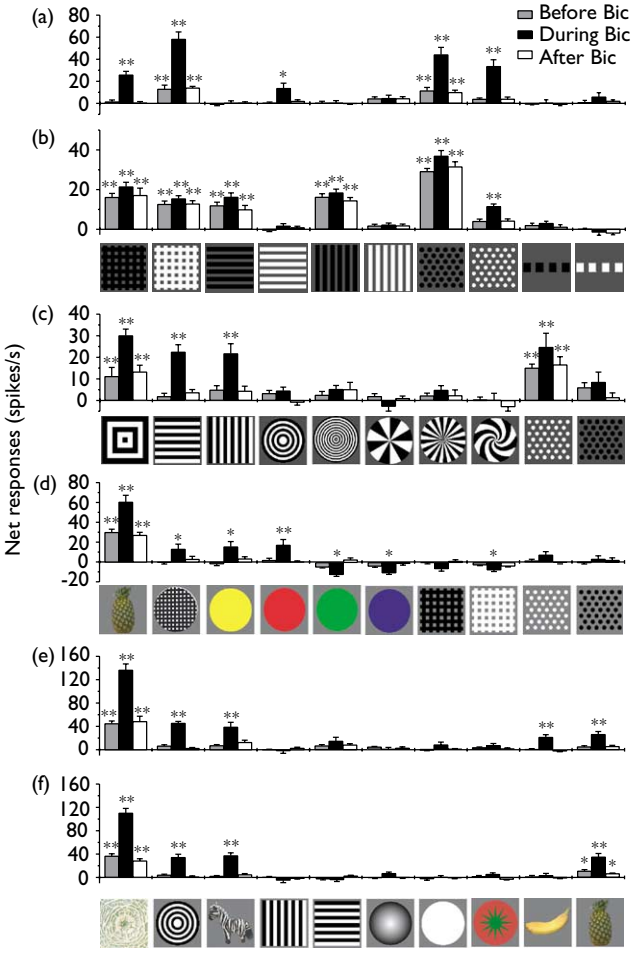

Fig. 1. Blockade of GABAergic inhibition altered texture selectivity of TE neurons in some particular feature domains. Cells in (**a**,**b**) became responsive to previously ineffective patterns with a luminance polarity opposite to the originally effective one. A cell shown in (**c**) began responsive to ineffective component features of a composite pattern and three other cells in (**d**–**f**) were responsive to a more complex natural texture stimulus. The three cells in (a,b,d) were recorded from a vertical penetration, (a) 225 μm below, (b) in the upper layers, and 1295 μm above (d), which was in the deeper cortical layers. Of 35 tested stimuli, 21 were texture stimuli. The cell in (c) was recorded from another monkey 1325 μm below the cortical surface. Of 30 tested stimuli, 10 were texture stimuli. The two cells shown in (e,f) were recorded 100 μm apart along a penetration in the upper cortical layers from the third monkey. Of 40 tested stimuli, 12 were texture stimuli. Among the stimuli used, only 10 are presented here for each cell. Gray, dark and light bars show the response magnitudes for each cell. $^{**}p < 0.01$, $^{*}p < 0.05$: the responses before Bic application, during Bic and after Bic application, respectively, elicited by a stimulus were compared with the spontaneous firing rate by *t*-test. Error bars = s.e.m.

change for arrays of white and black dots. It originally responded to the black dots and, during Bic application, gained a response to the white dots. The opposite effects presumably arose because the array of small squares formed by a grid is similar to an array of dots. It appears that the cell was originally sensitive to an array of darker dots on a lighter background and was induced to respond to an array of lighter dots on a darker background.

Another cell (Fig. 1b) responded only to texture stimuli under normal conditions, preferring best an array of black dots, but became responsive during Bic application to an array of white dots that was originally ineffective. This kind of luminance-contrast change was specific to the array of small dots, and did not occur for a line of large square dots or straight gratings (Fig. 1b). The two cells in Fig. 1a,b were recorded from at two sites 225 μm apart along a vertical penetration.

