RELATION BETWEEN THE NEURON ACTIVITIES IN CORTICAL AREA V4 AND THE METACONTRAST MASKING

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Abstract

Metacontrast masking is a phenomenon in the visual perception in which two brief visual stimuli, the test and mask stimuli, follow each other in rapid succession, which causes the test stimulus to become less visible or invisible even though the test and mask stimuli do not spatially overlap. In the present study, I investigated the relation between the neuron activities in cortical area V4 in the macaque monkey to the metacontrast masking in order to understand how the activities of V4 neurons correlate with the perception of the visual stimulus. First, I conducted psychophysical experiments of metacontrast masking in human subjects. I found that the visibility of the test stimulus was suppressed when the interval between the onset of the test and mask stimuli (stimulus onset asynchrony; SOA) was within a certain range. Maximum suppression of perception of the test stimulus occurred when the SOA was about + 30 to 50 ms and became gradually weaker with an increase in the SOA. The suppression lasted up to about 100 to 200 ms in the positive SOA. In the negative SOA, there was little inhibition of perception. Secondly, I conducted unit recording experiment in area V4 of macaque monkeys. In this part of the study, I studied the temporal characteristics of suppression in area V4 using a visual stimulus for metacontrast masking. Visual responses of V4 neurons to a brief test stimulus presented within the receptive field were recorded, and the effect of a mask stimulus that did not spatially overlap the test stimulus was examined. Responses to the test stimulus were suppressed by the mask stimulus, which either preceded or followed the test stimulus. To study the temporal

characteristics of suppression, the SOA between the test stimulus and the mask stimulus was varied. Maximum suppression occurred with a simultaneous presentation of the two stimuli, and the suppression gradually weakened as the SOA increased. The suppressive effect of the mask stimulus lasted on average about 77 ms in the negative SOA (forward masking) and 65 ms in the positive SOA (backward masking). These results indicate that surround suppression in V4 neurons has considerable temporal width, which is longer than that previously reported in areas V1 and V2. When I compare the time course of suppression in V4 neurons with that in the perception in psychophysical experiments, I found that there were two differences. First, the inhibition occurred only in the positive SOA in the psychophysical experiments but the inhibition was found in both positive and negative SOA in the responses of V4 neurons. Secondly, the duration of inhibition was longer in the positive SOA in the perceptual metacontrast masking than in the activities of V4 neurons. These results indicate that the activities of V4 neurons do not parallel the perception in metacontrast masking. However, the longer duration of suppression of V4 neurons compared with neurons in V1 and V2 which are located ealier in the visual processing suggest that activities in V4 may represent an intermediate stage of conversion of visual signals which finally makes the time course of the neural responses resemblance to the perception in the metacontrast masking.

1. Introduction

It has been known that the visual information of an object in the external world, which comes in the retina, is processed along several visual cortical areas in the brain and finally perception of the object (visual awareness) is established. Recent studies of monkey visual system have shown that the ventral visual cortical pathway from V1 to the inferotemporal cortex (IT) via areas V2 and V4 plays an important role for visual object perception such as shape and color perception and recognition (Gross et al., 1972; Dean, 1976; Mishkin et al., 1983; Desimone et al., 1984; Desimone and Schein, 1987; Heywood and Cowey, 1987; Komatsu et al., 1992; Schiller, 1993; Kobatake and Tanaka, 1994; Tanaka, 1996) (Fig. 1). Along this pathway, representation of the visual stimulus is transformed. It still remains unknown at which stage in the visual processing, the neural representation of object correlate with perception which may be key to understand where the visual awareness is established (Fig. 2).

One of the ways to investigate such problem is to study neuron activities in a situation in which physically presented stimulus does not correspond with the perception and examine whether the neural activities of visual cortical neurons are correlated with the physical parameters of the stimulus or the perceived contents of the stimulus. Metacontrast masking is one of such situations in which physical stimulus is dissociated from percept. Metacontrast, a kind of visual masking, is a perceptual phenomenon in which the temporal relationship in the interaction between two nearby stimuli is critical. In metacontrast, when two brief visual stimuli, the test and mask stimuli, follow

each other in a rapid succession, the test stimulus becomes less visible or even invisible (Alpern, 1953; Lefton, 1973; Breitmeyer and Ganz, 1976; Breitmeyer, 1984) (Fig. 3). The reduction of visibility of the test stimulus is strongly affected by the interval between the test and the mask stimuli. It has been shown that the reduction of visibility is maximal when the interval between the onset of the test and the mask stimuli (stimulus onset asynchrony; SOA) is approximately 30 to 80 ms and the effect is still observed when the SOA exceeds 100 ms (Alpern, 1953; Schiller and Smith, 1966; Kahneman, 1967; Lefton, 1973). So, in the metacontrast masking, even though the test stimulus physically stimulate the retinal cells, it does not cause visual awareness and is not perceived if an appropriate SOA is used. Thus metacontrast masking provides an interesting opportunity to study where in the visual pathway neuron activities dissociate from physical parameters of the stimulus and correlate with perception. However, there were few physiological studies to examine the neural correlates of metacontrast masking (Schiller, 1968; von der Heydt et al., 1997; Macknik and Livingstone, 1998).

A recent study done by von der Heydt et al. (1997) showed that the inhibition of the activities of neurons in areas V1 and V2 of the macaque monkey did not correspond with the perception of metacontrast masking and that the inhibition of the responses in V1/V2 neurons to the metacontrast stimulus occurred between -33 to +33 msec SOA. Their results indicate that the neural activities at the early cortical stages do not correlate with perception in metacontrast masking. One possibility is that neural mechanisms of

metacontrast masking resides in the higher visual cortical areas than V1/V2.

Area V4, a retinotopically organized extrastriate cortex in the ventral visual pathway, receives inputs from area V2 and is a major source of visual input to the inferotemporal cortex (Desimone et al., 1980; Shipp and Zeki, 1985; Gattass et al., 1988; Distler et al., 1993). This area is involved in several aspects of object vision (Heywood and Cowey, 1987; Walsh et al., 1992; Schiller, 1993; Kobatake et al., 1994; Merigan, 1996). It is interesting to know how neural responses in area V4 correlate with perception in metacontrast masking.

Neurons in various visual cortical areas including area V4 have suppressive mechanisms within and outside the receptive field (Hubel and Wiesel, 1968; Allman et al., 1985; Tanaka et al., 1986; Desimone and Schein, 1987; Schein and Desimone, 1990; Cheng et al., 1994). When the width or length of a visual stimulus is increased, the neural response initially increases, but if there is a suppressive mechanism, the response decreases with further increase in the size of the stimulus (Desimone and Schein, 1987) (Fig. 4A). It is thought that the suppressive mechanisms have an important role in the detection of local features such as curvature or termination of contours or junctions, or the global analysis of a scene such as figure-ground segregation or color constancy (Zeki, 1983; Allman et al., 1985; Tanaka K. et al., 1986; Desimone and Schein, 1987; Dobbins et al., 1987; von der Heydt and Peterhans, 1989; Schein and Desimone, 1990). The temporal aspects of these suppressive mechanisms, however, remain unknown (Fig. 4B). The situation in which the surround stimulus is presented in succession after the presentation of a central

stimulus corresponds well with the presentation of the test and the mask stimuli in the metacontrast masking. So, it is important to examine the time course of inhibition of the response of V4 neurons in order to know the correlation of V4 neuron activities with the metacontrast masking.

This study consists of two parts. In the first part, I studied the time course of suppression in the perceptual metacontrast masking in human subjects. The aim of this part was to know the time course of suppression in the metacontrast masking using the same apparatus and stimulus that would be used for the physiological recording experiment. In the second part of the present study, I investigated the temporal aspects of the suppression of the response of V4 neurons to the metacontrast stimulus in the monkey. I then compared the time course obtained in the psychophysical experiment with that obtained in V4 recording experiment. I found that the suppressive mechanism of the receptive fields of V4 neurons have a significant temporal width, but there were significant differences between the time course of the suppression of V4 neurons and that of human metacontrast masking.

2. Materials and Methods

2.1 Psychophysics

Experiments were done for three human subjects. The subjects sat facing a color CRT monitor 57 cm in front of them. Visual stimuli were displayed on the color monitor (60 Hz; 1024 x 768 pixel). The test stimulus was a uniformly colored circle, and the mask stimulus was an annulus of the same color as the test stimulus. The inner diameter of the mask stimulus was the same as the diameter of the test stimulus. Thus, the test and mask stimuli touched each other but did not spatially overlap.

In each trial, the test and/or mask stimuli were presented while the subjects looked at the fixation spot. The test and mask stimuli were located in the place which is shifted at the 6.7 degree eccentricity from the fixation point. The duration of either stimulus was 17 ms (one frame). In some trials, only the test stimulus or the mask stimulus was presented. In other trials, both test and mask stimuli were presented. The interval between the onset of each stimulus, SOA, was chosen from a range between -133 to +133 ms and varied from trial to trial. A negative SOA value indicates that the mask stimulus preceded the test stimulus and a positive SOA value indicates that the mask stimulus followed the test stimulus. The different types of trials and different SOAs were randomly selected for every trial. The luminance of the stimuli was 20 cd/m^2 against a background of 5 cd/m^2. Subjects were required to report the perceived brightness of the test stimulus at each SOA by rating the brightness of the test stimulus from 0 to 4. Value 0 indicates that the test stimulus was not perceived at

all, whereas value 4 indicates that the perceived brightness was the same as that of the test stimulus presented alone. The subject held a box with five buttons. By pushing one of five buttons, the subject reported the result of his rating. The data were averaged for 10 trials. To examine the effect of eccentricity and color of stimulus for metacontrast masking, the location and color of stimulus were changed in some experiments.

2.2. Electrophysiological recording

2.2.1 *Behavioral task*

Two awake monkeys (*Macaca fuscata*) were used for the recording experiments. During the experiments, the monkeys sat in a primate chair and looked at the screen of a color display. The monkeys were trained to perform a fixation task. A trial started when a small spot (fixation spot) appeared on the screen (Fig. 5). The monkey was required to foveate the fixation spot within 500 ms and to maintain its gaze within 1° from the spot. At the end of a successful trial, a drop of water was delivered as a reward, the fixation spot was turned off, and a 1-s intertrial interval started. Eye position was monitored using the magnetic search-coil technique (Robinson, 1963). If the monkey's eye deviated from the fixation point more than 1° during a trial, the trial was automatically terminated without reward and the intertrial interval started.

2.2.2 *Surgery and recording*

A stainless steel recording chamber and head holder were fixed to the

skull using standard sterile surgical techniques under sodium pentobarbital anesthesia (6-12 mg/kg/h). A search coil was placed in the eye and was connected to a plug on the top of the skull. After surgery, the monkey was allowed to recover for at least 1 week before the experiments began. During this period, antibiotic (Cefazolin sodium) was given every 12 hours. All procedures for animal care and experiments were in accordance with the NIH Guide for the Care and Use of Laboratory Animals (1996) and approved by the animal experiment committee of the Okazaki National Research Institute.

Single-cell activity was recorded from area V4 representing the parafoveal and peripheral visual fields. The recording chamber was placed above the posterodorsal surface of the cortex. A glass-coated Elgiloy microelectrode was advanced through the dura in a different location each day. Neural signals were amplified and discriminated on the basis of spike amplitude with time windows and converted pulse sequences were analyzed with a computer and displayed on line (Fig. 6). Eye positions were also displayed continuously.

2.2.3 *Visual stimuli*

Visual stimuli were displayed on a color monitor (60 Hz; 1024 x 768 pixel) 57 cm in front of the monkey. To determine the location and size of the receptive field (RF), a small rectangular stimulus (0.3° x 0.3°) was used. After determining the location of the RF, the color of the stimulus was changed to determine the color preference of the neurons.

Almost all V4 neurons had suppressive mechanisms within or outside the RF such that visual stimuli exceeding a certain size reduced the visual response. We studied the temporal characteristics of this suppressive mechanism as follows. Two stimuli (test and mask stimulus) were used for the experiment. The test stimulus was a uniformly colored circle and its size was always equal to or smaller than the size of the RF. The mask stimulus was an annulus of the same color as the test stimulus. The inner diameter of the mask stimulus was the same as the diameter of the test stimulus. The outer diameter of the mask stimulus was usually larger than the RF but in some cases it was smaller. The size of these stimuli were chosen such that the response to the test stimulus presented alone was much stronger than that of the mask stimulus presented alone.

In each trial, the test and/or mask stimuli were presented while the monkey's gaze was on the fixation spot. The duration of either stimulus was 17 ms (one frame). In some trials, only the test stimulus or the mask stimulus was presented. In other trials, both test and mask stimuli were presented. An example of the sequence of the test and mask stimuli is illustrated in Fig. 5. The SOA was chosen from a range between -133 to +133 ms and was varied from trial to trial. A negative SOA value indicates that the mask stimulus preceded the test stimulus and a positive SOA value indicates that the mask stimulus followed the test stimulus. For the positive SOA trials, the effect of masking was examined using a set of six SOAs (17, 33, 50, 67, 100, and 133 ms) for every neuron. For the negative SOA trials, a less dense sampling was made. For some neurons, a set of three SOAs (-33, -67, and -133 ms) was examined. For the

remaining neurons, two SOAs (-50 and -100 ms) were examined. The different types of trials and different SOAs were randomly selected for every trial. In these tests, neural responses for each condition were recorded for at least five trials. The luminance of the stimuli was 20 cd/m^2 against a background of 5 cd/m^2.

2.2.4. *Analysis of neural responses*

For the analysis of the temporal characteristics of suppression, we used the average firing rate during the 50 to 250 ms period after the presentation of the test stimulus. This period was chosen because the latency of the visual response of V4 neurons is approximately 50 ms and the response to the test stimulus rarely exceeded 250 ms. The discharge rate during the 200 to 700 ms before the presentation of the test stimulus was used as the background discharge rate and was subtracted from the discharge rate after the visual stimulation in order to obtain the magnitude of the response. In some cases, the spike activity during the 50 to 150 ms after the presentation of the test stimulus and during the 150 to 250 ms period were analyzed separately. I only analyzed the neurons in which the response to the mask stimulus alone was less than half of the magnitude of the response to the test stimulus alone. To analyze the temporal characteristics of the suppressive mechanisms, the magnitude of the response to the test stimulus presented alone was used as the control value. This value was compared with the response obtained when the test stimulus was paired with the mask stimulus. The relative response was calculated as a

ratio between the response in this paired condition and the control value for each SOA and this ratio was used as the measure of the effect of the mask stimulus on the response to the test stimulus. For brief presentation of a visual stimulus such as 17 ms used here, it is hard to distinguish between on and off responses. Since I am interested in the suppression of on-responses of V4 neurons, I attempted to exclude potential contamination of off-responses as follows. For every neuron, I tested the responses to the optimum visual stimulus using a longer duration (500 ms). If I found off-response to the test stimulus with longer duration of stimulus presentation, I excluded the cell from the analysis.

2.2.5. *Histology*

Upon completion of the last recording session, the monkeys were sacrificed under deep anesthesia with sodium pentobarbital and perfused through the heart with saline that was followed by 4 % paraformaldehyde. We penetrated pins at several locations surrounding the recording site. A tissue block containing area V4 was sectioned at 50 μm in the frontal plane and every second section was stained with cresyl violet. We were able to identify the holes made by the pins and thus were able to identify the recorded regions in the brain sections (Fig. 7). Examination of the stained sections confirmed that the electrode track was located in the cortex of the prelunate gyrus (Fig. 8).

