

# Flicker in the visual background impairs the ability to process a moving visual stimulus

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## Abstract

For the detection of a moving object, segregating the object from the background is a necessary first step. This segregation can be achieved by detection of differences in the spatial, temporal and spatio-temporal properties of the object and background. Here we investigate how flicker influences the perception of a moving object in man and monkey, and we examine the neuronal responses in extrastriate medial temporal and medial superior temporal areas (MT and MST) of two rhesus monkeys. The performance of humans and monkeys in a direction discrimination task was impaired in the presence of flicker in the background compared to the static background condition. A similar effect was found in recordings from 155 single units in areas MT and MST during the discrimination task. The discriminability ( $d'$ ) of the neuronal responses in preferred and nonpreferred directions was reduced by 33% on average in the presence of a flicker background compared to the static background. This reduction in discriminability was not caused by differences in variance of the neuronal activity for the two background conditions, but was due to a reduction of the difference between the activities in preferred and nonpreferred direction. This reduction in directional selectivity could be traced back to two different mechanisms: in 32 out of 155 neurons (21%), the decrease resulted from an increase in the response to the stimulus moving in the nonpreferred direction; in 62 out of 155 neurons (40%), the reduction in directional selectivity was due to a decrease in the response to the preferred direction. These results give deeper insights into how moving stimuli are processed in the presence of background flicker as present in natural visual scenes.

## Introduction

The correct processing of visual motion is of great importance for animals, humans and computer vision applications. The analysis of visual motion provides the input for image segmentation, structure-from-motion, time-to-collision, recovery of three-dimensional arrangement of objects, goal-directed behaviour and other visual tasks (for overview see Nakayama, 1985). An empirical indication for the importance of motion processing is the fact that human subjects are highly precise in the detection of velocity differences in a visual display (McKee, 1981; Orban *et al.*, 1984).

The basic properties of motion perception have been traditionally studied in the laboratory using small moving objects or patches of moving random dots presented against a dark, homogeneous background. In the real world, however, the situation is usually more complicated. When the moving object is presented in front of a highly structured visual background, the properties of the background interact with those of the object. An object moving across a homogeneous dark background can be reliably detected by many different features (luminance, flicker, contrast, colour, etc.). However, if the object moves across a highly structured background, some of these features become ambiguous or lose their power to separate object and background completely. The system has to reevaluate the relative importance of object segregation cues depending on the individual background situation.

The properties of a visual background can differ from the moving object either purely in the spatial (texture) domain or in the temporal (flicker) domain or in the spatio-temporal (motion) domain. When the spatial properties of the background match those of the moving object, the effect of luminance and contrast as segregation cues is abolished. Although the moving object is only segregated by its temporal and spatio-temporal properties, we are able to perceive the motion precisely (from Koffka, 1935 to Nakayama, 1985).

When a structured background is not stationary but dynamic (i.e. the elements change their position randomly like the leaves of a tree in a storm), a moving object cannot be separated by purely temporal segregation cues. The flicker induced by the object motion cannot be differentiated from the flicker induced by the dynamic random-dot background. Obviously, purely spatial as well as purely temporal cues are no longer valid for the object segmentation; the only class of segregation cues which is left for object detection are the spatio-temporal or motion cues. However, we are able to perceive this motion correctly (Zanker, 1993) and we are able to track it by smooth pursuit eye movements (Butzer *et al.*, 1997).

It is reasonable to assume that the above-mentioned losses of relevant cues for object detection could result in a reduction in the ability to perceive the motion of a stimulus. The effect of flicker on sensory and sensorimotor performance has been shown psychophysically in several earlier investigations (Macknik *et al.*, 1991; Scase *et al.*, 1996; Baccino *et al.*, 2001). It has been reported that flicker is able to increase the perceived velocity of slowly moving random dot patterns; this effect was named 'temporal capture' (Treue *et al.*, 1993). However, at higher stimulus velocities no influence of flicker was reported (Zanker & Braddick, 1999).

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TABLE 1. Comparison of the different setups used for the human psychophysics, monkey psychophysics and single-unit recordings

	Human psychophysics	Monkey psychophysics	Monkey recordings
Environment			
Ambience	Dim laboratory	Darkness	Darkness
Visualization	Monitor	Projector	Projector
Frame Rate	70 Hz	60 Hz	60 Hz
Viewing distance	70 cm	85.5 cm	85.5 cm
Size	32° width 23° height	74° width 66° height	74° width 66° height
Number of pixels	320 × 200	1280 × 1024	1280 × 1024
Background properties			
Luminance dots	2.0 cd/m <sup>2</sup>	1.9 cd/m <sup>2</sup>	1.9 cd/m <sup>2</sup>
Luminance back.	< 0.1 cd/m <sup>2</sup>	< 0.1 cd/m <sup>2</sup>	< 0.1 cd/m <sup>2</sup>
Dot density	4%	2%	2%
Flicker density	0, 1, 5, 10, 25, 50, 75, 100%	0, 100%	0, 100%
Stimulus properties			
Stimulus height	7°	10°	10°
Stimulus width	3.5°	3°	2.5°–5°
Horizontal startposition	3° left–3° right	0°	15° left–15° right*
Vertical startposition	1° down	1° down	6° up–8° down*
Stimulus duration	14, 43, 72, 100, 129 ms	100, 300, 500, 700, 900 ms	1500 ms
Stimulus speed	9°/s	10°/s	8–15°/s
Increment/frame	0.13°	0.17°	0.13–0.25°

\*Depending on receptive field position.

To address the question of how a moving stimulus is processed in the presence of flicker in the background, we performed two series of experiments. First, we investigated the effect of the temporal structure of the background on the perception of moving objects in humans and subhuman primates. Second, we analysed the neuronal responses recorded from motion areas MT and MST (medial temporal and medial superior temporal areas) depending on the background of a moving stimulus. The motion perception of the monkeys was also monitored during the single-unit recordings. Preliminary results have been published (Churan & Ilg, 2000).

## Materials and methods

To examine the influence of background flicker on the ability of humans and monkeys to detect the direction of a moving stimulus, we ran similar experiments with human subjects and rhesus monkeys. In addition, we recorded and analysed the neuronal processing in the monkey experiments.

### Human psychophysics

#### Subjects

Six subjects (three male and three female, ages between 26 and 40 years) participated in the experiments. All of them had a normal or corrected-to-normal visual acuity.

#### Stimulus presentation

The motion stimuli were presented on a 17-inch monitor (details in Table 1). The experiments consisted of single trials, during which a random dot background was presented with a dot density of 4% white dots on a dark screen. Different densities of flicker in the background were induced by random changes in the position of a certain percentage of the dots in each transition between two consecutive video frames while the other dots remained stationary (see Fig. 1A). The dots which changed their position were selected randomly in each transition between two frames. The percentage of changing dots was 0, 1, 5, 10, 25, 50, 75 or 100% of all dots.

At the onset of each trial, the fixation cross and the background were presented for 400 ms. After this period the fixation cross and the

background were presented together with a motion stimulus, which appeared in a random horizontal position on the screen, moving coherently in the leftward or rightward direction. The stimulus consisted of a rectangular bar of random dots (with dot size and dot density identical to the background) covering  $3.5^\circ \times 7^\circ$  of the visual field (Fig. 1B). The duration of the stimulus presentation was 1, 3, 5, 7 or 9 successive frame changes (i.e. 14, 43, 72, 100 and 129 ms). After the stimulus disappeared, the background and the fixation cross remained visible for another 400 ms.

The subjects were asked to fixate on the centre of a small red cross (size 40 min of arc) above the centre of the stimulus field during the entire trial. After the presentation of the moving stimulus, subjects had to report the perceived direction of the moving object by pressing one of two buttons. For each density of background flicker and for each duration of stimulus presentation 18 trials were carried out, resulting in 630 trials per subject. The duration of the experimental session never exceeded 30 min.

#### Data analysis

For each density of background flicker, the percentage of correct responses was calculated as a variable dependent on the duration of stimulus presentation ( $x$ ). A sigmoid psychometric function was fitted to the data using the equation:

$$y(x) = a/[1 + e^{-b(x-c)}] \quad (1)$$

The discrimination threshold was determined as the presentation duration at which the percentage of correct responses reached the level of 75%. To compare the discrimination thresholds for different flicker densities, a one-factorial ANOVA and a *post hoc* Scheffé test were used.