Figure 2 shows the selectivity change of a population of cells that appeared in particular stimulus dimensions of texture features. Responses of eight cells to an initially ineffective luminance pattern were enhanced by Bic from 3.2 ± 2.8 to 15.8 ± 6.3 spikes/s (mean $\pm$ s.d., $n = 8$; paired t-test, $p < 0.001$, right half of Fig. 2a). Of the cells selective for one of two orthogonal orientations of a straight grating, the selectivity of 27% (4/15) was abolished by Bic (t-test, $p < 0.05$, Fig. 2b). Their responses to the ineffective orientation were augmented from 1.3 ± 1.7 to 24.3 ± 3.6 spikes/s ($p < 0.001$, Fig. 2b). Results in Fig. 1a,b and Fig. 2a,b suggest that GABAergic inhibition contributes to the luminance or orientation selectivity of some TE neurons for a texture pattern by suppressing responses to the opposite luminance or orthogonal orientation.

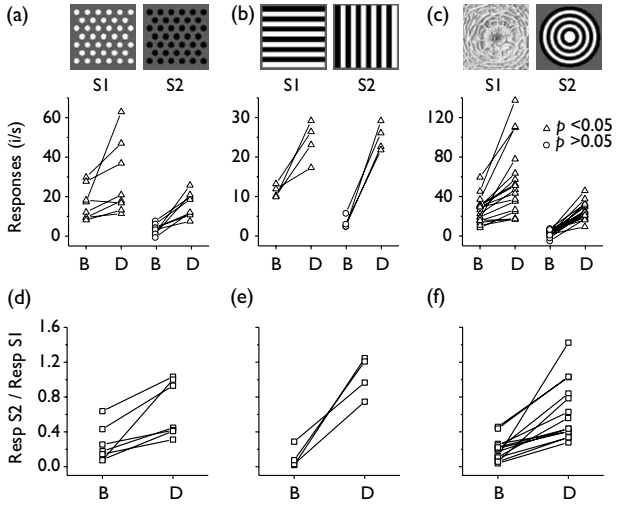

Fig. 2. Population data for specific effects of blocking GABAergic inhibition on the texture selectivity of TE neurons. The change of texture selectivity induced by Bic appeared (**a**) in the luminance polarity of patterns ($n = 8$), (**b**) in the orientation of straight gratings ($n = 4$), and (**c**) in component features of a complex texture stimulus ($n = 17$). The first column of each panel shows responses to originally effective stimuli and second column to the originally ineffective ones. Note that only responses to one stimulus were presented if a cell showed the behavior to more than one stimulus in (a) or (c) and that five cells showed two of the three kinds of behavior in (a,b,c). Triangles ($p > 0.05$) or circles ($p > 0.05$) joined by a line indicate responses (spikes/s) of each of the cells tested before and during Bic application (B and D). Pictures above the plots represent examples of texture stimuli used, and do not necessarily represent the exact stimuli presented for each cell. (**d–f**) Bic changed response ratios of the cells to two different stimuli. A pair of squares joined by a line indicate ratios of responses (Resp) of the cells in (a,b,c) to a pair of the originally ineffective (S2) and effective stimuli (S1) before and during Bic application, respectively. Four stimulus pairs were excluded because the ineffective stimuli evoked negative responses before Bic application, yielding nonsensical negative ratio values.

The disinhibitory effects of Bic application occurred more often in component feature dimensions: Of 36 cells responsive to a composite pattern or a complex texture stimulus, 17 (47%) appeared to receive inputs, masked by GABAergic inhibition, from simple components of the originally effective pattern or complex texture stimulus. For example, a cell (Fig. 1c) that originally responded to a black-and-white concentric square, but not to the horizontal and vertical gratings that are components of the square, began to respond robustly to these gratings upon Bic application ($p < 0.01$). The change was not due to a difference in the spatial frequency between the square grating and straight gratings, because no such change occurred in the responses evoked by concentric or radial gratings with a spatial frequency similar to or higher than that of the straight gratings (Fig. 1c).

Figure 1d–f shows the effects of Bic on the selectivity of TE neurons for complex natural texture stimuli. A cell (Fig. 1d) responded solely to a side view of a pineapple among the 35 stimuli tested. Bic made it responsive to a black grid on a white circle, as well as to yellow and red colors, which may represent components of surface characteristics of the pineapple. In contrast, Bic-induced disinhibition did not make it responsive to other ineffective stimuli such as green or blue color, a black or white grid, an array of white or black dots (Fig. 1d) or other gratings (see Fig. 1b,c for stimuli). It did not respond to any other stimuli in the set under either normal or disinhibited conditions. Thus, inhibitory inputs carrying information regarding the grid and the yellow and red color features appear to be essential for the cell to produce a selective response to the pineapple.