3. Results

3.1. *Psychophysics of metacontrast masking*

3.1.1. *Masking effect for the changes in the SOA*

Psychophysical experiments were done in three human subjects. The stimuli and the sequence of presentation are shown in Fig. 9. The perceived brightness of the test stimulus as a function of SOA for all three subjects are shown in Fig. 10. The test and mask stimuli were presented at 6.7 degree eccentricity from the fixation point on the horizontal meridian and the same color and luminance were used for both test and mask stimuli. The diameter of the test stimulus is 3.3 degree and the mask stimulus is 5.6 degree. The perceived brightness of the test stimulus was very low near the 0 msec-SOA (17~50 msec) in the positive SOA in either subject, indicating that the test stimulus is less visible in these periods. The inhibition of perceived brightness gradually decreases as the SOA becomes larger. The inhibition of the perceived brightness for the test stimulus was found between about 17 ~ 200 msec in subject 1, 17 ~ 100 msec in subject 2 and about 17 ~ 133 msec in subject 3. In contrast, there was little inhibition in the negative SOA for all three subjects, indicating that subjects clearly perceived the test stimulus when the mask stimulus preceded the test stimulus. As a result, the time course of the inhibition of the perception of the test stimulus was quite asymmetrical around 0 msec-SOA.

3.1.2. *The effect of eccentricity on the metacontrast masking*

The effect of the eccentricity of the stimulus presentation on the metacontrast masking is shown in Fig. 11. The same stimulus size and color was used for different eccentricities. The inhibition is stronger when the stimuli are presented in the peripheral visual field than in the foveal visual field. The maximal inhibition of the perceived brightness of the test stimulus occurred at similar SOAs for each condition but the magnitude of inhibition is much larger in the peripheral visual field than in the foveal visual field. The inhibition of the perceived brightness are found between 34 and 100 msec at 0 degree in eccentricity, between 17 and 150 msec at 6.7 degree and between 17 and 167 msec at 10 degree. The perceived brightness was similar between 6.7 degree and 10 degree conditions until 50 ms-SOA, but after this period, it became lower at 10 degree condition. These results indicate that the masking effect of the metacontrast is stronger in the peripheral visual field than in the foveal visual field.

3.1.3. *The effect of color for the metacontrast masking*

The effect of the color of the test and mask stimuli is shown in Fig. 12. The perceived brightness of the test stimulus was examined when the test and mask stimuli had the same color (green) and when they had different colors (the test stimulus was green and the mask stimulus was white). In these two conditions, the color of the test stimulus is same, and only difference is the color of mask stimulus. As shown in Fig. 10, the inhibition of the perceived brightness of the test stimulus was found in the same color condition. The inhibition was not

found when the color of the test and mask stimuli were different. This result indicates that the metacontrast masking is affected by the difference of the color between the test and the mask stimulus.

3.2. *Recording of V4 neuron activity*

3.2.1. *Response of V4 neurons to the metacontrast stimulus*

We recorded 101 single and multiple neurons from area V4 of two awake monkeys. The stimulus and the sequence of the presentation are shown in Fig. 5. The RFs of recorded neurons were located in the right lower visual field. The recordings were made from the parafoveal and peripheral representations, where the eccentricity of the RFs was within 3 to 15 °. Of these 101 neurons, 37 neurons showed a response to the mask stimulus that was less than half of that to the test stimulus. Since one neuron showed an off-response to a stimulus having a longer duration, it was excluded from the subsequent analysis. The results obtained from the remaining 36 neurons are discussed below. There was no systematic differences between the neurons that were analyzed and those that were rejected with regard to the receptive field sizes, response latencies, or preferred stimulus sizes.

3.2.2. *Inhibition of response of V4 neurons to the metacontrast stimulus*

A sample of responses of a typical V4 neuron is shown in Fig. 13a. Responses obtained when either the test stimulus or the mask stimulus was

presented alone are shown (Fig. 13A, left). A very short presentation (17 ms) of the test stimulus generated a clear response that lasted for approximately 100 ms. The onset latency was approximately 50 ms. The response to the mask stimulus was very weak compared with the response to the test stimulus. The response obtained when the test stimulus was paired with the mask stimulus at various SOAs is also shown (Fig. 13A, right). The response was strongly suppressed at an SOA of 0 ms. The amplitude of the response was much smaller compared with the control condition in which the test stimulus was presented alone and the duration of the response was much shorter. Inhibition was clearly observed at the 17-ms SOA wherein the initial part of the response was similar to the control condition but the late component of the response was truncated so that the duration of the response was much shorter than in the control condition. The inhibition was less marked at the 50-ms SOA. The early component of the response was inhibited at the -33-ms SOA when the mask stimulus preceded the test stimulus, but the inhibition of the late component was relatively weak. Figure 13B plots the responses of the same V4 neuron as shown in Fig. 13A as a function of the SOA.

Many neurons recorded in this study showed the inhibitions centered at the 0 ms SOA as shown in Fig. 13. But for a few neurons, the response to the test stimulus was little affected by the mask stimulus in any SOAs. Fig 14 shows an example of such a neuron. This neuron showed a phasic response to the test stimulus and almost no response to the mask stimulus (fig. 14a). At any SOA, the response showed no inhibition compared with the response to the test

stimulus presented alone (fig. 14b).

We found that most V4 neurons (31/36, 86.1%) exhibit a significant change in response as a function of the SOA ($p < 0.05$, ANOVA). In most cases, the clearest change was a suppression of responses at an SOA of about 0 ms. In 27 out of 31 neurons (87.1%), the response at the 0-ms SOA was significantly inhibited compared with the control value, which was the response to the test stimulus presented alone ($p < 0.05$, t-test) (fig. 15). An example of such a neuron is shown in Fig. 13.

Likewise, most of the cells recorded from area V4 exhibited a response to the test stimulus that was inhibited by presentation of the mask stimulus, and this inhibition became gradually stronger as the SOA approached zero. The inhibition of the responses was observed in both positive and negative SOAs. These results indicate that the inhibition due to the mask stimulus had considerable temporal width. However, the time course of the inhibition differed from cell to cell. Fig. 16 shows the responses of three examples of neurons that exhibited different time course of inhibition. Fig. 16A is the same neuron as shown in Fig. 13. The inhibition was nearly symmetrical around 0-msec SOA, and it lasted up to about + and - 100 msec. The neuron as shown in Fig. 16B exhibited more asymmetric time course of inhibition around 0 ms-SOA. Comparing between the positive and negative SOAs, the inhibition lasted longer in the positive SOA up to about 100 msec but it lasted shorter in the negative SOA up to about -70 msec SOA. There were neurons which showed a longer duration of inhibition in the negative SOA than in the positive SOA (data not

shown). Fig. 16C is another example of a neuron which exhibited very short duration of inhibition. The response is strongly inhibited at 0 ms SOA but there was little inhibition at other SOAs.

3.2.3. *Temporal width of inhibition*

To quantify the time course of the inhibition, we computed the "recovery time" for each of the 27 neurons that showed significant suppression at the 0-ms SOA. For each neuron, we computed the recovery time for positive and negative SOAs separately.

The sample for this analysis consisted of 15 neurons in the negative SOA condition in which responses were recorded at three different SOAs. In the positive SOA condition, we included all 27 neurons in the analysis. Spearman's rank correlation test was used to determine whether the gradual increase in the response with the increase in the absolute value of SOA was statistically significant. Twenty-six out of 27 neurons in the positive SOA condition and 13 out of 15 neurons in the negative SOA condition showed a significant correlation ($p < 0.05$) (fig. 15).

To analyze how long the inhibitions were found in the positive and the negative SOAs as a function of SOA, we computed the "recovery time" which is the absolute value of the SOA when the response recover to the level of the response obtained by the test stimulus alone. The distributions of the recovery times are shown in Fig. 17. In the positive SOA condition, the recovery times ranged from 22.4 ms to 190.4 ms, with a median of 64.5 ms. In the negative

SOA condition, the recovery times ranged from 22.7 ms to 181.4 ms, with a median of 77.3 ms. As a population, there was no significant difference ($p = 0.71$, unpaired t-test) in the distribution of the recovery times between the negative and positive SOAs. A comparison of the recovery times for negative and positive SOAs for 13 individual neurons for which the recovery times were obtained for both positive and negative SOAs is shown in Fig.18. There was a slight tendency towards a longer recovery time in the negative SOA condition, although the difference was not statistically significant ($p = 0.66$, paired t-test).

3.2. 4. *Inhibition of response in a population of V4 cells and psychophysical experiment of metacontrast masking*

In almost all the cells recorded from V4, the response to the test stimulus was inhibited by presentation of the mask stimulus and the inhibition became gradually stronger as the SOA approached zero. The inhibition of the responses was observed in both positive and negative SOA. We computed the average of the normalized response of each neuron for each SOA. Maximum suppression was observed at the 0-ms SOA (Fig. 19A), and the averaged response monotonically increased with an increase in the absolute value of the SOA. When we compared the averaged responses obtained at the same absolute values of SOAs, e.g. +33 ms vs -33 ms, +67 ms vs -67 ms, and +133 ms vs -133 ms of SOA, there was no significant difference ($p>0.2$, unpaired t-test). The recovery times computed from this graph were 65.4 ms for the positive SOAs and 77.4 ms for the negative SOAs which is very similar to the median values of

the recovery times of the sample of cells as described before.

Fig. 19B shows the average of the results from psychophysical experiments of metacontrast masking for three human subjects which were shown in Fig. 10. The inhibition of the perceived brightness is strongest at the short positive SOAs (17, 33 and 50 ms-SOAs) and gradually decreases as the SOA increases in the positive SOA. On the other hand, the inhibition of perceived brightness is not found in the negative SOA.

Comparing between the results in V4 neurons and psychophysical experiments, the temporal characteristics of suppression of V4 cells seems different from that of the metacontrast masking indicated in psychophysical experiments in two aspects (fig. 20). First, the duration of suppression in V4 neurons (65 ms on average in the positive SOA) is shorter than that of the metacontrast masking (100-200 ms). Second, the suppression was nearly symmetrical around zero SOA in V4 cells, whereas it was found only at the positive SOA in perceptual metacontrast masking. These comparisons show that there are marked differences in the time course of inhibition between the V4 neurons and metacontrast masking. Nonetheless, there were some similarities between the inhibition in V4 neurons and that in the perceptual metacontrast masking as described below.

3.2.5. *Effects of eccentricity for the V4 neuron activity and metacontrast masking*

Since I found in the psychophysical experiment that the strength of the inhibition is influenced by the eccentricity of the stimulus presentation, we

compared the inhibitions of V4 neuron activities between parafoveal and peripheral V4. Fig. 21 shows the results of the effects of eccentricity on the time course of the inhibition on V4 neuron activity. The comparison was done between the averaged relative response of 15 parafoveal V4 neurons and 11 peripheral V4 neurons. The suppression was overall stronger in peripheral V4 neurons than parafoveal neurons. The recovery time computed from this graph are 52.8 ms for the parafoveal V4 neurons and 84.7 ms for the peripheral V4 neurons, showing that the inhibition lasted longer in the peripheral V4 than in the parafoveal V4. Comparing the suppression of V4 neuron activity and that of metacontrast masking in the psychophysical experiment shown in fig. 11, the stronger suppression in the peripheral V4 seems to correspond to the result that the masking effect was stronger in the peripheral visual field than in the parafoveal visual field in the psychophysical experiment.

3.2. 6. *Effects of color for the V4 neuron activity and metacontrast masking*

Since I found in the psychophysical experiment that the effect of masking becomes weaker when the color of the mask stimulus is different from that of the test stimulus, we examined if the difference in the color between the test and mask stimuli affect the inhibition of V4 neurons. Fig. 22 shows the effect of color differences on the time course of inhibition of the responses of V4 neurons by the metacontrast stimulus. As was used in the psychophysical experiment, the green test stimulus and white mask stimulus were used in the different-color condition while both the test and mask stimuli were green in the

control condition. The stronger inhibition was found when the color of the test and mask stimuli was the same than when the color was different. The recovery times computed from this graph were 85.8 ms for the same-color condition and 28.9 ms for the different-color condition. Comparing the suppression of V4 neuron activity and that of metacontrast masking in the psychophysical experiment shown in fig. 12, there was a common tendency that the inhibition is stronger in the same-color condition than in the different-color condition for both V4 neurons and psychophysical experiment, however, the extent of the inhibition was different between V4 neurons and psychophysics, that is, there was a clear inhibition in V4 neuron activities in the different color condition while there was no inhibition in such a condition in the psychophysical experiment.

3.2.7. *Comparison of early and late components of the response*

One main difference in the time course of the inhibition between V4 neuron activities and perceptual metacontrast masking is that the former is nearly symmetrical around zero SOA whereas the latter is quite asymmetrical. I realized, however, that some V4 neurons exhibited inhibition which is skewed toward positive SOA and is asymmetrical. Fig. 23A shows the responses of one such example of V4 neurons. When the test stimulus was presented alone (control condition), this neuron responded with a latency of approximately 60 ms and the response lasted over 200 ms. The response to the mask stimulus was much weaker than that to the test stimulus. When the test stimulus was paired with the mask stimulus, the response was strongly inhibited at a 0-ms SOA. The

initial component of the response did not clearly change, but the duration of the response was much shorter than that in the control condition. At an SOA of 17 ms, a strong inhibition to the late component of the response was observed such that the response later than 150 ms after the presentation of the test stimulus was completely eliminated. As the SOA increased, the duration of the response became gradually longer. Inhibition of the late component was still observed at an SOA of 50 ms, but at an SOA of 100 ms, inhibition was not clear. At an SOA of -33 ms, the early component of the response to the test stimulus was reduced but the late component was not clearly inhibited. Fig. 23B plots the responses of the same V4 neuron as a function of SOA. The response was computed from the discharges during the 50 to 250 ms after presentation of the test stimulus. The recovery times computed from this graph were 83.8 for the positive SOA and –51.3 ms for the negative SOA, indicating that the inhibition was shifted to the positive SOA.

The responses at different SOAs suggest that the effect of SOA on the response is different between the early and late components of the responses. To examine this, I plotted the time course of inhibitions for the early (50 – 150 ms) and late component of response (150 – 250 ms) separately (Fig. 24). Compared with the time course of inhibition for the early component of response, the inhibition is shifted to the more positive SOA for the late component of the response. These results indicate that there are neurons in V4 that show inhibition which is more pronounced in the positive SOA than in the negative SOA and that, in such neurons, the asymmetry is particularly clear in the late

component of the response.

As can be seen in Fig. 13 and Fig. 23, the inhibition of the response is more clearly observed in the later component of the response when the SOA becomes larger. This suggests that the recovery time depends on the amount of the later component of the response. To examine this possibility, we analyzed the correlation between the amount of the late component relative to the early component of the response and the recovery time for the positive SOA. The early and late components of the response were defined as the mean discharge rate during 50 to 150 ms and that during 150 to 250 ms periods after the onset of the test stimulus, respectively. Figure 25 shows the results from 26 V4 neurons. The recovery time becomes larger as the ratio of the late component of the response becomes larger. There was a positive correlation between the amount of the late component of the response and the recovery time, indicating that the recovery time depends on the amount of the late component of the response.

4. Discussion

In the present study, I examined the responses of V4 neuron activity to the metacontrast masking stimulus in the monkey and compared them with the perception of the test stimulus in the perceptual metacontrast masking obtained in the psychophysical experiment in human subjects.

The psychophysical experiments of metacontrast masking for human subjects in this study showed that the visibility of the test stimulus was suppressed when the interval between the onset of the test and mask stimuli (stimulus onset asynchrony; SOA) was within a certain range. Maximum suppression of perception of the test stimulus occurred when the SOA was about + 30 to 50 ms and became gradually weaker with an increase in the SOA. The suppression lasted up to about 100 to 200 ms in the positive SOA. In the negative SOA, there was little inhibition of perception. Some previous psychophysical studies of metacontrast reported that the maximum suppression occurred at about 50 - 100 ms SOA which is longer than the result in the present study (Alpern, 1953; Schiller and Smith, 1966; Kahneman, 1967; Lefton, 1973; Breitmeyer, 1984). This discrepancy between the present and previous results can be explained by the relative strength of the mask stimulus; it is reported that when the strength of the test stimulus is less than that of the mask stimulus, the maximum suppression occurs earlier in the positive SOA. (Breitmeyer, 1978). In the present study, the strength (luminance x duration) of the mask stimulus was larger than that of the test stimulus, and it is expected that the maximum suppression occurs in a short SOA. With regard to the effect of the eccentricity of

the stimulus, it has been reported that the inhibition of metacontrast masking decreases when the stimuli are presented in the fovea while the inhibition increases as the stimuli are presented at progressively more peripheral visual field (Alpern, 1953; Stewart and Purcell, 1970). Present result is consistent with these results.