### Psychophysics and chronic single-unit recordings in trained rhesus monkeys

#### Surgical preparations and recording procedure

Two rhesus monkeys (F and G) were used in the single-unit recording experiments. Under sterile conditions and intubation anaesthesia (isoflurane), the monkeys received a dental cement implant including head holder and recording chamber as well as a subconjunctival

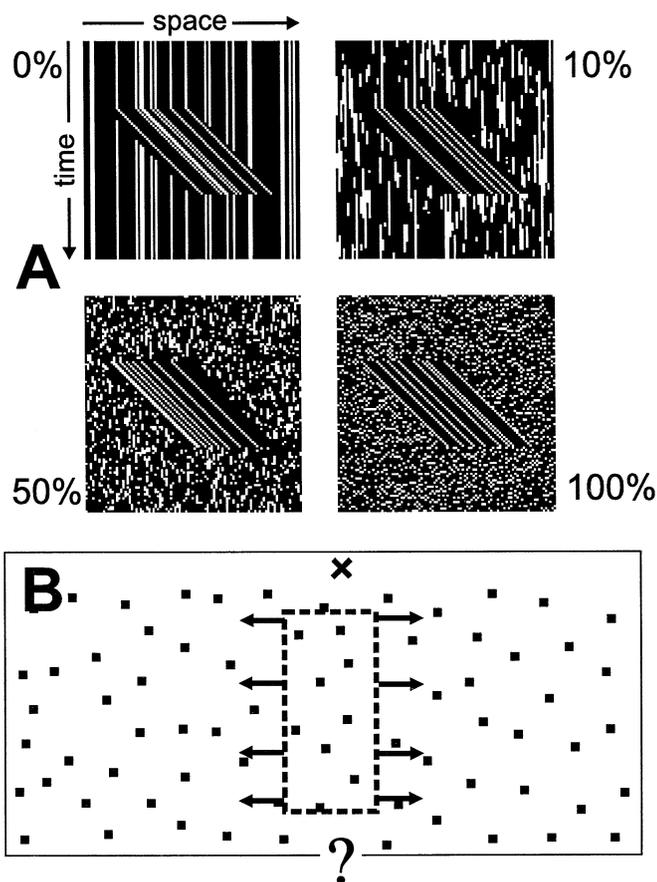


FIG. 1. (A) Space–time diagrams of the discrimination stimulus at four different densities of flicker in the background. (B) Sketch of the direction discrimination stimulus used in the experiments. A rectangular block (size  $3.5 \times 7^\circ$ ) of randomly placed dots moved coherently leftward or rightward. The background always had the same density of white dots (4%) as the object. The 'x' represents the fixation target.

search coil to precisely monitor the eye position (Robinson, 1963; Judge *et al.*, 1980). All animal procedures were carried out in accordance with the Guidelines for the use of Animals in Neuroscience Research laid down by the Society for Neuroscience and the German law, and were approved by the local ethics committee. The centre of each recording chamber was aimed at MST (lateral 19, posterior 3.5, dorsal 16 mm) tilted  $30^\circ$  upwards in a parasagittal plane. After recovery from surgery, the monkeys were familiarized to the laboratory, including the head restraint. After calibration of the eye movement signal, the monkeys learned to report the perceived direction of the stimulus by a saccade as indicated in Fig. 2. The single-unit activity was recorded using self-made glass-isolated tungsten electrodes whose high stability and stiffness allowed transdural tracks without using a guiding tube. The microelectrode signal was preamplified, low-pass filtered at 10 kHz and fed to a multispikes detector (MSD Alpha Omega, Nazareth, Israel). The temporal resolution of the sampling of the neuronal activity was 4 kHz. Horizontal and vertical eye position was sampled at 12-bit with 1 kHz per channel.

#### Visual response properties

For each neuron, the location of the receptive field was mapped using a manual procedure in which the investigator used a mouse-driven visual stimulus to determine the borders of the receptive field.

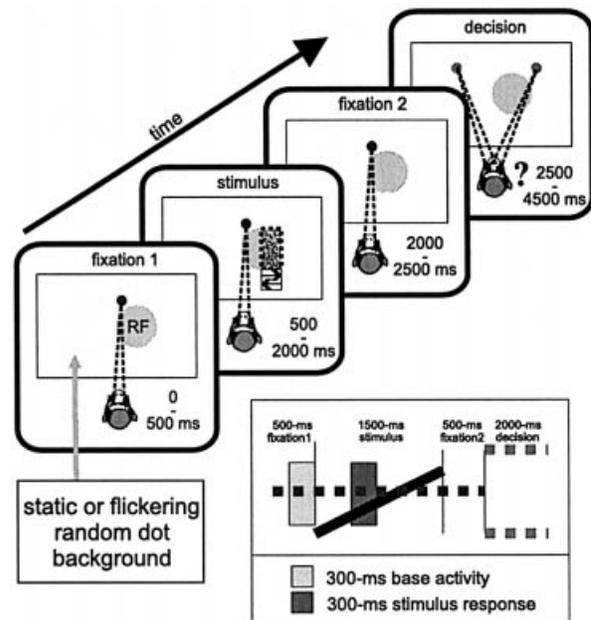


FIG. 2. Sketch of the events during a single trial. Each trial was subdivided into four periods. The monkey had to fixate a red dot in the first three periods while the static or flicker background (periods 1–3) and the motion stimulus (period 2) were presented. In the fourth period, the monkey reported the perceived direction of stimulus motion by a saccade towards the target located in the direction of the movement of the previously displayed stimulus. The base activity (i.e. the neuronal response to the static or flickering background before the presentation of the moving stimulus) of a neuron was obtained during the last 300 ms interval of the first fixation period. The neuronal response to the stimulus was obtained during the stimulus presentation in a time window of 300 ms, while the stimulus moved through the centre of the receptive field.

The directional and speed tuning were measured using a random dot pattern moving within a circular aperture positioned on the receptive field. The strength of the directional selectivity was calculated by the direction index ( $DI$ ), defined as:

$$DI = 1 - (A_{\text{non-pref}}/A_{\text{pref}}) \quad (2)$$

where  $A_{\text{non-pref}}$  is the mean of activity obtained during stimulus movement in non-preferred direction, and  $A_{\text{pref}}$  is the mean of activity during stimulus presentation in the preferred direction.

#### Direction discrimination task

In the monkey experiments, the motion stimuli used were nearly identical to those used for the human psychophysics. The stimuli were back-projected on a tangent screen by means of a video projector (Electrohome ECP 4100 Electrohome, Kitchener, Canada; for details see Table 1).

The sequence of events of the direction discrimination task is shown in Fig. 2. Like the human subjects, the monkeys fixated on a small red stationary target (diameter 20 min of arc) placed in the centre of the visual field. The size of the gaze control window was  $2^\circ$  in each dimension. At the onset of each trial, either a static (0%) or a 100% flicker random dot background was presented for 500 ms. The base activity of a neuron was determined in a 300-ms time interval during this period. The motion stimulus was then presented for 1000–1500 ms moving either in the leftward or rightward direction over the static or flickering background. The stimulus trajectory was adjusted to ensure that the bar crossed the centre of the receptive field during the presentation time. The height of the moving object was fixed to

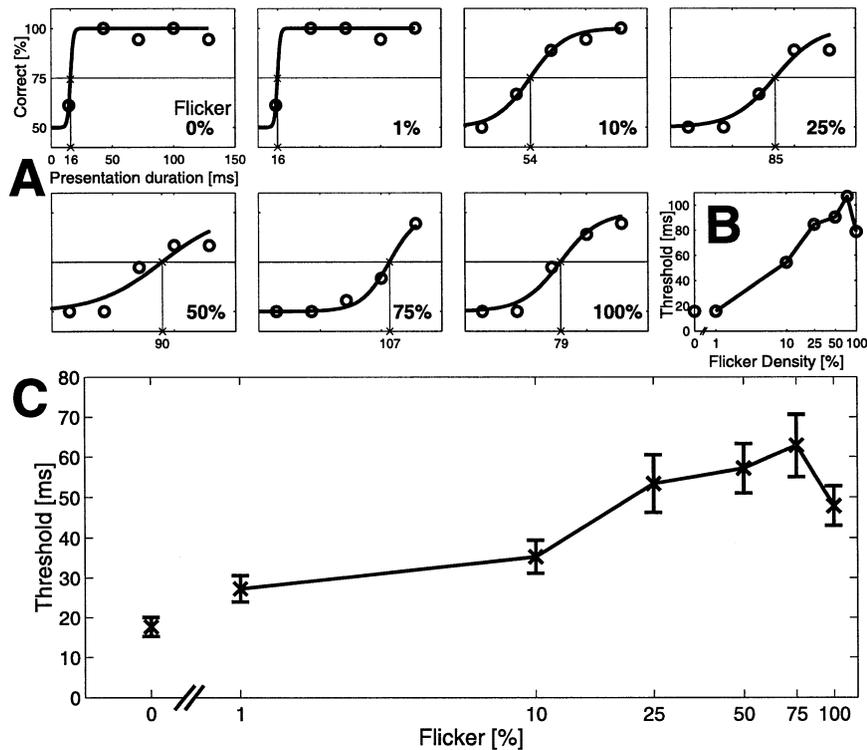


FIG. 3. Human discrimination thresholds during stimulus presentation with different densities of flicker in the background. (A) Percentages of correct responses plotted against the presentation time of the stimulus for one typical subject. Raw data and the fitted sigmoid function are shown. The vertical line indicates the position of the discrimination threshold calculated at 75% correct responses. (B) Discrimination thresholds plotted against the different densities of background flicker for the same subject. (C) Discrimination thresholds (mean and standard error) as a function of the different densities of background flicker for six subjects.