Two other cells (Fig. 1e,f) exhibit similar selectivity changes for a complex texture. Both cells preferred the bottom view of a melon, and were induced by Bic to respond to originally ineffective stimuli, a concentric ring and a zebra. Thus, it appears that the concentric circle and curved stripes, the features that are present in the melon, concentric ring and zebra, are inputs into these cells. Accordingly, the cells failed to respond to straight stripes. On the other hand, these cells were also unresponsive to a luminance gradient and a solid white circle, which are component features of the melon. Ineffective banana and pineapple activated the first cell upon Bic application ($p < 0.01$, Fig. 1e). Bic enhanced responses of the second cell to the pineapple ($p < 0.01$, Fig. 1f) relative to its original responses. The concentric circle, curved stripe and yellow color appeared to be component features critical for developing the first cell's specific selectivity for the melon to that it only responded among 40 stimuli tested. For the second cell, the concentric circle and the curved stripe appeared to be the salient features that it was sensitive to.

The two cells were located at nearby sites 100 μm apart along a recording track. Figure 2c shows that responses of 17 cells to one of ineffective component features were increased from 3.0 ± 3.4 to 25.2 ± 8.8 spikes/s by Bic ($p < 0.0001$; Fig. 2c). Of the 17 cells, 15 became responsive to ineffective pattern component features, four to color, and three to shape. The results in Fig. 1c–f and Fig. 2c suggest that the inhibition to input of some component features plays an important role in generating the selectivity of TE neurons for a composite pattern or complex natural texture.

Blockade of GABAergic inhibition changed texture selectivity of neurons: The effects induced by Bic were not simply generic changes in response gain, but were alterations in neuronal texture selectivity. Figure 2d–f plots the ratios of responses of the cells in Fig. 2a–c to a pair of the originally ineffective and effective stimuli (S1 and S2 in Fig. 2) before and during Bic application, respectively. If Bic had only a gain effect, the ratios of responses to two stimuli should be the same with or without Bic. However, the response ratios were obviously altered by Bic; on average increased by 0.51 ± 0.34 (mean $\pm$ s.d., $n = 25$). The cells thus changed their selectivity for the texture stimuli. One may argue that if responses to effective stimuli had reached saturation, Bic would increase responses only to ineffective stimuli, thereby changing the ratio. The following observations indicate that this was not the case. Most cells (79%, 38/48) significantly enhanced responses to effective texture stimuli ($p < 0.05$). Many of them responded more strongly either to ineffective texture stimuli than to originally effective ones during Bic application (e.g. Fig. 2b) or to suboptimal texture stimuli during Bic application than to the most effective one before and even during Bic application (Fig. 3a,b). Moreover, firing rates of a part of the cells to non-texture stimuli were higher than to texture ones with Bic (not shown).

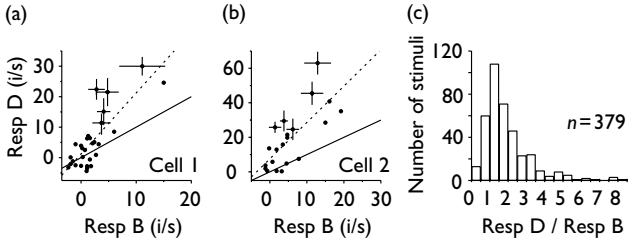

Fig. 3. Bic application does not simply scale responses of TE neurons. (**a**,**b**) Responses (spikes/s) during Bic application (RespD) were plotted against those obtained before Bic application (RespB) for two representative cells. Stimulus selectivities of the two cells were significantly altered by Bic application (drug $\times$ stimulus interaction, $p < 0.05$). Diagonal lines (slope = 1, solid lines), regression lines (slope = 2.000 (a) or 2.106 (b), broken lines), and s.e.m (crosses) of responses to a part of the stimuli beyond a linear increase predicted by the regression are displayed in the panels. Each point represents a stimulus. (a) includes non-texture stimuli and (b) only texture stimuli, showing no substantial difference in the effects of Bic between the texture and non-texture stimuli. (**c**) Histogram of ratios of responses evoked by a stimulus between during (Resp D) and before Bic application (RespB) across 379 texture stimuli for 58 cells. The stimuli that evoked responses < 3 spikes/s before Bic application or ≤ 0 during Bic application were excluded to avoid an unmanageably large ratio or nonsensical negative ratio.