Although area V4 is important for some aspects of object vision (Heywood and Cowey, 1987; Walsh et al., 1992; Schiller, 1993; Merigan, 1996), it is still unknown whether the activity of V4 neurons is correlated with awareness of visual attributes of an object, such as form and color. Several studies suggest that the neuronal activity in area V4 and inferotemporal (IT) cortex is more strongly correlated with the perception than V1 (Zeki, 1983; Crick and Koch, 1995; Leopold and Logothetis, 1996; Gur and Snodderly, 1997; Sheinberg and Logothetis, 1997). In order to examine the correlation between neural activity and perception, experimental situations in which physical stimuli are dissociated from perceptual contents are useful. Metacontrast masking is an example of a situation in which a physically presented test stimulus becomes invisible when paired with a surrounding mask stimulus. A unique feature of metacontrast masking is that the temporal factor of the suppressive mechanism is critical. Examination of V4 activity in metacontrast masking might thus provide useful information about how neuron activity in this area correlates with perception.

In V4, Desimone and Schein (1987) showed that most V4 neurons have silent suppressive mechanisms inside and outside of the receptive field. However, it has not been examined whether the suppression occurred when the

center and the surround stimulus are presented with some temporal gaps and how long the suppression lasts. The present study for the first time revealed that the suppression of activity of V4 neuron has a considerable temporal width. The suppressive effect was observed when the onset of the test and mask stimuli were within approximately 50 to 100 ms (65 ms at the positive SOA and −77 ms at the negative SOA on average). Many neurons showed the suppression in both the positive and negative SOAs, and the suppression was fairly symmetrical, centered at zero SOA.

Comparing the time course of the suppression in V4 neurons with that of the perceptual metacontrast masking (Fig. 26), there were differences in two aspects. First, V4 neurons tended to have a shorter duration of suppression; suppression of responses of V4 neurons is observed when the SOA is on average within 65 ms in the positive SOA, whereas suppression of metacontrast masking is observed when the SOA exceeds 100 ms. Second, the suppression of the responses of V4 neurons is fairly symmetrical around zero SOA whereas the suppression of perceptual metacontrast masking tends to be asymmetrical. In particular, clear suppression occurs in V4 neurons at periods with a negative SOA, but perceptual metacontrast shows no suppression. These results indicate that activities of V4 neurons do not parallel the perception in metacontrast masking.

Nonetheless, the effect of eccentricity and color shows a similar tendency for V4 neuron and psychophysical study. With regard to the eccentricity of the stimulus presentation, the inhibition is found more strongly in

the peripheral visual field than in the foveal visual field. The result in the recording experiment may be related to the observation that neurons in the peripheral representation tend to exhibit more sustained activity. With regard to the color of the stimuli, it was found that the inhibition decreases when the colors of the test and mask stimuli are different. Previous study in the monkey V1 showed that the horizontal connections run between the blobs of similar color opponency (Ts'o and Gilbert, 1988). Although it has been unknown whether a similar connections exists in V4. If they exist, it would be possible that the interaction is more strong when the test and mask stimulus have the same colors than when the colors are different.

Several studies have examined neuronal activity using visual masking paradigms (Schiller, 1968; Rolls and Tovee, 1994; Kovacs et al., 1995; von der Heydt et al., 1997; Macknik and Livingstone, 1998; Thompson and Schall, 1999). von der Heydt et al. (1997) demonstrated that the activity of neurons in areas V1 and V2 in the monkey do not correlate with metacontrast masking. They found that cells that responded to a uniform test stimulus covering the RF were not affected by the mask, and cells that responded to the edge of the test stimulus were only inhibited when the test and mask stimuli were nearly simultaneous (0 ± 33 ms SOA). No neurons were suppressed at an SOA of over 50 ms. Moreover, the cells with sustained activity were not found in V1 and V2. They suggested that the stimuli that are masked in perception are fully represented in areas V1 and V2, and metacontrast masking occurs beyond V1 and V2. In the present study, suppression was observed with an SOA of over 50 ms, and some

cells with sustained activity exhibited suppression that skewed to the positive SOA. Therefore, compared with the study by von der Heydt et al. (1997), the present results indicate that the time course of inhibition of V4 neurons is longer than that of neurons in V1 and V2 (Fig. 26).

Recently, Macknik and Livingstone (1998) reported that after-discharge or off-response of V1 neurons is inhibited when the mask stimulus follows the test stimulus. In the present study, only the on-response to the test stimulus was tested. Thus, our results differ from those of Macknik and Livingstone (1998) in the sense that on-response, not off-response of the V4 neurons was suppressed by the metacontrast stimulus. Of course, the present findings do not deny the possibility that the lack of an off-response is somehow involved in metacontrast masking.

The responses of IT neurons in backward masking using face (Rolls and Tovee, 1994) and pattern stimuli (Kovacs et al., 1995) have been examined. It is shown that, in IT, suppression of responses gradually increases as the SOA becomes shorter and that some neurons exhibit a sustained response to a brief visual stimulus. These results are similar to the responses of V4 neurons in the present study. Their studies differ from the present study in an important aspect, however; in their study, the test and mask stimuli are presented at the same location and are thus spatially completely overlapping, whereas in the present study these two stimuli are not spatially overlapping.

Recently, the response of frontal eye field neurons to the backward masking was examined in the behaving monkeys (Thompson and Schall, 1999).

It was shown that the neurons in the frontal eye field is activated by the masked stimulus which the monkey cannot detect, indicating that the information of masked stimulus is transmitted to the frontal eye field. In the present study, the response of V4 neurons to the masked test stimulus was not inhibited completely but partially inhibited even at the SOA when the masking effect is maximum. These results may indicate a possibility that all components of the neural response do not contribute to the perception of the visual stimulus.

Breitmeyer and Ganz (1976) hypothesized that the metacontrast is produced by a temporal overlap between the transient inhibitory process and sustained excitatory process. The present results suggest that when a surrounding mask stimulus is presented, some active process occurs to suppress the response evoked by the test stimulus. This process is by itself silent but is assumed to have some duration. Suppression is assumed to occur when the excitatory process induced by the test stimulus and the inhibitory process induced by the mask stimulus are temporally overlapping. The time course of the suppression might result from the change in the temporal overlap between the excitatory process and the inhibitory process as SOA changes.

Present study shows that the V4 cells with larger amount of the late component of the activities show more prolonged suppression in the positive SOA, and that the time course of the inhibition of the late component of the response has a clear asymmetry which is skewed toward the positive SOA. Thus, if we consider only the late component of the response, the time course of the suppression by the masking stimulus becomes more similar to the perceptual

metacontrast than when we take account both early and late components. Several recent studies suggest that a late component of the visual response of cortical neurons plays an important role in the extraction of the information of objects (Lamme, 1995; Zipser and Lamme, 1997; Sugase et al., 1999), so it may be possible to assume that the late component of the responses of V4 neurons may have close relevance to the formation of perception in metacontrast masking. The difference of the temporal width of inhibition between V4 and V1/V2 neurons can be explained by the fact that the cells with sustained activity were found in V4 but not in V1/V2.

A marked difference of the inhibition at the negative SOA was found between V4 neurons and metacontrast masking. The inhibition was found in V4 but not in psychophysics. In V1/V2 cells, the inhibition was also found in the negative SOA (von der Heydt et al., 1997). If the late component of response of sustained activity is analyzed as shown in Fig. 24, the time course of inhibition is shifted to the more positive SOA. This is explained by the following model. If the surround inhibition evoked by the masked stimulus have a certain latency and duration, and the inhibition is the temporal overlapping between the excitatory response evoked by the test stimulus and the surround inhibition by the mask stimulus, then the inhibition of the late component of response is shifted to the positive SOA.

The present result that the time course of inhibition is longer in the V4 neurons than in V1/V2 neurons might show that the activities of V4 neurons contributes more to the representation of perception than that of V1/V2 neurons

while the activities of V1/V2 are more correlate with the physical stimulus. However, even the late component of V4 neuron activities do not seem to parallel the perception. Therefore, V4 might be at an intermediate stage of transformation from the representation of physical stimulus to that of perception. Anatomical study in the monkey shows that V4 is an intermediate stage in the ventral visual pathway, that is, the area to receive inputs from V2 and send outputs to IT (Desimone et al., 1984; Shipp and Zeki, 1985; Distler et al., 1993). Recent studies of binocular rivalry and other studies showed that the number of neurons whose activities correlate with the perception are small in V1, intermediate in V4 and large in IT (Leopold and Logothetis, 1996; Gur and Snodderly, 1997; Sheinberg and Logothetis, 1997). Therefore, it may be possible that, in IT, neuron activities are correlated with the perception of the metacontrast masking. Neurons in IT cortex tend to have a longer latency and some IT neurons respond to a brief visual stimulus for a long duration (Rolls and Tovee, 1994), so it is expected that the time course of inhibition would be prolonged to the late positive SOA. It will be of interest to examine whether suppression of IT neurons by a surrounding mask stimulus has a time course similar to that of metacontrast masking.

Acknowledgements

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Figure Legends

Fig.1 Schematic illustration of the ventral visual cortical pathway in monkey. A lateral view of the monkey brain (top). Each area connects anatomically from V1 to IT via V2 and V4 sequentially (bottom).

Fig. 2 Schematic illustration of the physical stimulus and its perception. One way to investigate which cortical stages are important for the transformation of the representation of physical stimulus to the representation correlated with perception is to examine whether the neural activity of visual cortical neurons is correlated with the physical stimulus or the perceived stimulus while using a stimulus for which the physically presented stimulus does not correspond with the percept.

Fig. 3 Schematic illustration of the stimulus and the sequence of presentation in metacontrast masking. The test and mask stimuli are circle- and ring- shaped stimulus, respectively. The test and mask stimuli do not overlap spatially and the edge of the test stimulus is aligned with the inner edge of the mask stimulus (top left). The mask stimulus precedes or follows the test stimulus with an SOA (stimulus onset asynchrony) (bottom). When the test stimulus follows the mask stimulus with a short positive SOA, it becomes less visible or invisible (top right).

Fig. 4 Schematic illustration of the lateral inhibition in area V4. Strong response of V4 neuron occurs when the visual stimulus is presented in the

receptive field (RF) (top left). The response of V4 neuron is strongly inhibited by the presentation of a stimulus which surrounds the central stimulus (top right). The sequential presentation of the center and the surround stimulus in the metacontrast masking (bottom).

Fig. 5 Schematic illustration of the fixation task. The trial started when a small spot (fixation spot) appeared on the screen. The monkeys were required to foveate the fixation spot and to maintain its gaze on the fixation spot. At the end of a successful trial, a drop of water was delivered as a reward.

Fig. 6 Schematic illustration of the experimental equipment. Neural signals were amplified and discriminated and converted pulse sequences of spike activity were analyzed with a computer and displayed on line. Eye position were monitored with an eye coil.

Fig. 7 An illustration of the region of recorded V4 areas. The lateral view of the monkey brain is shown (top). The coronal section is shown in bottom. The dotted area is the regions in which the recording the neuron activity was done in the present study. la; lateral sulcus, st; superior temporal sulcus, lu; lunate sulcus, io; inferior occipital sulcus.

Fig. 8 A photomicrograph of the track of a recording electrode in a brain section stained by Cresyl Violet. The track is located in the prelunate gyrus. An arrow

indicates the track of electrode.

Fig. 9 Schematic illustration of the presentation of the visual stimuli in the psychophysical experiments in human subjects. A: Each box indicates the display. The small spot is the fixation spot, the circle is the test stimulus and the ring indicates the mask stimulus. Four boxes illustrate the sequence of the display. The mask stimulus had an inner diameter that was the same as the diameter of the test stimulus. The mask stimulus preceded or followed the test stimulus. B: Time course of the presentation of visual stimuli. The sequence of an example of a trial with a paired presentation of the test and the mask stimuli is shown. During the fixation, the test and the mask stimuli were presented in a rapid succession. SOA (stimulus onset asynchrony) is the interval between the onset of the two stimuli. The duration of both test and mask stimuli was 17 msec.

Fig. 10 Perceived brightness of the test stimulus as a function of SOA in three subjects. The abscissa is the SOA; the ordinate is the average values of rating across 10 trials. Error bar indicates standard error (SE).

Fig. 11 Effect of the eccentricity of stimulus presentation on the metacontrast masking. The location of the test and mask stimulus was at 0 degree (rectangle), at 6.7 degree (circle) and at 10 degree (triangle). The abscissa is the SOA; the ordinate is the average values of rating across 10 trials.

Fig. 12 Effect of color of the test and mask stimuli on the metacontrast masking. The color of both test and mask stimulus was green in the same-color condition (rectangle). The test stimulus was green and the mask stimulus was white in the different-color condition (circle). In both condition, the luminance and size of the stimulus was the same. The diameter of the test stimulus was 1.3 degree and that of the mask stimulus was 3.3 degree. The stimuli were presented at a position (H = 1.3 degree, V = 6 degree) from the fixation point. The abscissa is the SOA; the ordinate is the average values of rating across 10 trials.

Fig. 13 A. Responses of a V4 neuron to the test stimulus alone and mask stimulus alone (left column) or the combination of these stimuli with a specific SOA (right column). For each condition, histograms and rasters are made from six trials. Rasters and histograms are aligned at the onset of the test stimulus that is indicated by a long vertical line. Below each histogram, the duration of the test (top) and the mask stimulus (bottom) are indicated by a thin horizontal bar. All stimuli were 17 ms long. The short vertical lines on the raster display indicate cell discharges and the peristimulus time histogram (PSTH) is the sum of the discharges of all the trials. The tick marks on the abscissa are at 100-ms intervals. In these histograms, bin width is 5 ms and the calibration bar at the left of each histogram indicates 100 spikes/s. B. Summary of results of the experiments as shown in A. Responses to the test stimulus that was paired with the mask stimulus at various SOA are plotted as open squares. The abscissa is the SOA; the ordinate is the average of responses across trials. Error bar

indicates standard deviation (SD). To the left of the graph, a filled square and a filled circle indicate the responses to the test stimulus and the mask stimulus presented alone, respectively. For this graph, the average firing rate during the 50 to 250 - ms period after the presentation of the test stimulus was used for the analysis.

Fig. 14 Responses of a V4 neuron which showed no inhibition. Histograms in A and the graph in B are made in the same format as in Fig. 13.

Fig. 15 The number of neurons which was analyzed in the present study. Of the 101 neurons recorded, 36 neurons showed a response to the mask stimulus that was less than half of that to the test stimulus (top). Of these neurons, 31 neurons showed a significant change in the response as a function of SOA ($p<0.05$, ANOVA). Of these 31 neurons, 27 neurons showed a significant inhibition compared with the control value ($p < 0.05$, t-test) (middle). Of these 27 neurons, 26 neurons in the positive SOA and 13 neurons in the negative SOA showed monotonic increases in the response with an increase in the absolute value of SOA ($p<0.05$, Spearman's rank correlation test) (bottom).

Fig. 16 Responses of three examples of V4 neurons. These responses are plotted in the same format as in Fig. 13. A: a neuron showing a nearly symmetrical inhibition around 0 msec SOA. This is the same neuron as shown in Fig. 13. B: a neuron showing an asymmetrical inhibition in which the inhibition

has a longer duration in the positive SOA than in the negative SOA. C: a neuron showing a very short duration of inhibition.