10°, while the width was adjusted between 2.5° and 5° so that it was always smaller than the width of the receptive field of the recorded neuron. The velocity of the moving stimulus was usually 10°/s; it was varied sometimes in the range from 8 to 15°/s to obtain a better directional selectivity. The response of the neuron to the stimulus was determined during a 300-ms period, when the stimulus crossed the centre of the receptive field. After the stimulus disappeared, the monkeys had to maintain fixation for another 500 ms. Subsequently, they had to report, within 2000 ms, the perceived direction of stimulus motion by making a saccade to one of two alternative targets (diameter 20 min of arc, green colour) which were presented 20° left and right of the fixation point. For a correct response the monkeys were rewarded with a small portion of water or apple juice.

To address the effects of the temporal background structure on motion perception of the monkeys, we varied the presentation duration of the stimulus moving across a stationary (0%) or flickering (100%) background. We used a sigmoid function (Eqn 1) to fit the obtained results and to determine the discrimination threshold in the same way as for the human subjects.

Table 1 informs of the details of the setups used in the human psychophysics, the monkey psychophysics and the single-unit recording.

#### Histology

Following the experimental period of  $\approx 3$  years, one monkey was killed and the brain was histologically processed to verify the recording positions. After perfusion of the animal, the brain was cut parasagittally in 40- $\mu$ m sections. The sections were stained for cell

bodies (Nissl) and for myelination (Gallyas). Area MT in the posterior bank of the superior temporal sulcus (STS) was determined by the dense myelination visible in the Gallyas staining. The reconstruction of the recording sites was made possible by injections of fluorescent tracers into sites that were identified during the time of data collection as areas MT and MST, based on response properties. The second monkey is currently being used in an ongoing related study.

## Results

### Psychophysics

For each density of flicker in the background, the percentage of correct responses was calculated for the different durations of stimulus presentation, as shown in Fig. 3A for one typical subject. The data was fitted with a sigmoid function (Eqn 1) and the thresholds for 75% correct responses (shown as vertical lines in the figure) were calculated from this function. The summarized dependence of the thresholds on the percentage of flickering dots is shown in Fig. 3B for the same subject. The thresholds of all subjects increase with the flicker density of the background (Fig. 3C) from 17 ms on average in the absence of flicker to  $\approx 63$  ms with a flicker density of 75% ( $P < 0.001$ , Scheffé test). The effect of the flicker background shows a saturation. The thresholds for flicker density of 25% and above were never significantly different from each other.

We also investigated in one monkey (G) whether the same influence of flicker in the background can be demonstrated. When

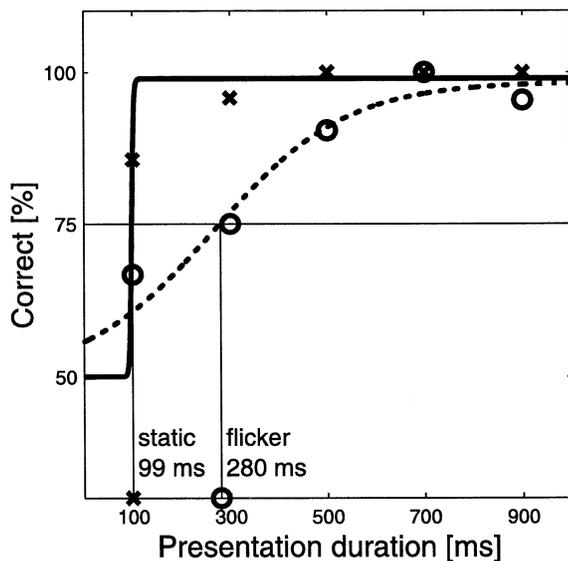


FIG. 4. Effect of the temporal structure of the background on performance in the motion discrimination task for one monkey (G). The percentages of correct responses are shown plotted against the presentation duration; solid line at flicker density of 0% and dashed line at 100%. The vertical lines indicate the position of the discrimination threshold calculated at 75% correct responses.

densities of 0% and 100% flicker in the background were compared, qualitatively the same effects could be shown for the performance of the animal (Fig. 4). Similar to what we found for human subjects, the presence of flicker in the background results in an increase in stimulus duration required for motion discrimination from 99 to 280 ms. However, it must be noted that the stimulus durations in the monkey experiment are clearly larger than those in the human experiments.

To ensure that the stimulus crossed the receptive field of the recorded neuron, we presented the stimulus for 1500 ms in the single-unit recordings. Despite this long stimulus presentation period, the direction discrimination performance varied significantly between the static and the flicker backgrounds. The monkeys reached on average 90% correct trials during presentation on a static background and 72% during presentation on a flicker background ( $P < 0.001$ ,  $t$ -test,  $n = 155$ ) during the recordings of all neurons.

#### Single-unit responses

Having shown that the temporal structure of the background affected the perception of a moving stimulus in humans and monkeys, we investigated the neuronal processing of visual motion in our monkeys. We recorded single-unit activity in areas MT and MST from two monkeys performing the direction discrimination task with either static or flicker background with 100% flickering dots.

#### Visual response properties

Our data sample obtained from two monkeys consisted of 65 neurons recorded from area MT and 90 neurons from area MST. All neurons in our sample had to show a significant directional selectivity to horizontal stimulus movement, i.e. the response to a stimulus moving in the preferred direction had to be significantly larger ( $P < 0.01$ ,  $t$ -test) than the response to a stimulus moving in the nonpreferred direction. For methodological reasons it was impossible to adjust the direction of stimulus movement to the actual preferred direction of the recorded neuron. The differentiation between areas MT and MST

at the time of the experiment was based on the 3-D coordinates of the recording location together with the ratio of eccentricity and size of the receptive field. As expected, the receptive field size of both areas increased linearly with eccentricity; the fields in area MST were significantly larger than the receptive fields in area MT at the same eccentricity ( $P = 0.005$ ) (Komatsu & Wurtz, 1988). In addition, the presence of an extra-retinal signal during the execution of smooth pursuit eye movements (Newsome *et al.*, 1988) was used as an indicator for recordings from area MST. The separation of areas based on these parameters was confirmed in one monkey by the anatomical postmortem reconstruction, showing that the recordings from area MST were located within the floor of the STS where the subarea MSTl (the lateral part of area MST) was described (Komatsu & Wurtz, 1988) (Fig. 5).

#### Direction discrimination task

The trajectory of the stimulus, the eye movements of the monkey, and the responses of an individual MT neuron during the different parts of a discrimination trial, as explained in the Materials and Methods section, are shown in Fig. 6. The stimulus moved on a static background in the preferred direction of the neuron. Note that the monkey correctly reported every presentation of the stimulus, as indicated by the saccades at the end of each trial.

#### Discriminability with static and flicker backgrounds

Because the flicker background impaired the discrimination thresholds for the direction of a moving stimulus, we investigated whether changes in the strength of the directional selectivity of individual neurons parallels the described psychophysical differences.

For each neuron we calculated a discriminability index ( $d'$ ) where

$$d' = 2 \times (A_{\text{pref}} - A_{\text{non-pref}}) / (\text{STD}_{\text{pref}} + \text{STD}_{\text{non-pref}}), \quad (3)$$

and  $A$  and  $\text{STD}$  are the mean and standard deviation of activity obtained in the two directions of stimulus movement.

Figure 7A shows the discriminability expressed as  $d'$ -values of neurons from our sample recorded with the static and flicker backgrounds. The presence of the flicker background caused a reduction in  $d'$  in most neurons recorded from areas MT and MST. The average reduction of  $d'$  by flicker was 33% for all recorded neurons. The reduction in  $d'$  was not significantly different in neurons from areas MT (36%) and MST (30%) (Fig. 7B,  $P = 0.47$ ,  $t$ -test).