Figure 3a,b is another demonstration that Bic did not generally enhance neuronal responses to all stimuli, but rather that some stimulus inputs were more affected by GABAergic inhibition than others. Responses of the cell in Fig. 1c and of another cell during Bic application were plotted against responses before Bic application. Responses to many stimuli were distributed along the diagonal (solid) line without obvious changes. In contrast, some responses deviated from this line and beyond the linearly increasing responses predicted by regression analysis (broken line) between the responses before and during Bic application, showing a considerable qualitative change in stimulus selectivity.

We further analyzed the ratio of responses of a cell to a stimulus during and before Bic application across 58 cells. Figure 3c shows the distribution of the ratios for 379 texture stimuli. If Bic significantly enhanced neuronal responses, the ratio should be considerably > 1. Further, if Bic only changed the gain of responses, this ratio would be almost the same for all stimuli tested to a cell. Figure 3c shows that ratios were widely distributed from 0 to 8.5, and asymmetrically (skew = 1.75) biased toward larger values. Of the ratios, 21% (81/379) were > 2.5. Bic enhanced neuronal responses to these stimuli. In contrast, other 44% (168/379) were between 0.5 and 1.5. Bic did not obviously change responses. Therefore, Bic changed the selectivity of cells for the stimuli to which the response ratio was markedly changed. Bic thus did not simply scale responses to all texture stimuli, maintaining the spectrum of relative original responsiveness, but specifically augmented neuronal responses to certain texture stimuli. A general change in the neuronal excitatory threshold or spontaneous firing rate cannot explain this phenomenon.

DISCUSSION

Blockade of GABAergic inhibition changed the selectivity of TE neurons for textures. A substantial portion of cells selective for the luminance polarity or orientation of a texture pattern can be induced to respond to the originally non-evocative luminance polarity or pattern orientation. Cells preferring a complex texture can become responsive to originally ineffective component features of the texture. It appears as though information regarding the opposite luminance polarities and orthogonal orientations of the patterns and component features of the complex texture is suppressed by GABAergic inhibitory interneurons, but is in fact transmitted to these cells. The cells received inputs related to different aspects of a texture feature often recorded along a vertical penetration. These results suggest that a group of cells code a texture feature. The selectivity of TE neurons for textures is thus built up on inputs of texture patterns with a feature different in a particular parameter dimension, or of component features related to a complex texture stimulus via inhibitory interaction mediated by GABAergic interneurons.

At earlier stages of the ventral pathway for object vision, neurons in areas V1, V2, V4 and TEO can only extract the simple features, such as orientation, luminance, size, density and shading direction of texture elements on a relatively small region of an object surface [13–17]. TE neurons can represent more complex and integrated texture features in a

large visual field [7–9,18]. The present study suggests that the processing of global texture feature occurs at different levels. The cells in Figs 1a–c and 2b may represent the primary level of this process. These cells extract a particular feature of relatively simple patterns, such as luminance and orientation information, or construct a particular composite pattern from inputs of its component features. At a higher level of the processing stage, cells (Fig. 1d–f) signal more complex texture features combined with shape and/or color. Under normal conditions, some cells have a specific selectivity for a complex natural texture, such as the cells in Fig. 1d,e, that only responded to a pineapple or a melon among 35 or 40 stimuli tested, which included some other objects, such as faces, an apple, a tomato, a pepper, and laboratory items. They process complex texture features combined with the shape and color of a complex natural stimulus. Indeed, TE neurons selective for a feature composed of a simple pattern together with shape and/or color information have been described previously [8,9,18,19]. These cells may be located at intermediate processing levels. Finally, TE neurons, such as those depicted in Fig. 1a,b,d, located at different processing levels and related to processing a complex texture feature, were clustered within a local cortical region [10,20,21]. The coordinated activity of the group of cells signals some aspects of visual features of the pineapple [22]. It is plausible that activity of a subset of these cells together with others (neighbors or distant ones) can process different aspects of features of the pineapple or other object features.

CONCLUSION

Our results show that TE neurons code texture features of visual objects by different mechanisms. Some cells detect a relatively simple texture pattern with suppression of GABAergic inhibition to stimulus input in a particular feature domain of the pattern at low levels of the texture processing. Others signal a complex texture feature with suppression to some component features of the texture at high levels. The cells at different levels of processing of a texture feature can be found at a local cortical region. A local GABAergic inhibitory circuit is crucially involved in the process.

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