Fig. 17 Distribution of the recovery time of the suppression in the negative SOA (A) and positive SOA (B). The abscissa represents the recovery time; the ordinate is the number of neurons. The median is -77.3 msec in the negative SOA and 64.5 msec in the positive SOA.

Fig. 18 Comparison of the recovery time in the negative and positive SOAs for 13 individual neurons in which the recovery time was obtained in both conditions. Each line connects the values for the positive and negative SOAs obtained in the same neuron. The recovery time in the negative SOA condition is shown to the left and that in the positive condition is shown to the right. The ordinate is the recovery time.

Fig. 19 Comparison of the time course of suppression between V4 neuron activities and psychophysical experiment. A: Population average of suppression of the responses of V4 neurons to the test stimulus when paired with the mask stimulus. The abscissa represents the SOA; the ordinate is the average of the normalized response. The averaged data was taken from 26 V4 neurons in the positive SOA condition and 13 V4 neurons in the negative SOA condition. Error bar: SE. B: Average of the results of psychophysical experiment obtained in three human subjects as shown in Fig. 10. The abscissa represents SOA; the

ordinate is the average rating of relative brightness of the test stimulus. Dotted line shows the SOA-0 msec.

Fig. 20 Summary of the differences between the time course of inhibition in physiological experiments in V4 and psychophysical experiments.

Fig. 21 The effect of eccentricity of stimulus presentation on the responses of V4 neurons. Averages of the relative responses at each SOA among neurons recorded from the parafoveal and peripheral representation in V4 are shown. Closed circle represents the averaged relative response of 11 peripheral V4 neurons and open rectangle shows that for 15 parafovea V4 neurons. The abscissa represents SOA; the ordinate is the average of the relative response.

Fig. 22 The effect of color of the stimuli on the responses of V4 neurons. Open rectangle indicates the averaged relative response of a V4 neuron when the test stimulus and the mask stimulus had the same color, and solid circle indicates responses when the test and mask stimuli had different colors. The abscissa represents SOA; the ordinate is the average of the relative response.

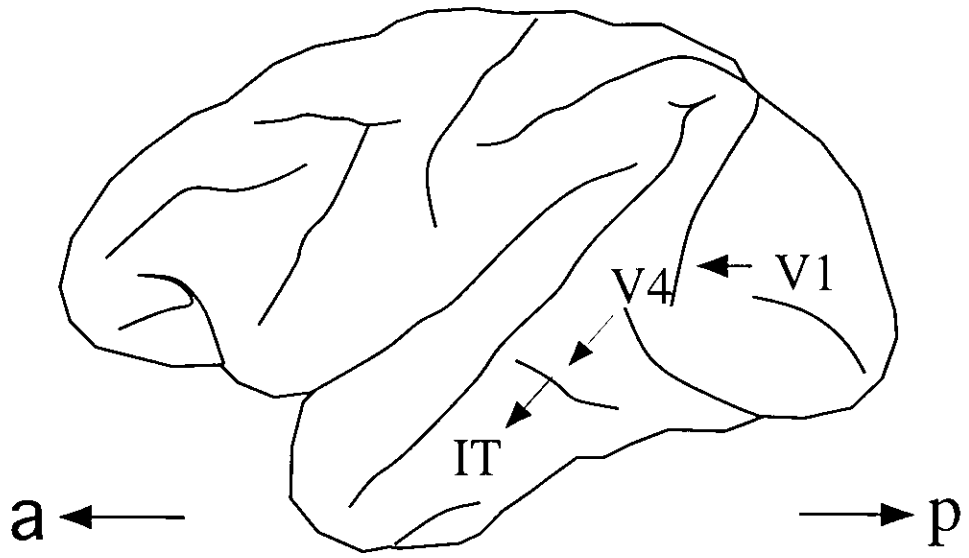
Fig. 23 An example of a V4 neuron with a sustained response to the test stimulus. This Figure is drawn in the same format as that of Fig. 14. The response is calculated as the mean discharge rate during 50 - 250 ms after stimulus presentation.

Fig. 24 Time course of the inhibition in the early and late components of the response. A: The time course of inhibition of the early component of the response (50 – 150 msec after the onset of test stimulus). B: The time course of inhibition of the late component of the response (150 – 250 msec). The abscissa represents the SOA and the ordinate is the response of spike activity. A filled square and a filled circle indicate the responses to the test stimulus and the mask stimulus presented alone, respectively.

Fig. 25 Relationship between the relative amount of the late component of the response and the recovery time in the positive SOA for the 26 V4 neurons analyzed. The abscissa represents the relative ratio of the late component of the response (150 to 250 ms after the presentation of the stimulus) to the early component (50 to 150 ms after the stimulus presentation). Ordinate is the recovery time at the positive SOA. A line indicates the linear fitting of the data ($y=107.96x + 61.26$; $r = 0.649$).

Fig. 26 Schematic illustration of the comparison between the results in the present study and those in a previous study in areas V1/V2 (von der Heydt et al. 1997).

Fig. 1



ventral visual pathway (object vision)

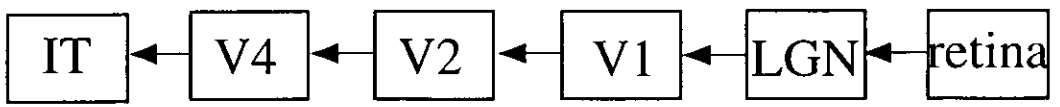
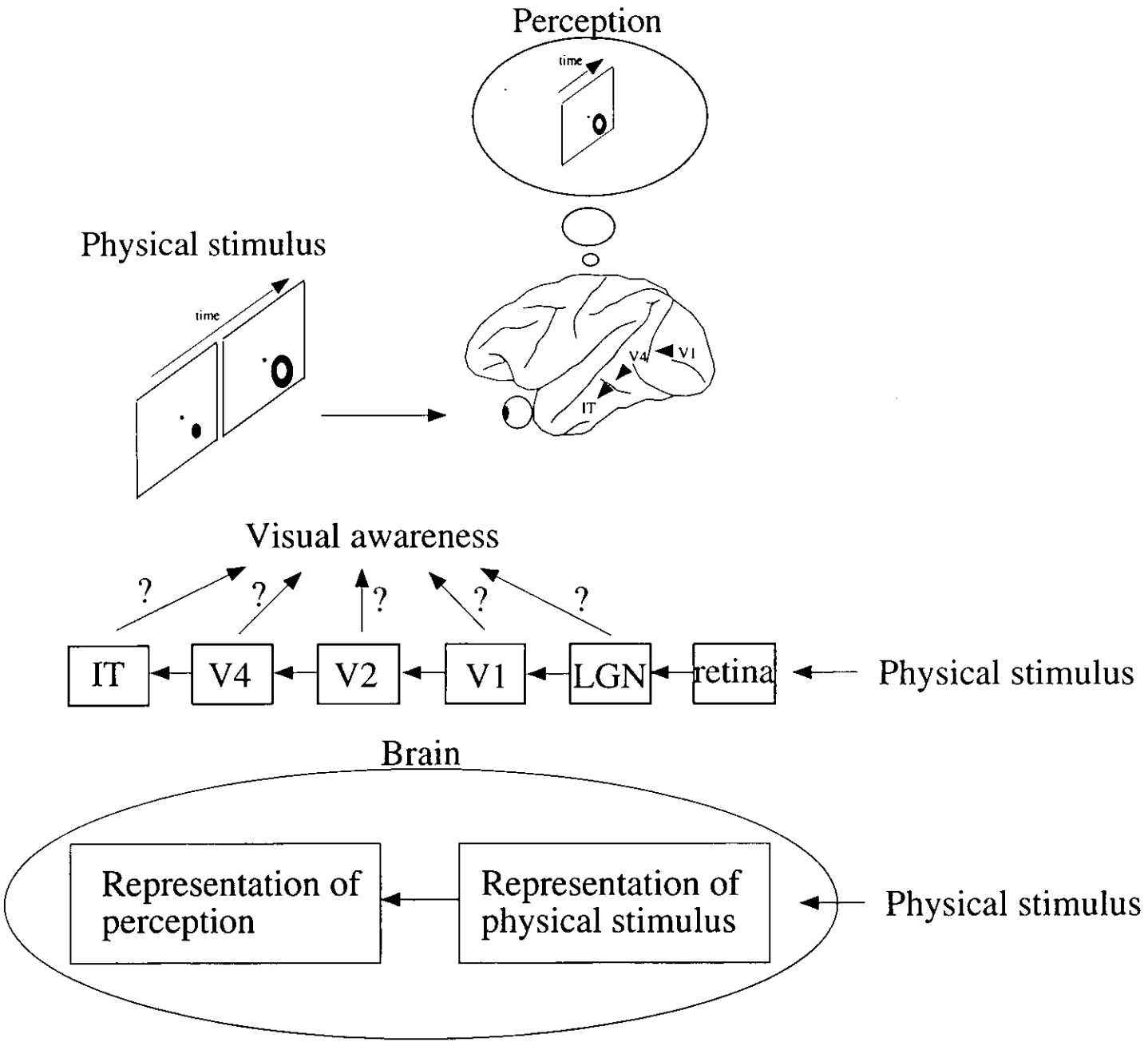


Fig. 2


Perception
time
Physical stimulus
time
V4
V1
IT
Visual awareness
?
?
?
?
?
IT
V4
V2
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LGN
retina
Physical stimulus
Brain
Representation of perception
Representation of physical stimulus
Physical stimulus