According to the calculation of  $d'$  (see Eqn 3), a reduction in the discriminability can arise from changes in either separation or spread of the neuronal responses. In Fig. 8, the standard deviations (SD) of neuronal activities for motion in the preferred and nonpreferred directions are shown. For motion in the nonpreferred direction, the SDs were not significantly different for the presentation on static and dynamic backgrounds ( $P = 0.27$ ,  $t$ -test, Fig. 8A). For motion in the preferred direction the SDs were significantly smaller for the presentation on flicker background than for the presentation on static background ( $P < 0.001$ , Fig. 8B). Because this significant effect potentially increases the  $d'$ -value in the presence of flicker background, the reduction of discriminability for presentation on the flicker background can not be traced back to changes in variance of the data in the two distributions.

For the investigation of changes in the differences in mean activity between preferred and nonpreferred directions, the direction index ( $DI$ ) was calculated. Figure 9A shows the  $DI$  values of neurons from our data sample recorded with the static and flicker backgrounds. The presence of the flicker background caused a reduction of  $DI$  in most

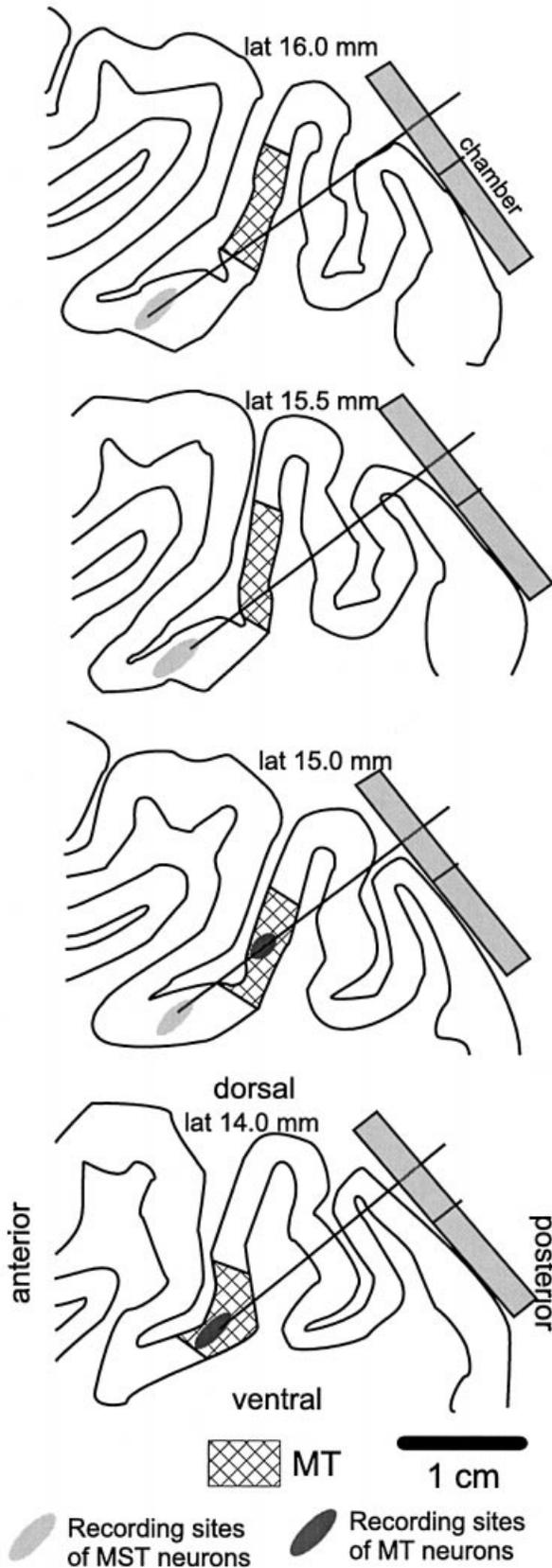


FIG. 5. Drawings of four parasagittal sections of monkey F's cortex, laterality as indicated. Borders of area MT were plotted based on dense myelination determined from Gallyas staining. The position of the recording chamber and direction of the microelectrode penetrations are shown and the sites where MT and MST neurons were recorded are labelled with grey ovals.

neurons recorded from areas MT and MST. The average reduction of *DI* by flicker was 22.5% for all recorded neurons. The reduction in *DI* was not significantly different in neurons from areas MT (22.8%) and MST (22.2%) (Fig. 9B;  $P = 0.92$ , *t*-test).

According to the calculation of *DI* (see Eqn 2), a reduction in the directional selectivity can arise from different sources: either the activity during motion of the stimulus in the preferred direction can be reduced, or the activity during stimulus motion in the nonpreferred direction can be increased. In the following, we investigated whether a single source, both sources independently, or a combination of the two sources was responsible for the reduction in *DI* in our data sample.

*Different possibilities for DI reduction*

The flicker-dependent reduction in *DI* could be due to an increase in the response elicited by movement in the nonpreferred direction without change in the neuronal response to the stimulus moving in the preferred direction. Figure 10 shows a typical example of a neuron decreasing its directional selectivity in this way in the presence of a flicker background. The discharge rate during presentation of the stimulus moving in the nonpreferred direction was increased in the presence of flicker.

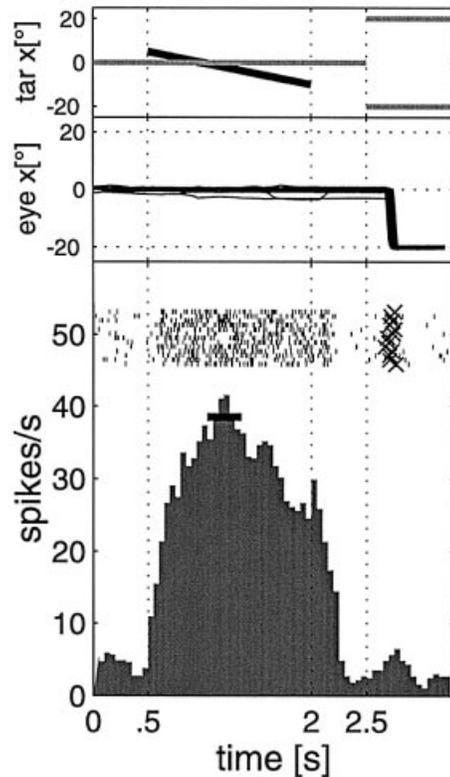


FIG. 6. The response of a typical MT neuron during the direction discrimination trials. The upper row shows the horizontal position of the moving stimulus (black line), fixation point at 0° and response targets at ±20° (grey lines). In the middle row, the horizontal eye position, consisting of fixation over the first three parts of the trial and a saccade indicating the perceived direction of the motion at the end of each trial, is shown for 15 trials. In the lower part, the neuronal activity is shown as raster display and peri-stimulus-time histogram (PSTH; bin size 50 ms). The time of onset of saccades, which is taken as the reaction time, is marked with an × in the raster display. The thick horizontal line in the PSTH specifies the time interval in which the neuronal response to the stimulus was calculated and the mean value of this response.

A subpopulation of 32 out of 155 neurons (21%) showed a significant ( $P < 0.01$ ,  $t$ -test) increase in activity during stimulus motion in the nonpreferred direction when the flicker background was presented, compared to when a static background was presented. From here on, we will term this subgroup 'flicker incremental' (FI)

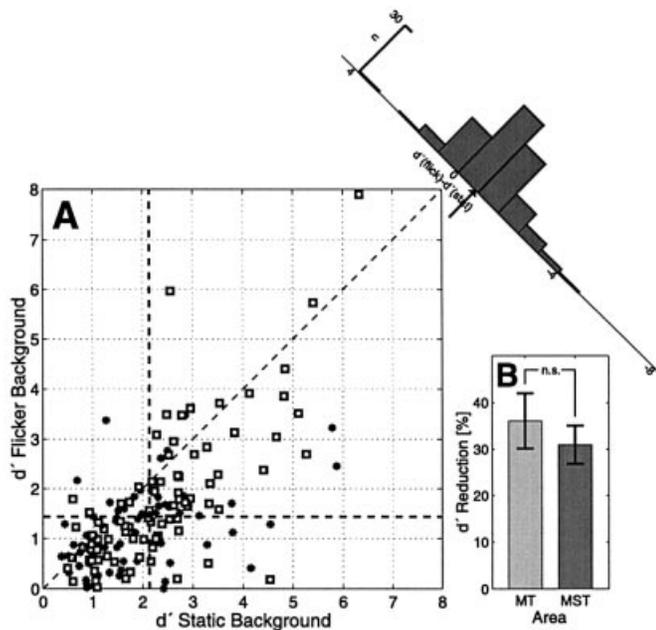


FIG. 7. (A) Comparison of discriminability ( $d'$ ) of the neuronal responses to stimulus movement in the preferred and nonpreferred directions for the stimulus on static and flicker backgrounds. Generally  $d'$  was lower (on average by 33%) in the presence of a flicker background (mean 1.4, dashed horizontal line) than in the presence of a static background (mean 2.1, dashed vertical line). The legend indicates whether the neuron was recorded from area MT (asterisks) or MST (squares). In the diagonal histogram the distribution of the  $d'$ -differences between the two background conditions is shown; the arrow represents the mean of this distribution. (B) There was no significant difference between MT and MST neurons in the changes of  $d'$  with static and flicker backgrounds ( $P = 0.47$ ,  $t$ -test).