Fig. 3

metacontrast masking

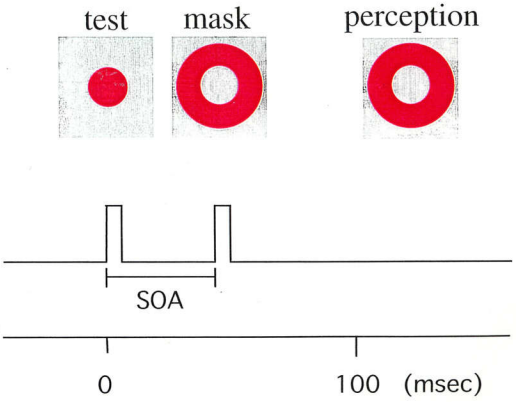


Fig 4

Lateral inhibition in area V4

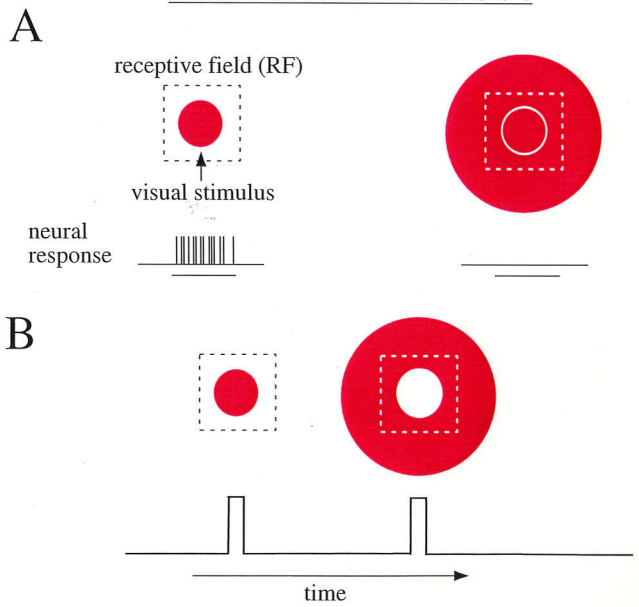


Fig. 5

Fixation task

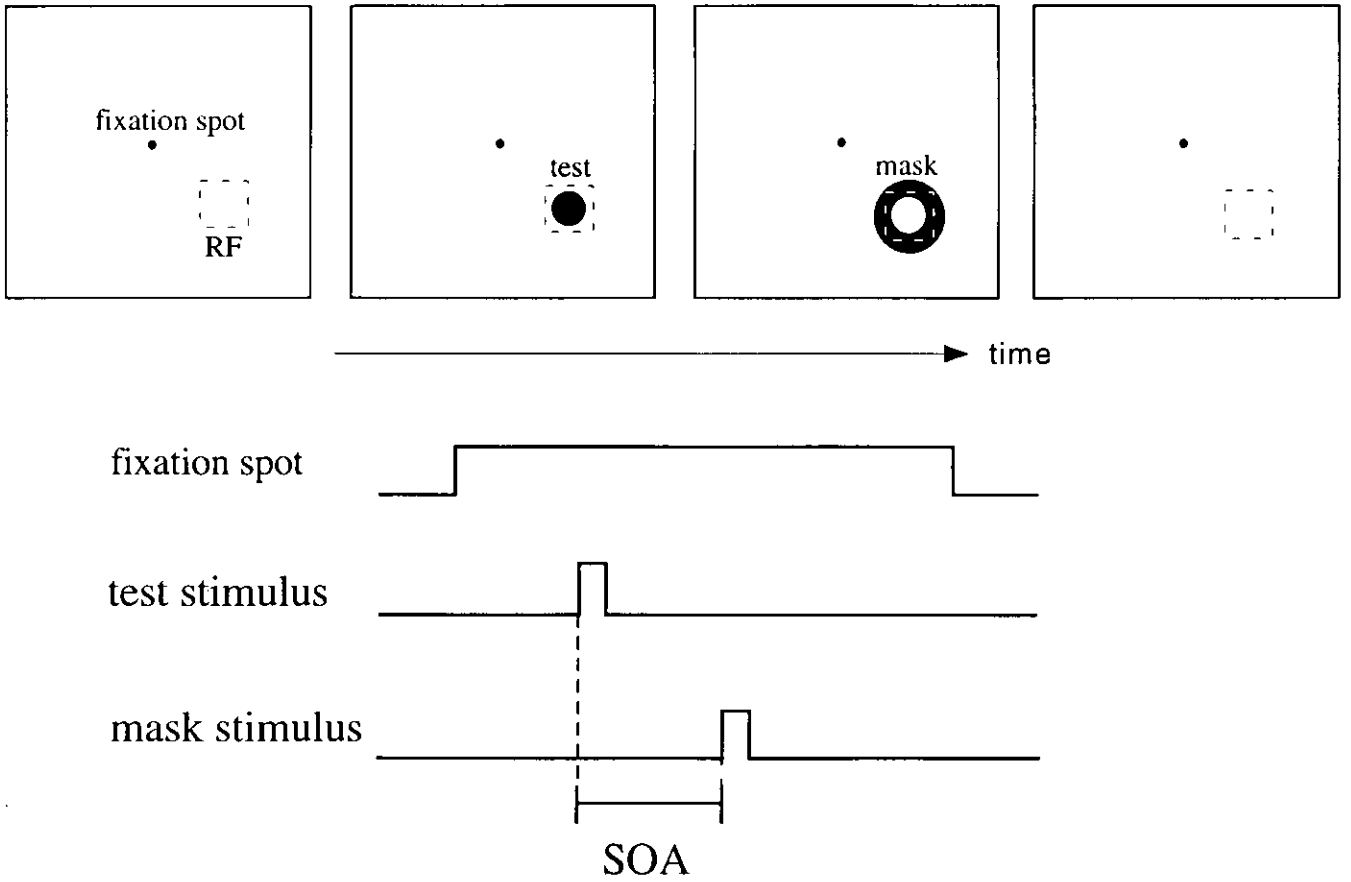


Fig. 6

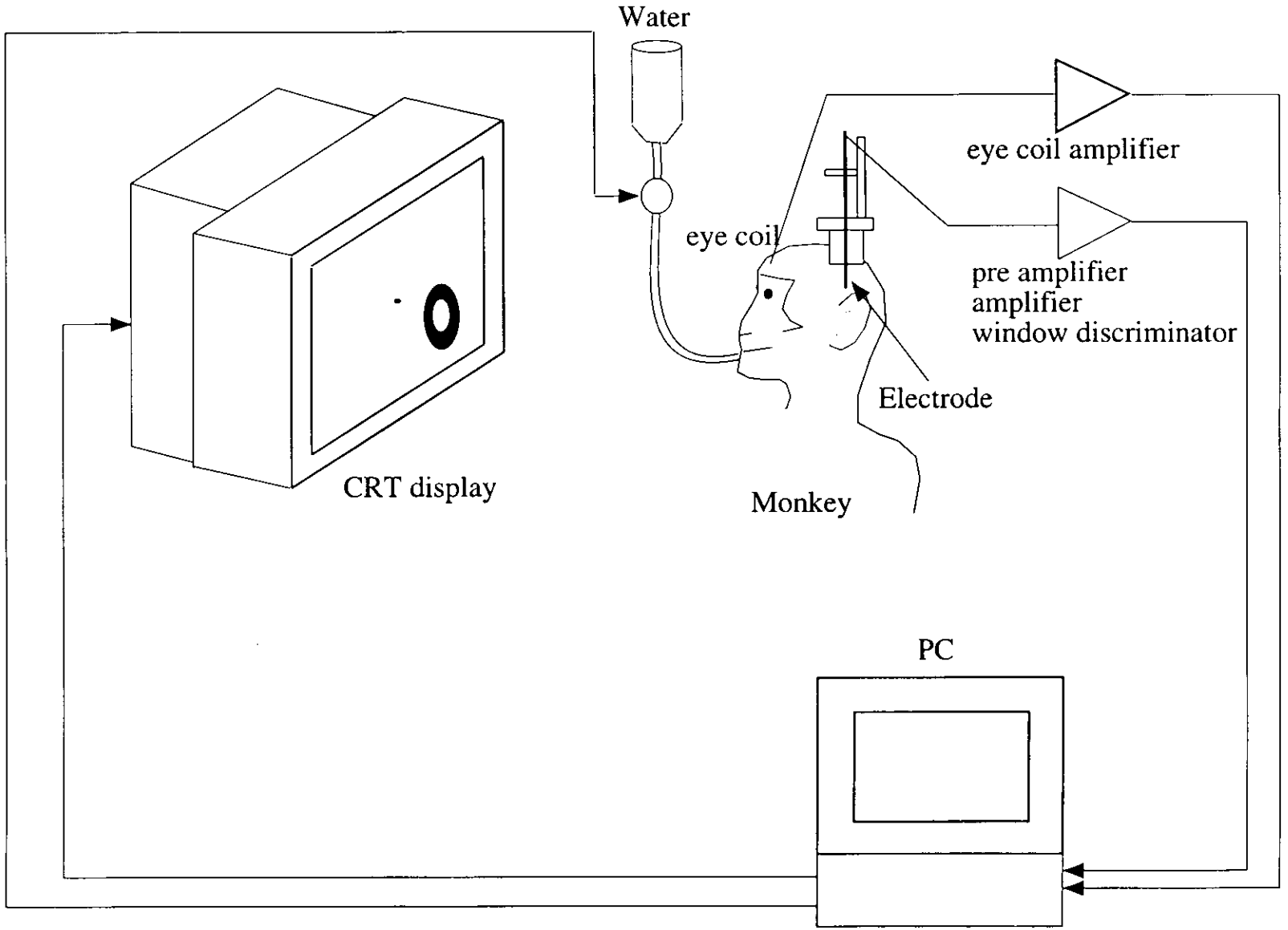

Water
eye coil amplifier
eye coil
pre amplifier
amplifier
window discriminator
Electrode
CRT display
Monkey
PC

Fig. 7

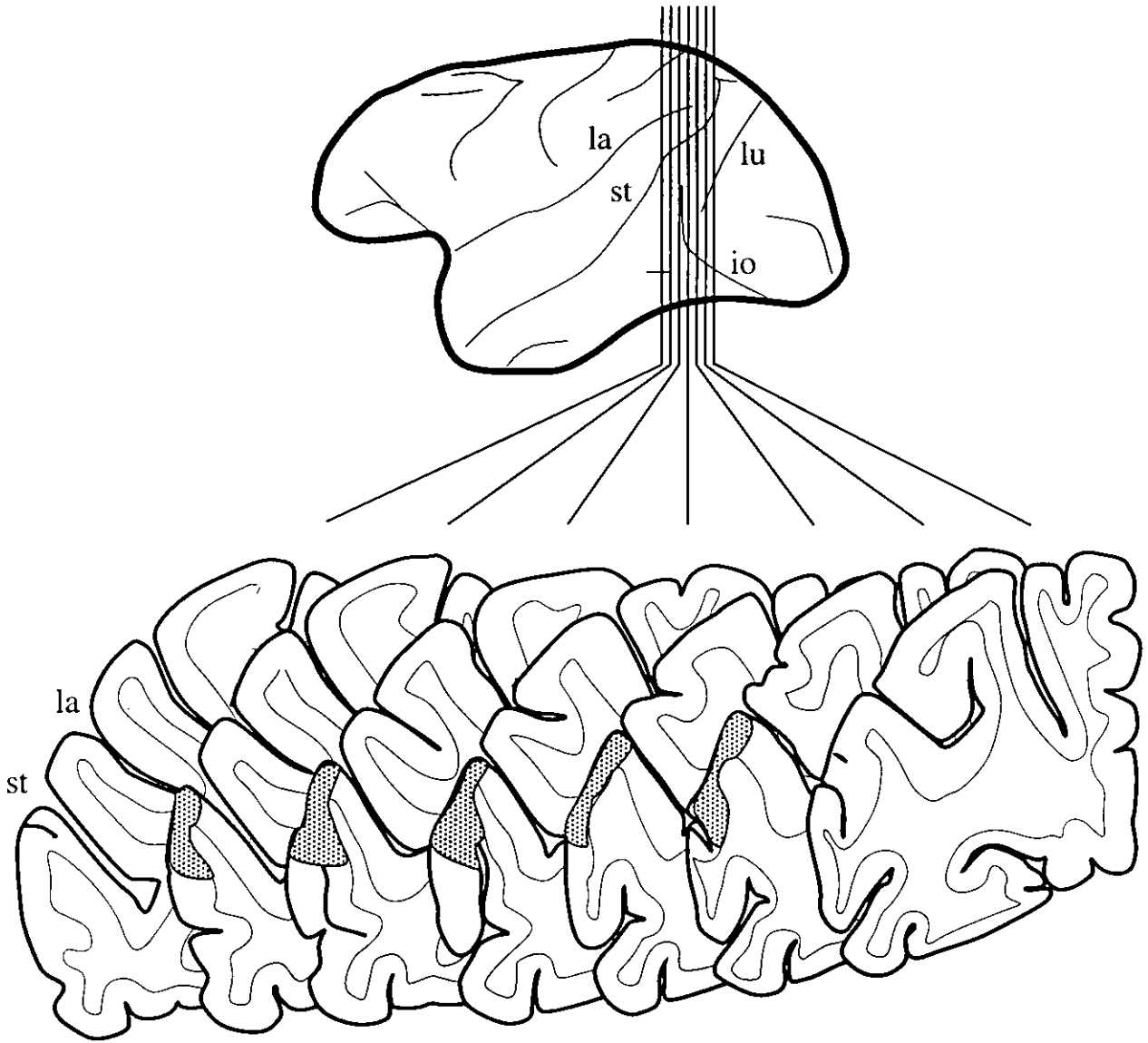


Fig. 8

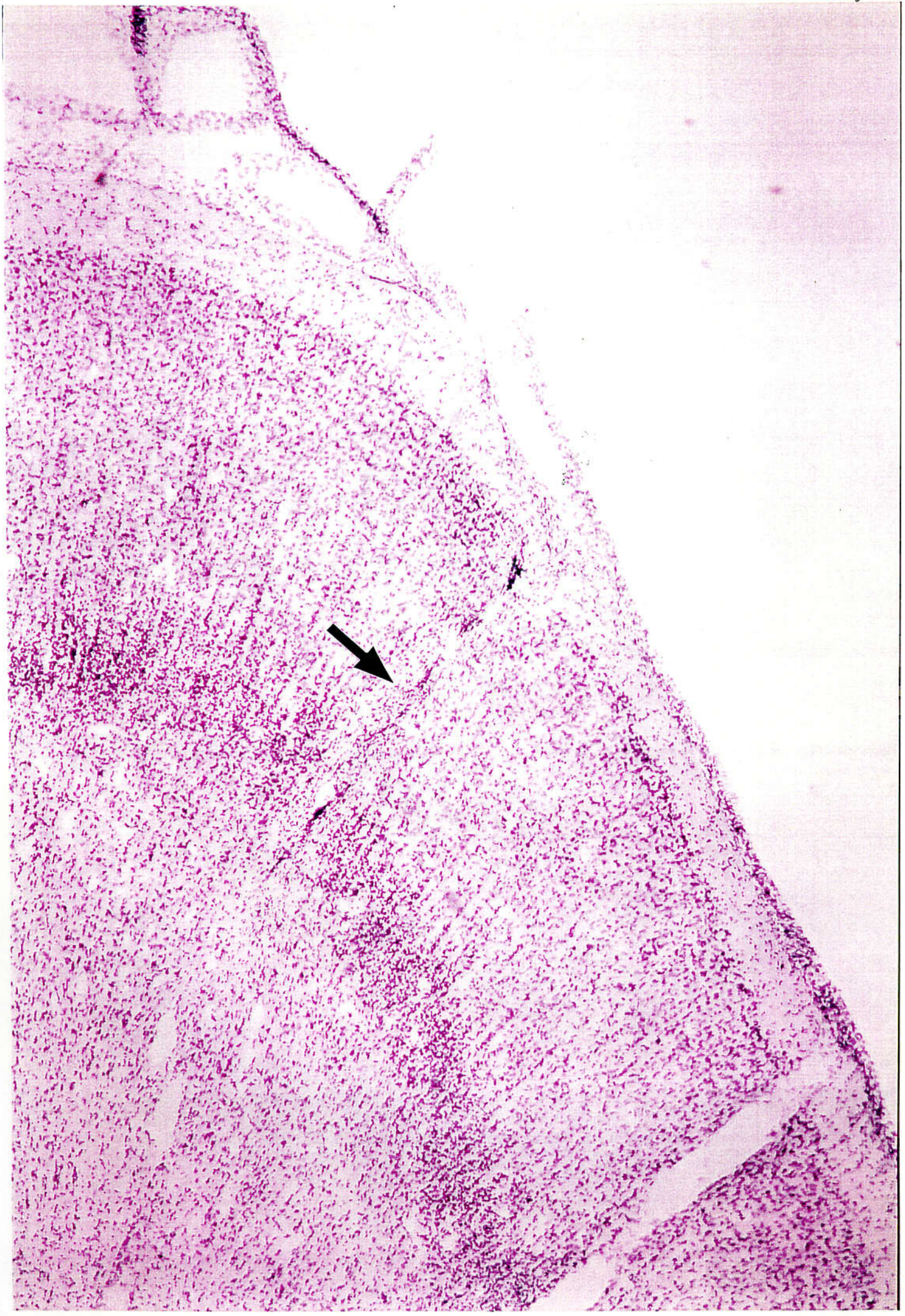


Fig. 9

metacontrast - psychophysics

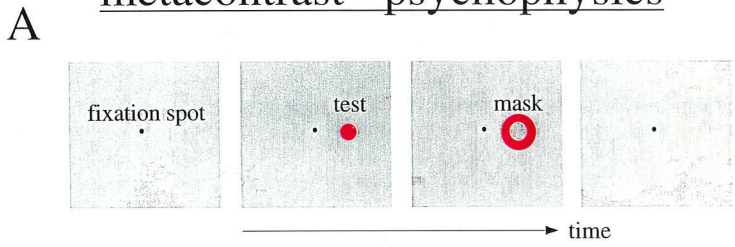


Fig. 10

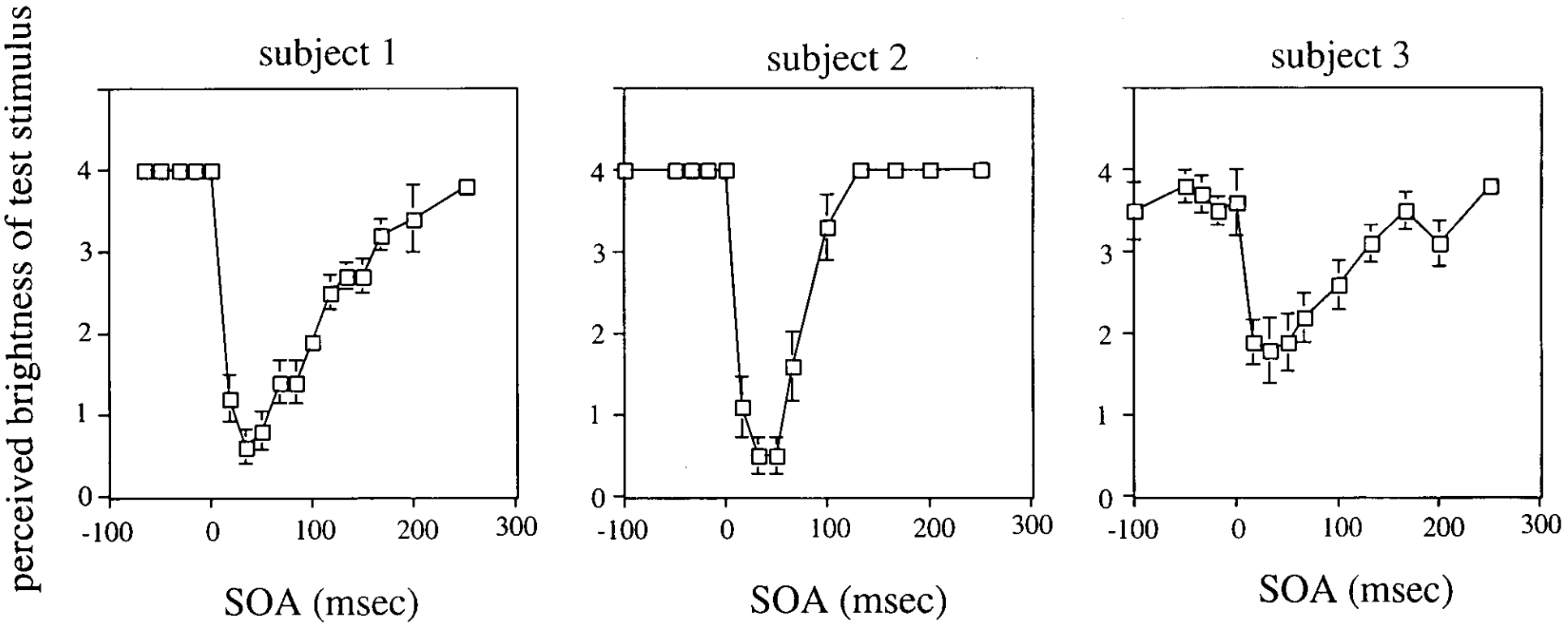

perceived brightness of test stimulus
subject 1
subject 2
subject 3
0
1
2
3
4
-100
0
100
200
300
SOA (msec)

Fig. 11

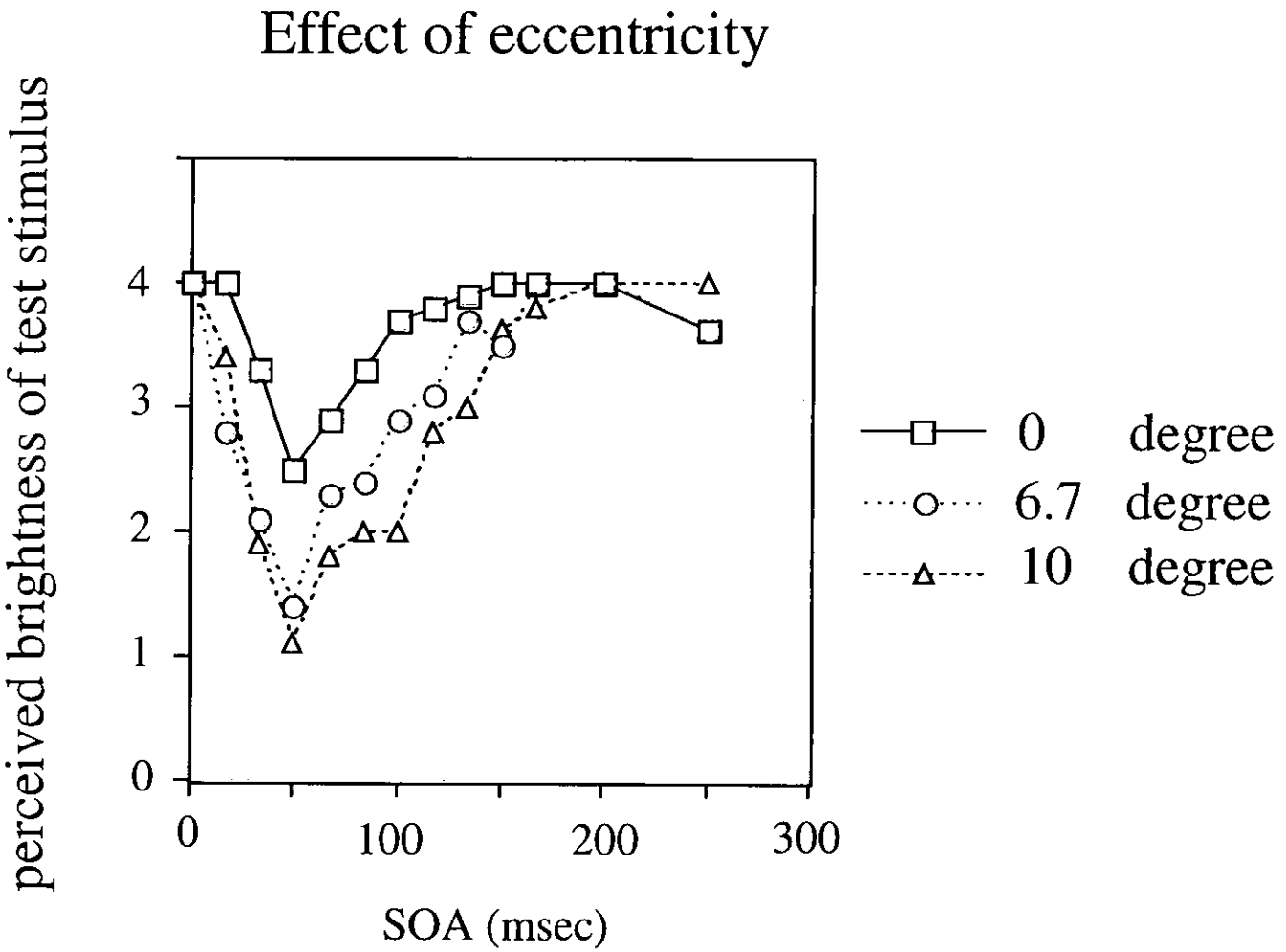

Effect of eccentricity
perceived brightness of test stimulus
0
1
2
3
4
0
100
200
300
SOA (msec)
0 degree
6.7 degree
10 degree

Fig. 12

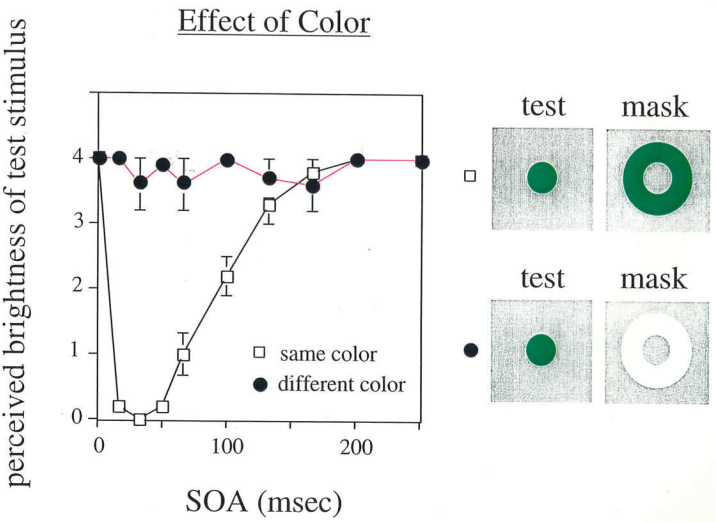
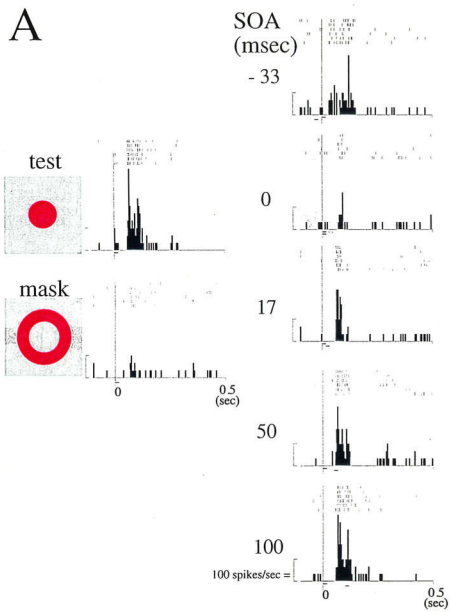

Effect of Color
perceived brightness of test stimulus
4
3
2
1
0
0
100
200
SOA (msec)
same color
different color
test
mask
test
mask

Fig. 13


A
SOA (msec)
- 33
test
0
mask
17
0
0.5 (sec)
50
100
100 spikes/sec =
0
0.5 (sec)

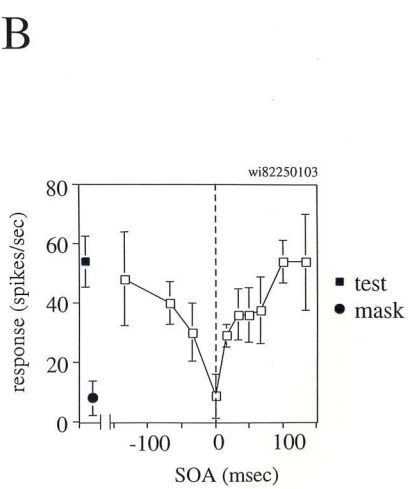
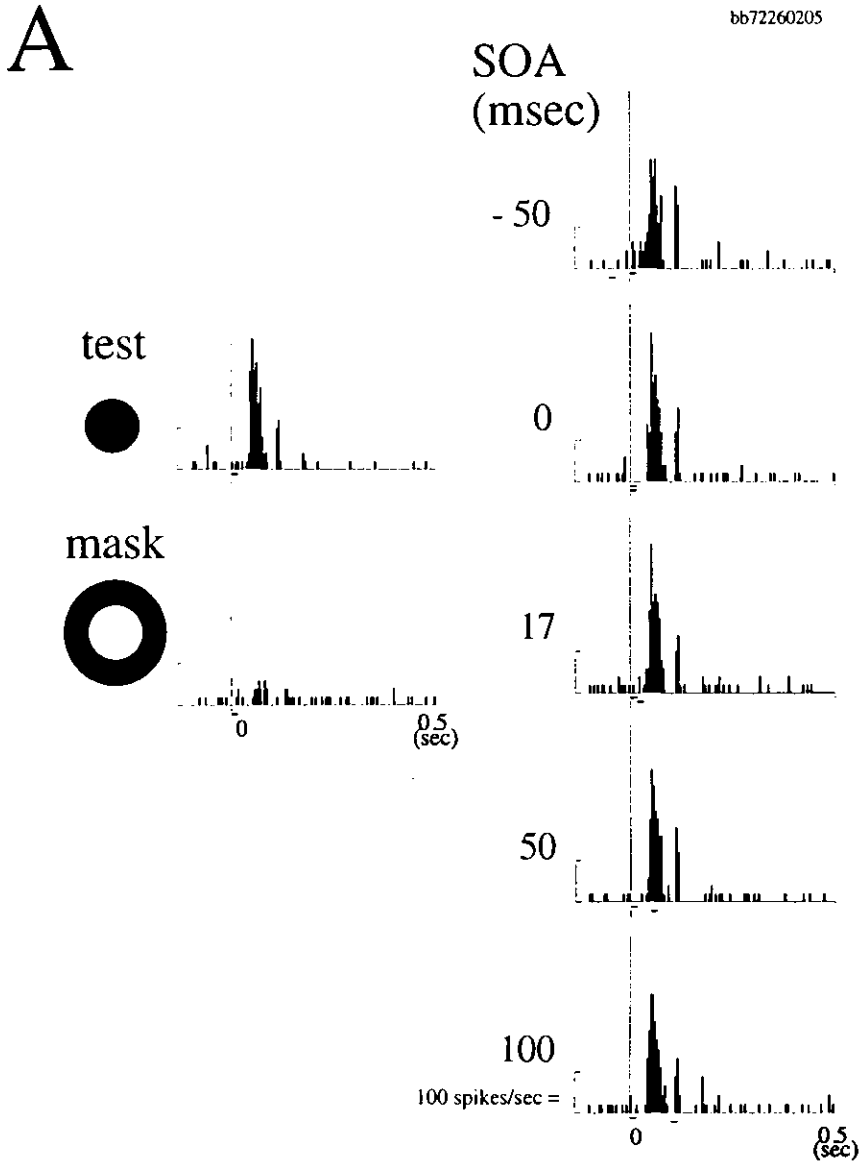

B
wi82250103
80
60
40
20
0
response (spikes/sec)
-100
0
100
SOA (msec)
test
mask

Fig. 14


A
bb72260205
SOA
(msec)
- 50
test
0
mask
17
0
0.5
(sec)
50
100
100 spikes/sec =
0
0.5
(sec)

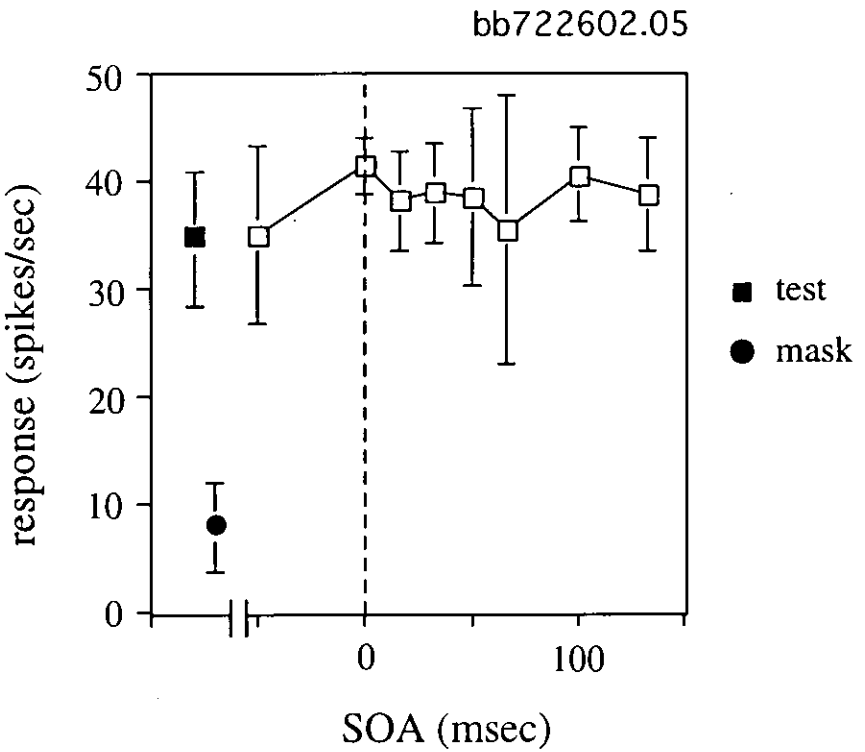

B
bb722602.05
response (spikes/sec)
50
40
30
20
10
0
0
100
SOA (msec)
test
mask

Fig. 15

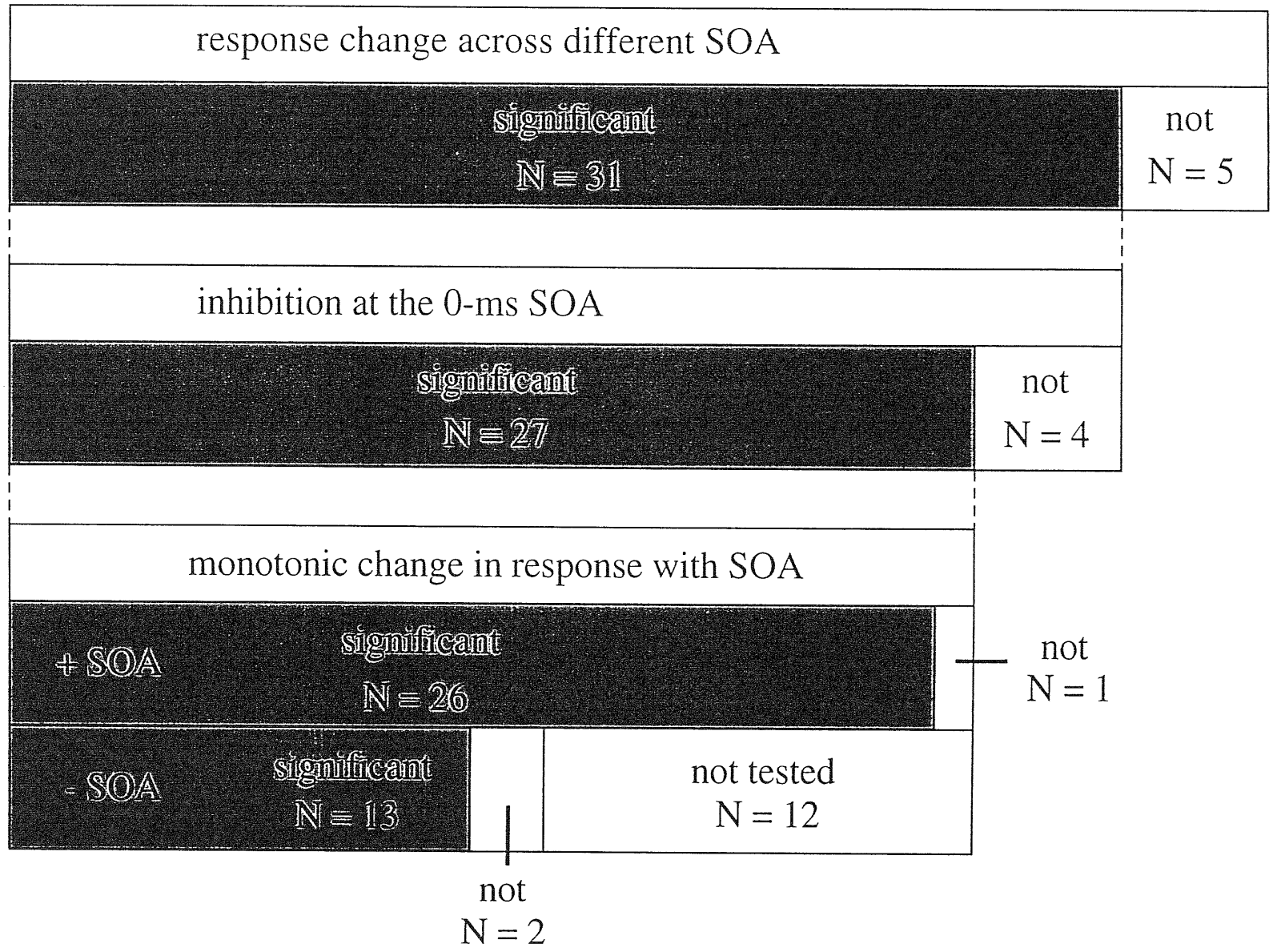

response change across different SOA
significant
N = 31
not
N = 5
inhibition at the 0-ms SOA
significant
N = 27
not
N = 4
monotonic change in response with SOA
+ SOA
significant
N = 26
not
N = 1
- SOA
significant
N = 13
not tested
N = 12
not
N = 2