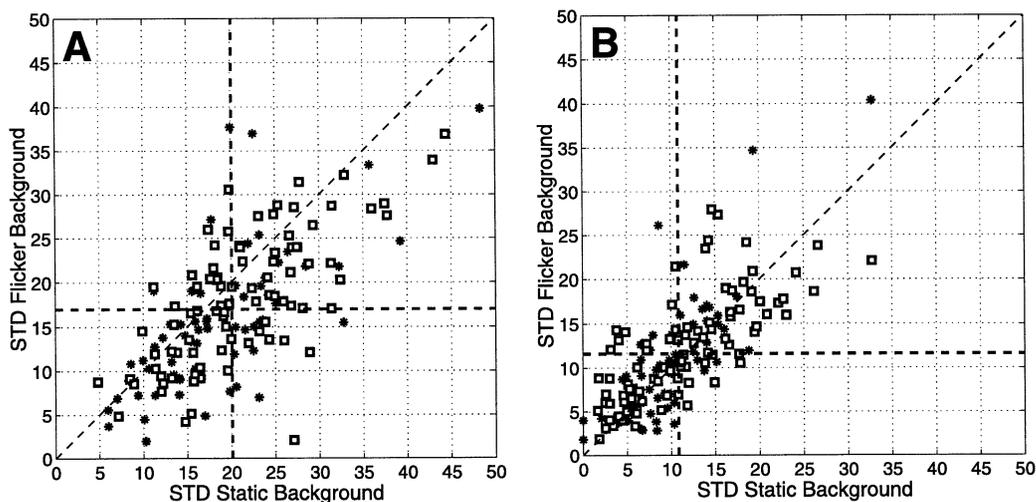


FIG. 8. Comparison of the standard deviations (SD) of the activity during stimulus presentation on static and flicker background. (A) For stimulus motion in nonpreferred direction the SDs are not significantly different ( $P = 0.27$ ,  $t$ -test). (B) For stimulus motion in preferred direction the SDs for motion on flicker background are significantly lower than for static background ( $P < 0.001$ ,  $t$ -test).

neurons. The activity of the FI neurons during stimulus movement in the nonpreferred direction was increased by 66% on average. The changes in responses of all other neurons did not differ significantly from zero. There were no significant differences between areas MT and MST; the frequency of occurrence of FI neurons was not significantly different between the two (14% in MT, 26% in MST,  $P = 0.08$ ). In addition, the mean increase in activity in response to stimulus movement in the nonpreferred direction due to the flicker background did not differ significantly between the two areas ( $P = 0.53$ ,  $t$ -test).

Figure 11 shows another typical neuron reducing its directional selectivity due to the flicker background in a different way. In contrast to the neuron presented in Fig. 10, the discharge rate elicited by a stimulus moving in the nonpreferred direction did not change depending on the background. Alternatively, during stimulus motion in the preferred direction, the response of the neuron was lower in the presence of the flicker background than in the presence of the static background.

Out of 155 neurons, 62 (40%) showed a significant decrease in activity during stimulus motion in the preferred direction when the flicker background was presented. From here on, we will term this subgroup 'flicker decremental' (FD) neurons. The discharge rate of FD neurons during presentation of stimulus motion in the preferred direction on flicker background was on average 52% lower than on the static background; in all other neurons the change was not significantly different from zero. We did not observe significant differences between areas MT and MST; the frequency of occurrence of FD neurons did not differ significantly between the two areas (46% in MT, 36% in MST,  $P = 0.19$ ), and the mean increase in activity did not differ significantly between the two areas ( $P = 0.53$ ,  $t$ -test).

#### Effects of the background on the base activity

When only the static or the dynamic background were presented without a moving stimulus, the activity of the neurons was affected by the background condition. This effect is visible in the responses of the example neuron in Fig. 9. In Fig. 12, the base activities with static and flickering background are compared. As shown in Fig. 12A, the base activity for the flicker background was significantly larger ( $P < 0.001$ ,  $t$ -test) than for the static background. On average, the

base activity for a flicker background was 32% higher than for a static background.

Because the background was able to influence the activity of the neurons even before stimulus presentation and because the moving stimulus never filled the entire receptive field, it is important to investigate the dependency of the changes in base activity on the above-described categories. In a one-factorial ANOVA and the subsequent *post hoc* Scheffé test, the group of FI neurons showed a significantly larger increase in base activity with the flicker background (Fig. 12B) than did the group of FD neurons ( $P < 0.001$ , Scheffé test) and the remaining neurons ( $P = 0.02$ , Scheffé test). No significant differences have been found between the group of FD neurons and the remaining neurons ( $P = 0.12$ , Scheffé test).

No significant differences in changes of base activity were found between neurons from areas MT and MST ( $P = 0.30$ , *t*-test; Fig. 12C).

#### Independence of the FI and FD mechanisms of reduction of directional selectivity

So far, the incremental and decremental effects of flicker have been demonstrated separately. However, the question of whether the two effects are independent or whether they constitute two parts of the same mechanism remains open. As shown above, a subpopulation of 32 FI neurons (21%) showed a significant increase in activity in the nonpreferred direction during the motion trials with flicker background. Another subpopulation of 62 FD neurons (40%) showed a significant decrease in activity in the preferred direction. Only a small

number of neurons (13/155; 8%) showed a combination of both effects.

As an indicator of the difference between the responses to stimulus motion on the two background conditions, a 'background index' (*BI*) was calculated as follows.

$$BI = (A_{\text{flicker}} - A_{\text{static}}) / [\text{maximum}(A_{\text{flicker}}, A_{\text{static}})], \quad (4)$$

Where  $A_{\text{flicker}}$  and  $A_{\text{static}}$  are the mean activities obtained with flicker and static backgrounds, respectively. If the responses elicited by static and flicker backgrounds are identical, *BI* is 0. Values above 0 indicate an increase in activity by the flicker background; values below 0 indicate a decrease. *BI* values of all recorded neurons for the preferred and the nonpreferred stimulus directions are shown in Fig. 13A, including the separation of the populations of FI and FD neurons. It also shows a group of 61 neurons (39%) showing no significant changes in activity in the two directions (marked by dots) and a small group of neurons (8%, marked by '+') showing other effects. To describe more precisely the distribution of the neurons along the different axes, and thereby describe the different types of effects induced by the flicker background, we subdivided the data shown in Fig. 13A into 12 radial segments of 30° each. Segment number 1 is shown as an example; the other segments follow in the clockwise direction. Figure 13B shows the resulting histogram showing a bimodal distribution with maxima near the segments representing the FI neurons (segment number 3, increase of response in the nonpreferred direction) and FD neurons (segment number 6, decrease of response in the preferred direction). The bimodal distribution can be well approximated by a sum of two gaussian functions (significantly better than by a single gaussian fit  $P = 0.03$ , correlation comparison). This bimodal distribution, together with the small number of neurons (8%) showing incremental as well as

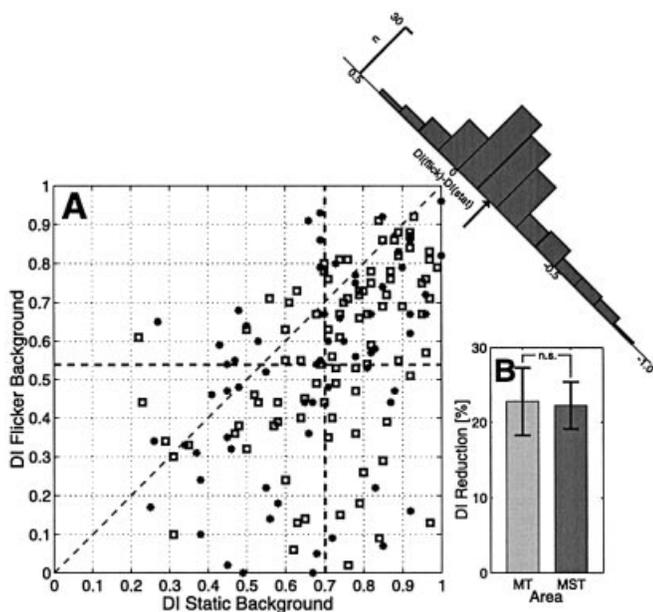


FIG. 9. (A) Comparison of directional selectivity of all neurons for the stimulus on static and flicker backgrounds. Generally the *DI* was lower (on average by 22.5%) in the presence of a flicker background (mean 0.54, dashed horizontal line) than in the presence of a static background (mean 0.70, dashed vertical line). The neurons recorded from area MT are marked as asterisks neurons from area MST as squares. In the diagonal histogram the distribution of the *DI*-differences between the two background conditions is shown; the arrow represents the mean of this distribution. (B) There was no significant difference between MT and MST neurons in the changes of *DI* with static and flicker backgrounds ( $P = 0.92$ , *t*-test).