Fig. 16

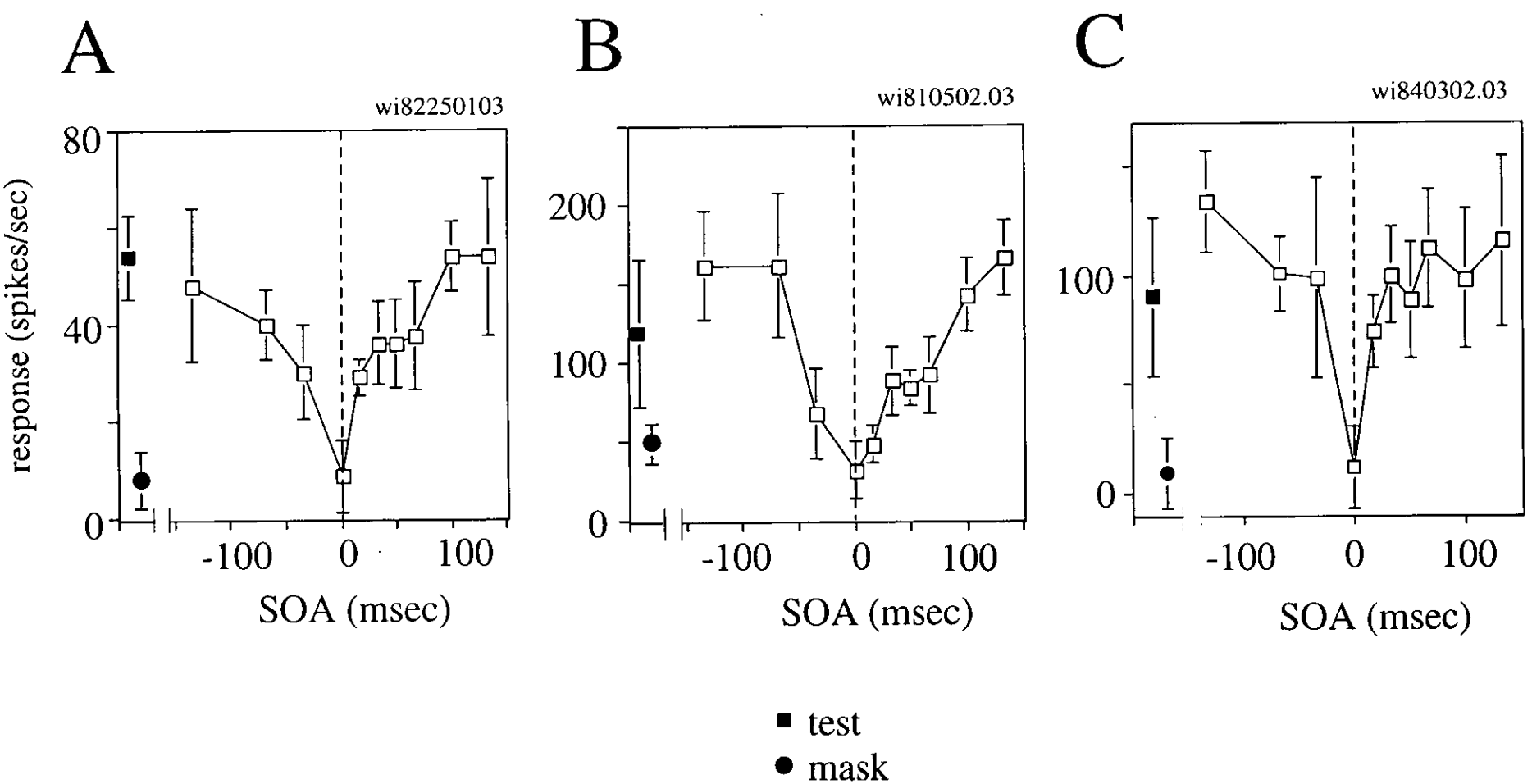

A
wi82250103
80
40
0
response (spikes/sec)
-100
0
100
SOA (msec)
B
wi810502.03
200
100
0
-100
0
100
SOA (msec)
C
wi840302.03
100
0
-100
0
100
SOA (msec)
test
mask

Fig. 17

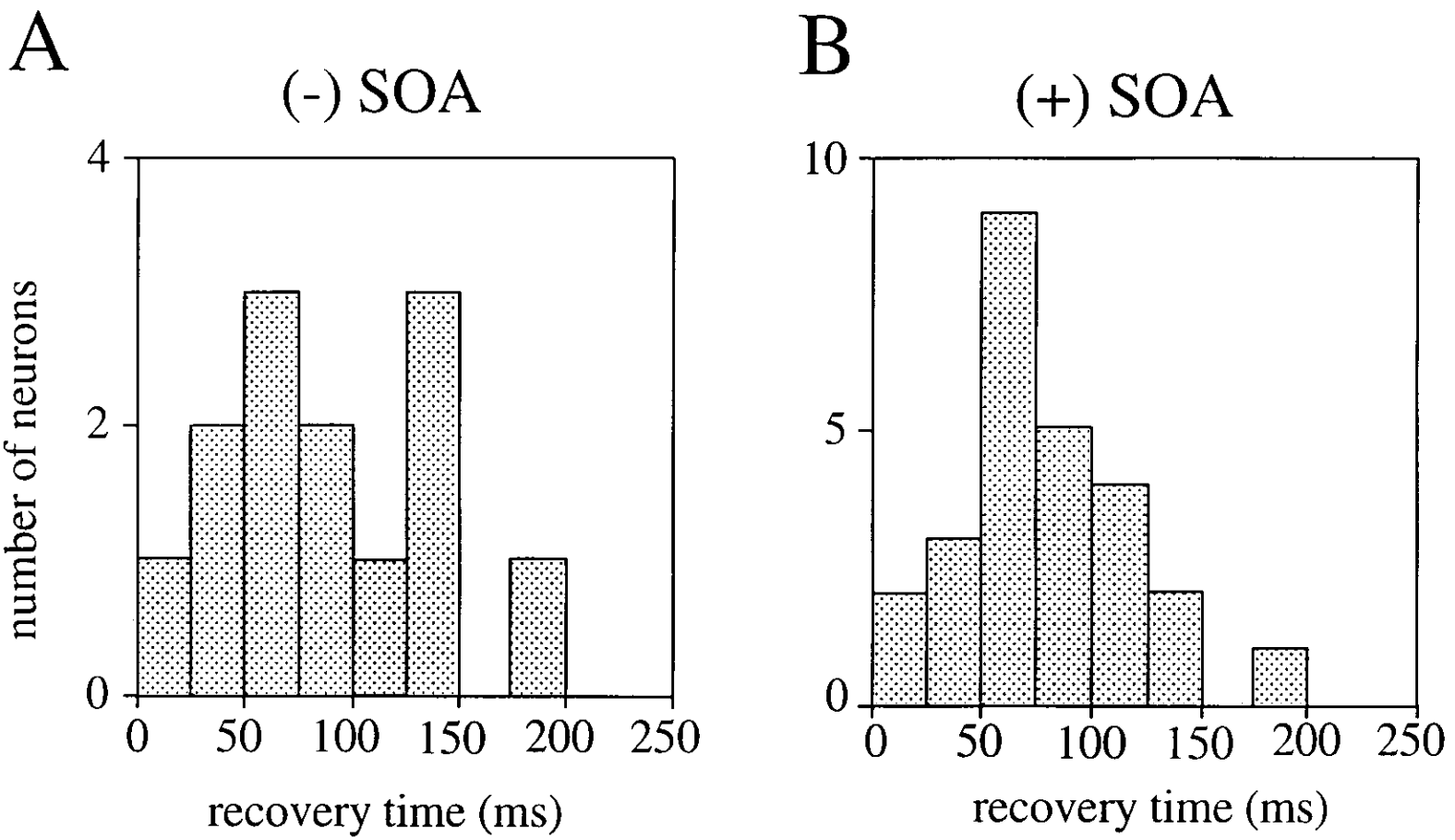

A
(-) SOA
number of neurons
4
2
0
0
50
100
150
200
250
recovery time (ms)
B
(+) SOA
10
5
0
0
50
100
150
200
250
recovery time (ms)

Fig. 18

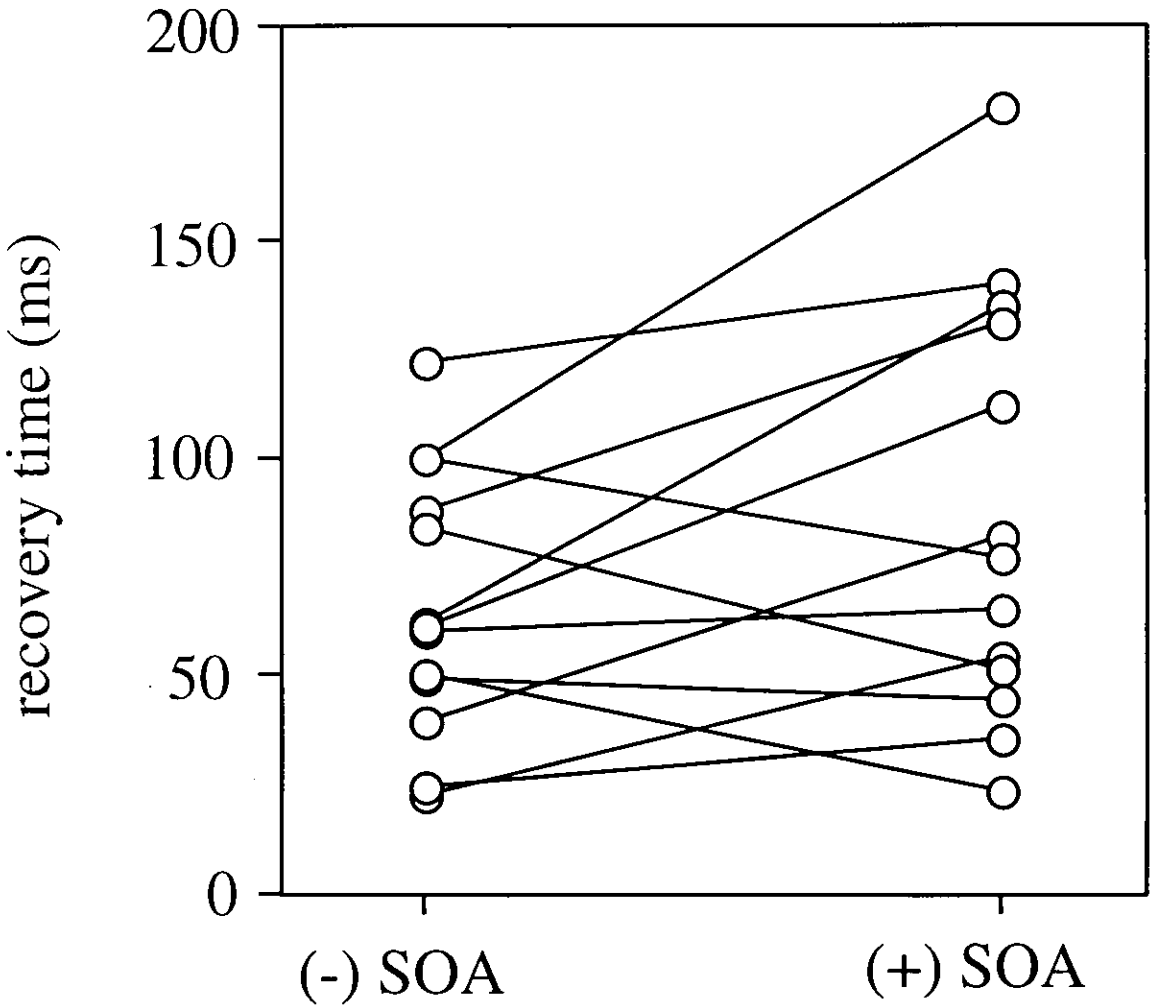


Fig. 19

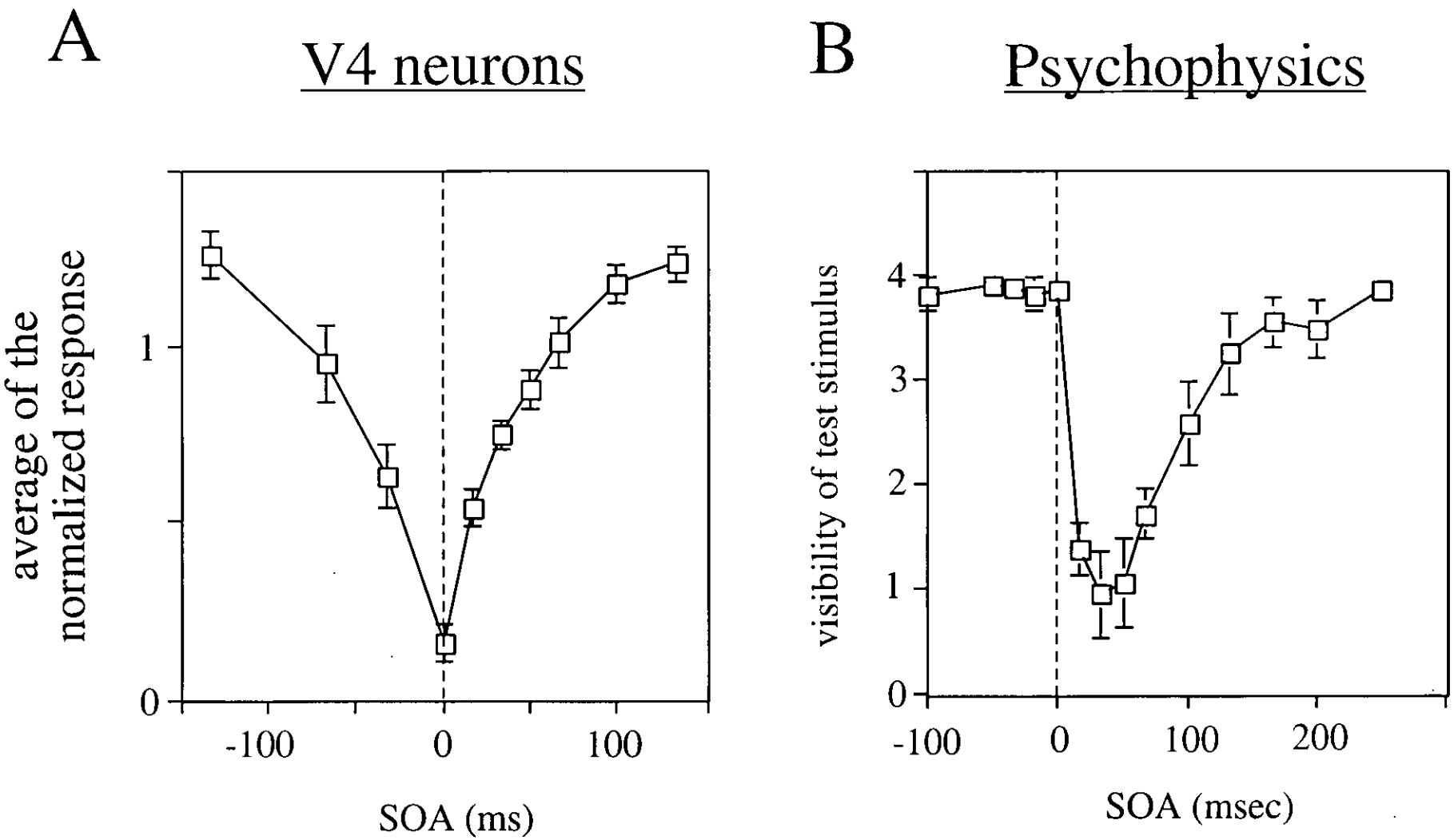

A
V4 neurons
average of the normalized response
1
0
-100
0
100
SOA (ms)
B
Psychophysics
visibility of test stimulus
4
3
2
1
0
-100
0
100
200
SOA (msec)

Fig. 20

Summary of differences between the time course of inhibition in V4 and psychophysics

	V4 neurons	Psychophysics
Time course of inhibition	Shorter duration (65 msec on average)	Longer duration (100-200 msec)
Inhibition in negative SOA	Inhibition	No inhibition

Fig. 2

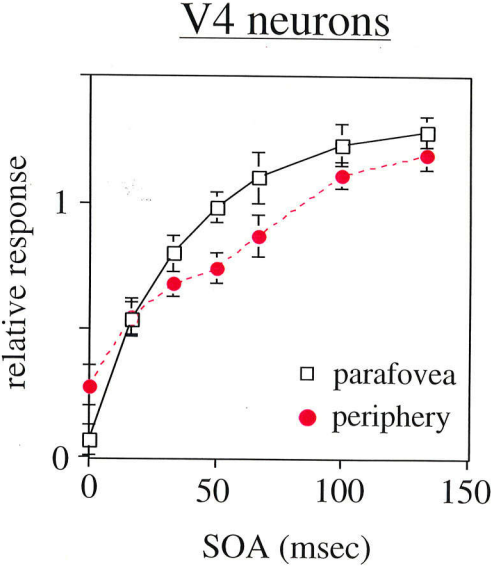

V4 neurons
relative response
1
0
0
50
100
150
SOA (msec)
parafovea
periphery

Fig. 22

Color effect

V4 neurons

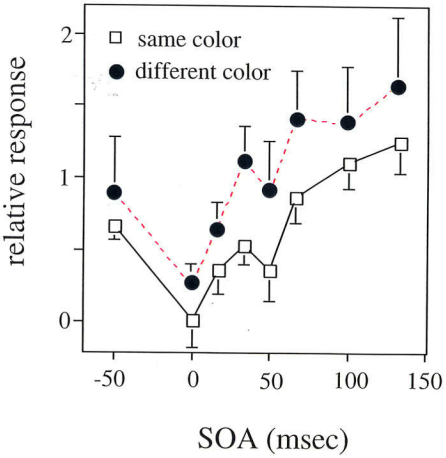
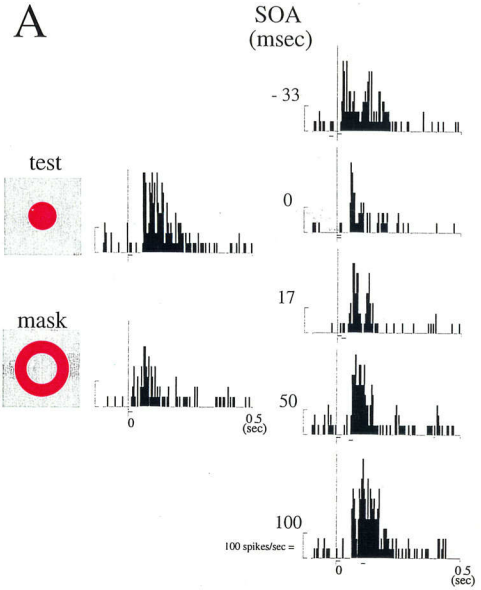


Fig. 23


A
SOA
(msec)
- 33
test
0
17
mask
50
0
0.5
(sec)
100
100 spikes/sec =
0
0.5
(sec)

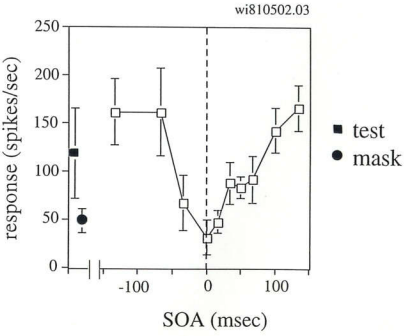

B
wi810502.03
response (spikes/sec)
250
200
150
100
50
0
-100
0
100
SOA (msec)
test
mask

Fig. 24

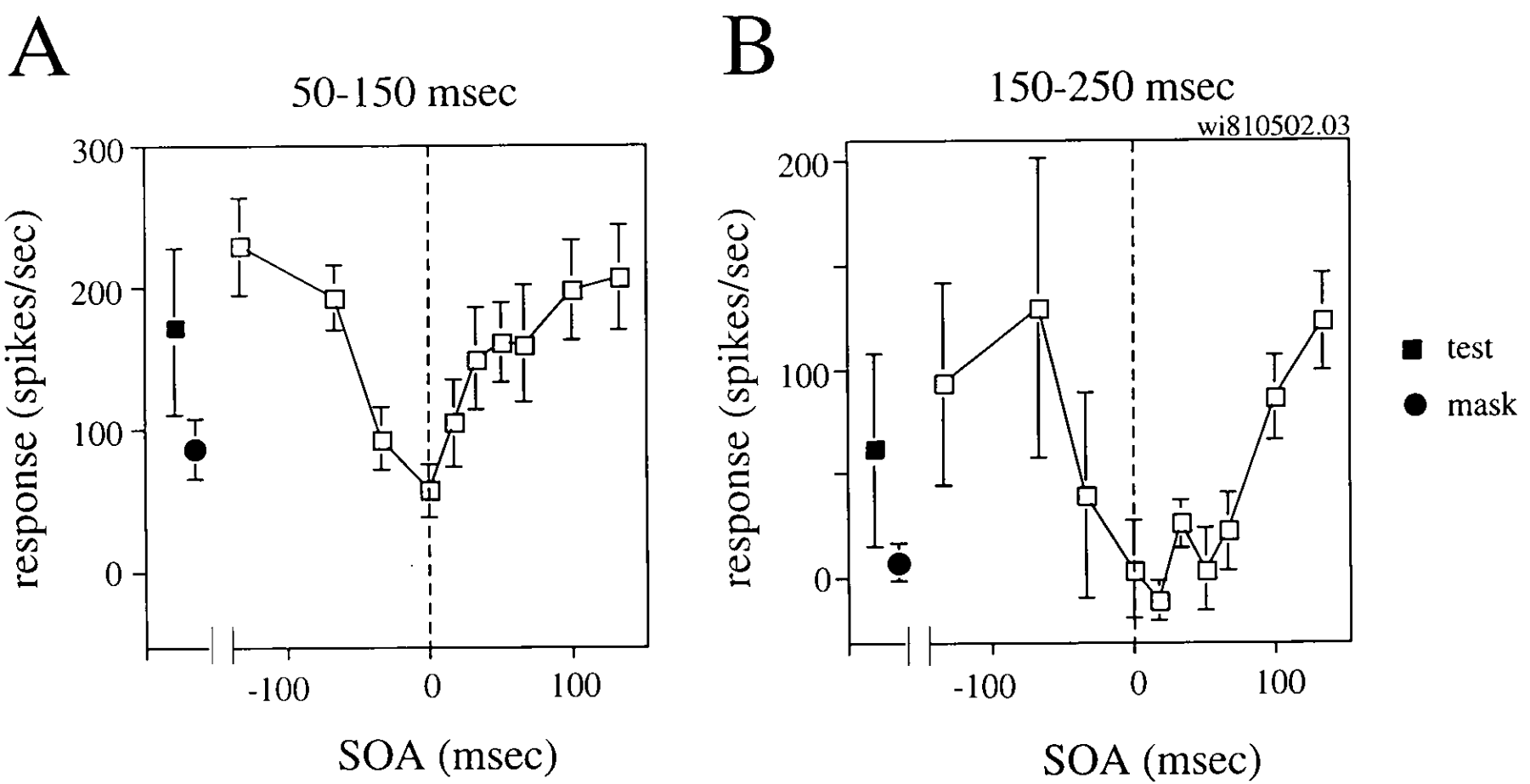

A
50-150 msec
300
200
100
0
response (spikes/sec)
-100
0
100
SOA (msec)
B
150-250 msec
wi810502.03
200
100
0
response (spikes/sec)
-100
0
100
SOA (msec)
test
mask

Fig. 25

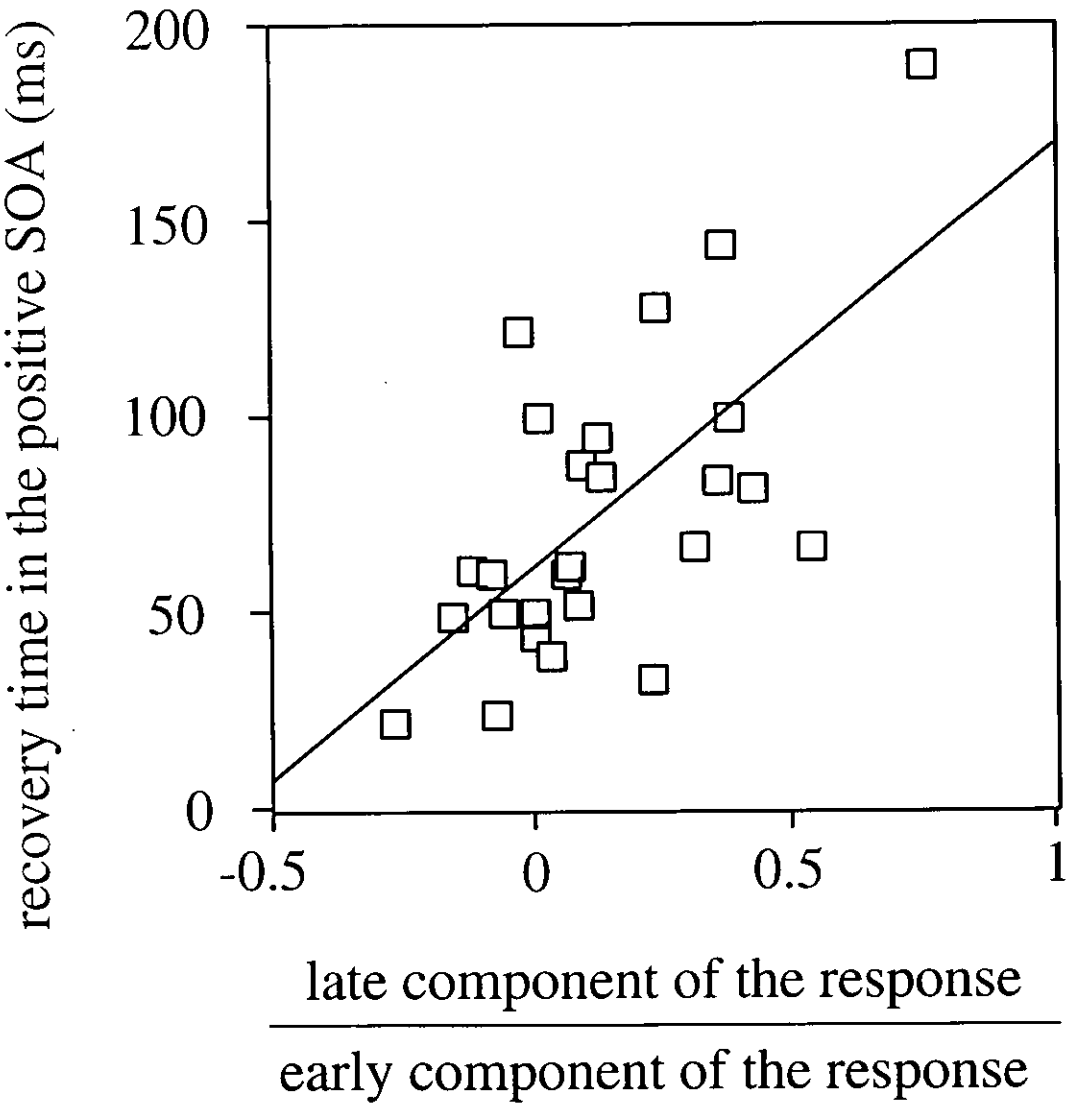
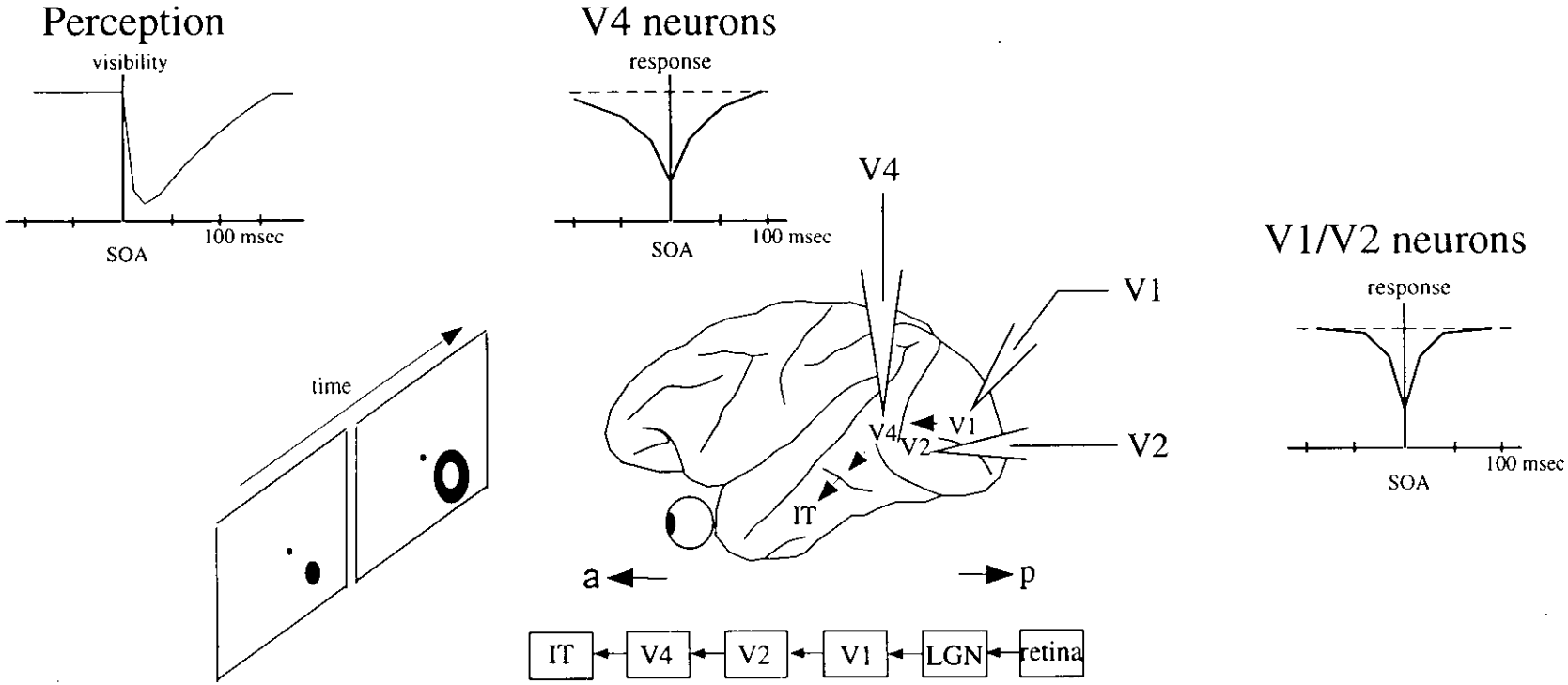

recovery time in the positive SOA (ms)
200
150
100
50
0
-0.5
0
0.5
1
late component of the response
early component of the response

Fig. 26



	Time course of inhibition		Sustained activity
	(+) SOA	(-) SOA	
Perception	~100-200 msec	No inhibition	
V1/V2	~33 msec	~ -33 msec	No
V4	~150 msec (average 65 msec)	~ -150 msec (average -77 msec)	Yes

(V1/V2 data, von der Heydt et al., 1997)