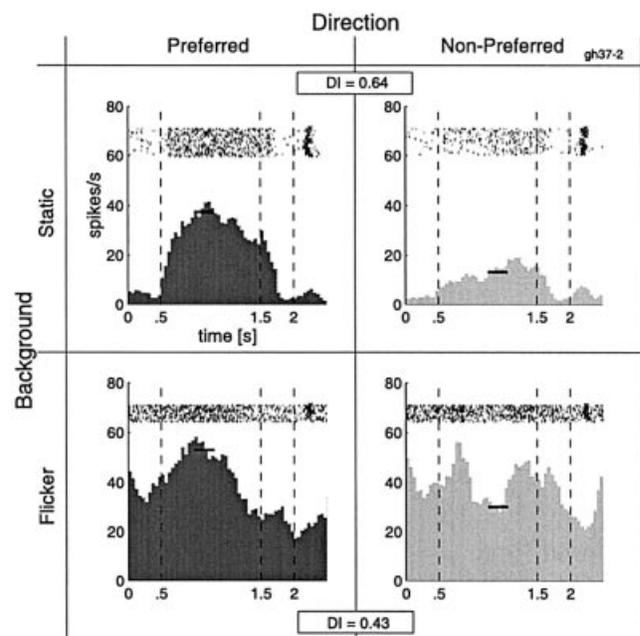


FIG. 10. Responses of a typical flicker incremental (FI) neuron from area MT, whose directional selectivity in the presence of the flicker background was reduced by an increase of activity in the nonpreferred direction. See Fig. 6 for details. For reasons of simplicity, the recorded stimulus and eye position data are not shown. The direction index was reduced from 0.64 with static background to 0.43 with flicker background.

decremental effects, suggests that the two mechanisms are indeed two independent effects whose interaction is rather weak.

The same evaluation as for the neuronal responses was employed for the net responses (stimulus-evoked activity – base activity)

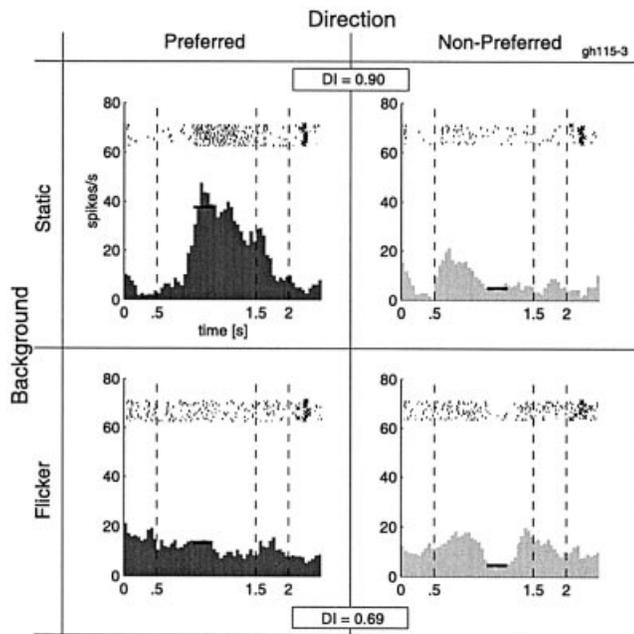


FIG. 11. Responses of a typical flicker-decremental (FD) neuron from area MT, whose directional selectivity in the presence of flicker background was reduced by a decrease in activity in the preferred direction. See Fig. 6 for details. The direction index was reduced from 0.90 with static background to 0.69 with flicker background.

(Fig. 14). As shown above, in FI neurons the changes in base activity were much higher than in all other types of neurons. The subtraction of base activity has therefore the strongest effect on the population of FI neurons in Fig. 14 while the FD neurons maintain as a distinct group within the plot. The circular histogram (Fig. 14B) reveals a mostly unimodal distribution having its maximum in the area of FD neurons (although a small maximum in the position of FI neurons is still present), demonstrating that only the inhibitory effect is still present independent of the changes in the base activity due to the flicker background.

## Discussion

The presented results demonstrate a similar deteriorating effect of the temporal structure of the background on the perception of a moving stimulus for humans and monkeys, and on the sharpness of neuronal responses to the moving stimulus in areas MT and MST of trained rhesus monkeys.

### *Effects of temporal background structure on motion perception*

Humans and monkeys showed a significant increase in the duration of stimulus presentation which is needed to discriminate motion direction in the presence of a flicker background compared to a static background. In the presence of flicker in the random dot background, the spatial as well as the temporal structure are no longer useful cues for the figure-ground segmentation, and so the coherent spatio-temporal signal of the moving object remains the only valid segmentation cue. The increase in motion discrimination thresholds indicates that the loss of temporal structure as a segmentation cue between figure and background could not be fully compensated for by the use of spatio-temporal cues.

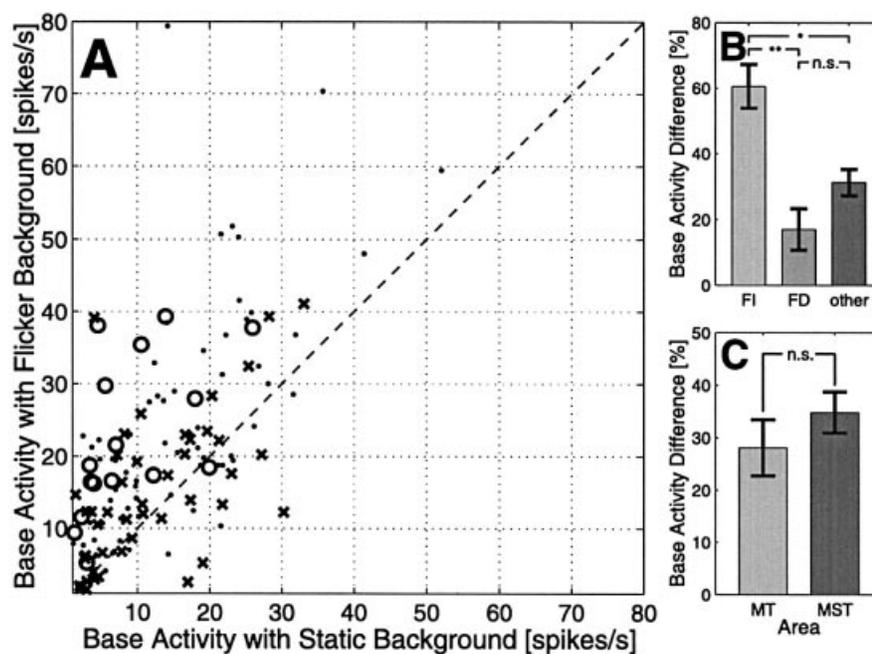


FIG. 12. (A) Activity of the neurons with static and flicker background in the time period before the presentation of the motion stimulus. The legend indicates whether a neuron was previously defined as an FI neuron ( $\circ$ ), FD ( $\times$ ) or remaining part of the population ( $\cdot$ ). (B) The increase in base activity for flicker background was significantly higher for the FI neurons than for the FD neurons ( $P < 0.001$ , Scheffé test) and for the remainder of the population ( $P = 0.02$ , Scheffé test). No significant difference was found between the population of FD neurons and the remainder of the population ( $P = 0.12$ , Scheffé test). (C) There was no significant difference between MT and MST neurons in the changes of base activity with static and flicker backgrounds ( $P = 0.30$ ,  $t$ -test).

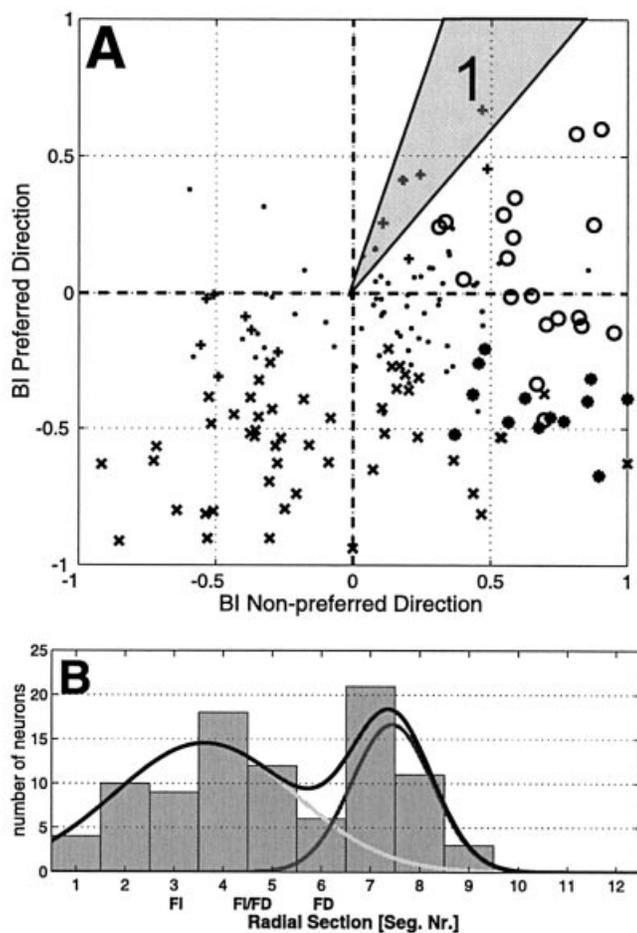


FIG. 13. (A) Comparison of the effects of flicker background on directional-selective neurons in the preferred and nonpreferred directions. Groups of neurons showing different responses to flicker background are marked separately. FI neurons ( $\circ$ ) significantly increase their activity in the nonpreferred direction. FD neurons ( $\times$ ) significantly decrease their activity in the preferred direction. Neurons showing a combination of both effects are marked differently ( $\bullet$ ). There is a small group of neurons (8%) showing other effects (+) and a bigger group of neurons (39%) showing no significant differences ( $\cdot$ ). (B) Histogram of the examined neuron types, grouped according to the influence of flicker background on their activity in the preferred and nonpreferred directions. The black line shows the sum of two gaussian functions (grey lines) fitted to the distribution.

Although we only used flicker densities of 0% and 100% in our monkey psychophysical study, the results were qualitatively identical to the results of the human study. Nevertheless, the measured thresholds were approximately five times higher than those measured in humans. These differences in threshold between the human subjects and the monkey (18 ms to 99 ms for flicker density of 0%, 49 ms to 280 ms for flicker density of 100%) most probably arose from the different experimental conditions and different motivational states, rather than from fundamental differences in motion perception of humans and monkeys (see Table 1). The differences between the human and monkey setups were rather small; therefore they can probably only account for minor differences in the measured data. A more important factor might be the difference in duration of an experimental session: we were able to ask our subjects to perform the experiment within 30 min. There is no reason to assume that the motivation of the subjects changed much during this short period of time. In contrast, because the monkeys determined the pace of the

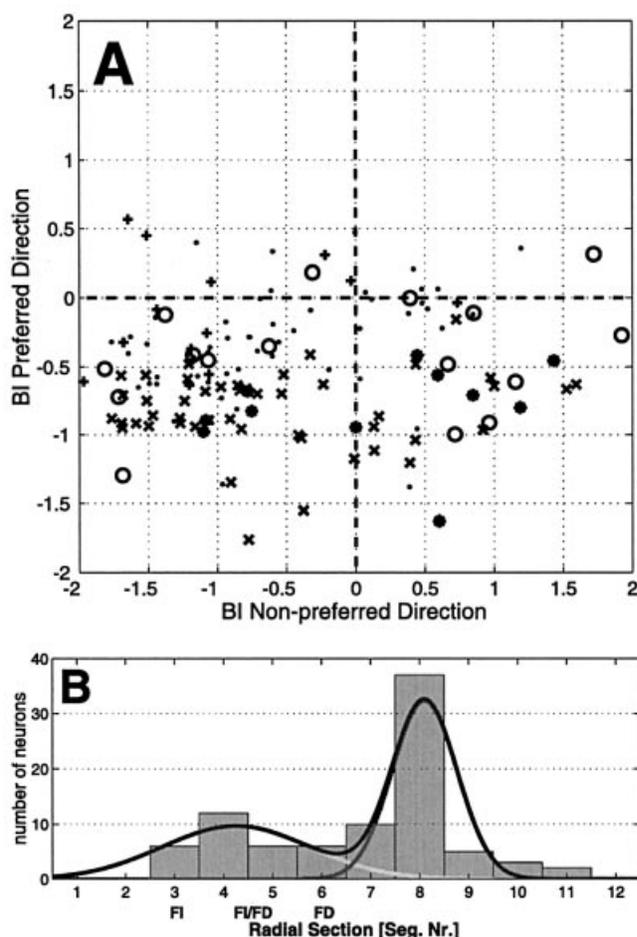


FIG. 14. (A) Comparison of the effects of flicker background on net activity of the investigated neurons in the preferred and nonpreferred directions. Groups of neurons showing different responses to flicker background are marked separately in the same way as in Fig. 13. (B) Histogram of the examined neuron types, grouped according to the influence of flicker background on their net-activity in the preferred and nonpreferred directions. The distribution can be fitted by a gaussian function (black line).

experiment themselves, the data collection sometimes lasted for several hours. Obviously, there were substantial changes in the motivation of the monkeys during this long period.

#### Quantitative comparison between psychophysics and neuronal responses

In the course of our experiments we quantitatively determined the background-induced changes in the discharge rates in primate areas MT and MST, and we also quantitatively measured the background-induced changes in the perception of man and monkeys. However, it is impossible to link these two measurements directly. There is no reason to assume that the activity in area MT and MST determines exclusively the motion perception; motion processing is not yet completed at the level of these areas (Felleman & van Essen, 1991). For later stages of processing, the effects of flicker was shown to decrease (see Lagae *et al.*, 1994). Therefore, the deleterious effect of flicker on the perception could be smaller than would be predicted from the effects on the discharge rates in areas MT and MST. In addition, the motion perception performance was different in human subject and rhesus monkeys as already discussed above. Obviously, the assumed differences in motivational states would affect the

performance in our discrimination task more severely than the discharge rates in areas MT and MST.

Taken together, although single-unit behaviour might not parallel perception quantitatively, qualitatively the same effect was shown for both parameters.

#### *Comparison of neuronal responses recorded from areas MT and MST*

In our results, we found no significant differences between neurons recorded from areas MT and MST. This result appears to conflict with some previous reports. When flicker and motion stimuli were presented separately, the responses of neurons in area MT to flicker were 40–50% of the responses to motion stimuli moving in the preferred direction (Lagae *et al.*, 1994; Qian & Andersen, 1994); however, in area MSTd the responses to flicker were only 17% of the responses to motion (Lagae *et al.*, 1994). In order to compare our data with this report, in which flicker and motion stimuli were presented separately, we also compared the base activities obtained during the presentation of a flicker background with the responses to a random dot pattern moving in the preferred direction of the neuron without background. Lagae *et al.* (1994) described the sensitivity of neurons for flicker and motion using a percentage index defined as follows.

$$I = 100 \times (A_{\text{motion}} - A_{\text{flicker}}) / (A_{\text{motion}} + A_{\text{flicker}}), \quad (5)$$

where  $A_{\text{motion}}$  is the activity observed during presentation of the motion stimulus moving in the preferred direction of the neuron, and  $A_{\text{flicker}}$  is the mean activity elicited by the flicker stimulus. For MT neurons, an average index of 49 was reported, which means that the response to motion is about three times as high as the response to flicker. This fits well with the average index of 38 for our sample of MT neurons. However, there are substantial differences between the reported results and our data collected from the MST neurons. Lagae *et al.* (1994) reported an index of 71, whereas we calculated an average index of 35 for our area MST neurons, which was not significantly different from our MT sample ( $P = 0.79$ ,  $t$ -test).

This difference between our results and the results reported by Lagae *et al.* (1994), as well as the similarity in responses from area MT and MST in our study, can be explained by the locations of our recordings. The anatomical reconstruction of the recording sites in one monkey showed that all MST recordings were located within the floor of the STS, where the lateral part of area MST (MSTl) is located (see Fig. 5). The properties of the visual responses of areas MT and MSTl neurons are quite similar (Komatsu & Wurtz, 1988); the major difference is pursuit-related responses (Newsome *et al.*, 1988) which are present in a subpopulation of neurons in area MSTl. In the above-mentioned study, the responses of neurons recorded in area MT were compared with those from neurons in the dorsal part of area MST (MSTd) located in the anterior bank of STS. The visual properties of neurons in MSTd are different from those of area MT, especially the selective responsiveness to complex motion patterns (Geesaman & Andersen, 1996; Duffy & Wurtz, 1997). Thus, it seems reasonable to suggest that the effect of flicker may be different between areas MSTl and MSTd, explaining the difference between our results and the results from the literature.

#### *Effect of flicker on neuronal activity at different stages of the visual pathway*

In order to compare the neuronal processing of a moving stimulus and the processing of flicker in different regions of the visual system, several human brain imaging studies (Sunaert *et al.*, 1999; Cheng

*et al.*, 1995) and single-unit recordings in monkeys (Britten *et al.*, 1993; Lagae *et al.*, 1994; Qian and Andersen, 1994) have been carried out in the past. It was shown that flicker produces a strong activation of human area V1, the first stage of visual processing in the cortex (Sunaert *et al.*, 1999). This flicker-induced activation was quantified as 63% of the response to a stimulus moving in the preferred direction for directional selective V1 neurons in monkeys (Qian and Andersen 1994). This effect is not restricted to directionally selective neurons in area V1; nondirectionally selective neurons in primate area V1 are reported to be highly sensitive to changes in luminance as well (Richmond *et al.*, 1990).

Beyond area V1, the neuronal responses to flicker diverge between the ventral ('what') and the dorsal ('where') pathway which includes the processing of visual motion (Ungerleider & Mishkin, 1982). It was shown in an fMRI study (Sunaert *et al.*, 1999) that areas in the ventral stream respond well to flicker at all levels of the hierarchy, while the responsiveness of neurons in the dorsal pathway to flicker is reduced in higher areas.

The effects of differences in temporal structure between object and background were reported for areas MT and MST in some studies. It could be shown that motion direction of stimuli which were segregated from the background only by temporal structure (drift-balanced motion Chubb & Sperling, 1988) is encoded by a subpopulation of neurons in areas MT (Albright, 1992; Churan & Ilg, 2001) and MST (Churan & Ilg, 2001).

Britten *et al.* (1993) investigated the effect of flicker on responses of neurons in area MT to translational flow fields. Dots moving coherently in a given direction (signal dots) were merged with dots which were replotted in random positions (flicker dots) (Newsome & Pare, 1988) whereby different proportions of signal and flicker dots were used. An increase in activity during stimulus motion in the nonpreferred direction, as well as a decrease in activity for motion in the preferred direction, resulting in a reduction of directional selectivity, were observed as a consequence of an increasing proportion of flicker dots (Britten *et al.*, 1993). However, Britten and colleagues did not differentiate explicitly between the response patterns described here as 'FI' and 'FD'. Other differences between both studies are, that in the study of Britten *et al.* (1993) the signal and the flicker dots were not spatially segregated, and that an increase in flicker dots resulted in a reduction in signal dots. Therefore, it remains unclear whether the reported effects were caused by an increase in flicker or by a decrease in the motion signal.

Although the responsiveness to flicker decreases in the ascending hierarchy of the processing in the visual system, it is not completely eliminated. This finding parallels our psychophysical finding that the temporal structure of the background does affect motion perception in man and monkey.

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#### Abbreviations

BI, background index; DI, direction index; FD, flicker decremental; FI, flicker incremental; MST, medial superior temporal area; MSTd, dorsal part of area MST; MSTl, lateral part of area MST; MT, medial temporal area; STD, standard deviation; STS, superior temporal sulcus.

## References

- Albright, T.D. (1992) Form–cue invariant motion processing in primate visual cortex. *Science*, **255**, 1141–1143.
- Baccino, T., Jaschinski, W. & Bussoloni, J. (2001) The influence of bright background flicker during different saccade periods on saccadic performance. *Vision Res.*, **41**, 3909–3916.
- Britten, K.H., Shadlen, M.N., Newsome, W.T. & Movshon, J.A. (1993) Responses of neurons in macaque MT to stochastic motion signals. *Vis. Neurosci.*, **10**, 1157–1169.
- Butzer, F., Ilg, U.J. & Zanker, J.M. (1997) Smooth-pursuit eye movements elicited by first-order and second-order motion. *Exp. Brain Res.*, **115**, 61–70.
- Cheng, K., Fujita, H., Kanno, I., Miura, S. & Tanaka, K. (1995) Human cortical regions activated by wide-field visual motion: an H2 (15)O PET study. *J. Neurophysiol.*, **74**, 413–427.
- Chubb, C. & Sperling, G. (1988) Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *J. Opt. Soc. Am. A*, **5**, 1986–2007.
- Churan, J. & Ilg, U.J. (2000) Does the temporal structure of the background affect the perception of first- and second-order motion? – A study in human psychophysics and primate single unit recording. *Soc. Neurosci. Abstr.*, **26**, 671.
- Churan, J. & Ilg, U.J. (2001) Processing of second-order motion stimuli in primate middle temporal area and medial superior temporal area. *J. Opt. Soc. Am. a Opt. Image Sci. Vis.*, **18**, 2297–2306.
- Duffy, C.J. & Wurtz, R.H. (1997) Medial superior temporal area neurons respond to speed patterns in optic flow. *J. Neurosci.*, **17**, 2839–2851.
- Felleman, D.J. & van Essen, D.C. (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cort.*, **1**, 1–47.
- Geesaman, B.J. & Andersen, R.A. (1996) The analysis of complex motion patterns by form/cue invariant MSTd neurons. *J. Neurosci.*, **16**, 4716–4732.
- Judge, S.J., Richmond, B.J. & Chu, F.C. (1980) Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Res.*, **20**, 535–538.
- Koffka, K. (1935) *Principles of Gestalt Psychology*. Lund Humphries, London.
- Komatsu, H. & Wurtz, R.H. (1988) Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *J. Neurophysiol.*, **60**, 580–603.
- Lagae, L., Maes, H., Raiguel, S., Xiao, D.K. & Orban, G.A. (1994) Responses of macaque STS neurons to optic flow components: a comparison of areas MT and MST. *J. Neurophysiol.*, **71**, 1597–1626.
- Macknik, S.L., Fisher, B.D. & Bridgeman, B. (1991) Flicker distorts visual space constancy. *Vision Res.*, **31**, 2057–2064.
- McKee, S.P. (1981) A local mechanism for differential velocity detection. *Vision Res.*, **21**, 491–500.
- Nakayama, K. (1985) Biological image motion processing: a review. *Vision Res.*, **25**, 625–660.
- Newsome, W.T. & Pare, E.B. (1988) A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *J. Neurosci.*, **8**, 2201–2211.
- Newsome, W.T., Wurtz, R.H. & Komatsu, H. (1988) Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. *J. Neurophysiol.*, **60**, 604–620.
- Orban, G.A., de Wolf, J. & Maes, H. (1984) Factors influencing velocity coding in the human visual system. *Vision Res.*, **24**, 33–39.
- Qian, N. & Andersen, R.A. (1994) Transparent motion perception as detection of unbalanced motion signals. II. Physiology. *J. Neurosci.*, **14**, 7367–7380.
- Richmond, B.J., Optican, L.M. & Spitzer, H. (1990) Temporal encoding of two-dimensional patterns by single units in primate primary visual cortex. I. Stimulus-response relations. *J. Neurophysiol.*, **64**, 351–369.
- Robinson, D.A. (1963) A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE BME*, **10**, 137.
- Scase, M.O., Braddick, O.J. & Raymond, J.E. (1996) What is noise for the motion system? *Vision Res.*, **36**, 2579–2586.
- Sunaert, S., Van Hecke, P., Marchal, G. & Orban, G.A. (1999) Motion-responsive regions of the human brain. *Exp. Brain Res.*, **127**, 355–370.
- Treue, S., Snowden, R.J. & Andersen, R.A. (1993) The effect of transiency on perceived velocity of visual patterns: a case of ‘temporal capture’. *Vision Res.*, **33**, 791–798.
- Ungerleider, L.G. & Mishkin, M. (1982) Two cortical visual systems. In Ingle, D.J. et al., eds. *Analysis of Visual Behavior*. MIT Press, Cambridge, pp. 549–586.
- Zanker, J.M. (1993) Theta motion: a paradoxical stimulus to explore higher order motion extraction. *Vision Res.*, **33**, 553–569.
- Zanker, J.M. & Braddick, O.J. (1999) How does noise influence the estimation of speed? *Vision Res.*, **39**, 2411–2420.