European Journal of Neuroscience, Vol. 11, pp. 2044–2058, 1999

Decision-related activity in the macaque dorsal visual pathway

Alexander Thiele,* Claudia Distler and Klaus-Peter Hoffmann
Allgemeine Zoologie und Neurobiologie, Ruhr-University Bochum, 44780 Bochum, Germany

Keywords: attention, direction discrimination, MST, MT, stimulus expectation, STPp, V3A

Abstract

Brain areas at higher levels of cortical organization are thought to be more involved in decision processes than are earlier, i.e. lower, sensory areas. Hence, neuronal activity correlated with decisions should vary with an area's position in the cortical hierarchy. To test this proposal, we investigated whether a change in neuronal activity during error trials depends in a systematic way on cortical hierarchical position. While macaque monkeys discriminated the direction of moving visual stimuli, the activity of direction-selective neurons was recorded in four extrastriate visual areas: V3A, the middle temporal area, the middle superior temporal area and the posterior part of the superior temporal polysensory area. Neuronal activity was significantly reduced in all areas when the monkeys made errors in judging the direction of stimuli moving in the preferred direction with low and intermediate luminance contrast. The amount of activity reduction was ≈50% in all of the visual areas. Thus, the activity on error trials is reduced in early visual processing, independent of the hierarchy in the dorsal visual pathway. The activity reduction depended on stimulus contrast and the direction of the decision relative to the stimulus motion. It was profound and significant in all areas at low stimulus contrast. However, it was nonsignificant at high stimulus contrast. Our data suggest that activity reduction on error trials is due to lack of attention in association with stimulus expectation.

Introduction

Well-trained humans and monkeys perform visual discrimination tasks with high accuracy. On some trials, however, they may fail to report the correct answer, either because the task is difficult or because the subject has wrong expectations or pays no attention to the stimulus. The neuronal activity concurrent with these errors must differ from the activity associated with correct decisions at some brain levels, and one may expect this difference to increase along the hierarchy of sensory processing. For example, activity differences might be absent in primary visual cortex but pronounced at later stages such as the parietal (Shadlen & Newsome, 1996) or the prefrontal cortex (Goldman-Rakic, 1995). To shed light on this issue we recorded activity of neurons in visual area V3A, the middle temporal area (MT), the superior middle temporal area (MST), and the posterior part of the polysensory area of the superior temporal sulcus (STPp), which are assumed to be at different hierarchical levels of the dorsal visual pathway (Mishkin *et al*., 1983; Felleman & Van Essen, 1991; Young, 1992; Cusick *et al*., 1995; Hilgetag *et al*., 1996). Additionally all these areas are likely to be involved in motion analysis. While this has been repeatedly demonstrated for area MT and MST (Dubner & Zeki, 1971; Albright, 1984; Britten *et al*., 1992; Celebrini & Newsome, 1994), the contribution of area V3A to motion processing is less clear. Though the number of direction-selective neurons in V3A is comparatively low (Zeki, 1978; Galletti *et al*., 1990), functional magnetic resonance imaging in humans has revealed high motion selectivity (Tootell *et al*., 1997). Another reason why area V3A was selected is its similarity to MT and MST; area V3A and MT both remain visually active when V1 is lesioned or inactivated (Rodman *et al*., 1989; Girard *et al*., 1991), and like MT and MST (Bremmer *et al*., 1997), area V3A contains a high number of gaze-dependent visual neurons (Galletti & Battaglini, 1989). With respect to visual activity, little is known about area STPp (Hikosaka *et al*., 1988; Scalaidhe *et al*., 1995). Its posterior region, however, contains a significant proportion of direction-selective neurons, many of which predict a monkey's directional decision in the absence of visual motion (Thiele & Hoffmann, 1996). Anatomical investigations indicate that STPp is located very high in the visual hierarchy (Cusick *et al*., 1995).

As we sampled activity from a wide range of visual cortical levels, our data should help to clarify whether decision-related activity changes depend on position in the visual cortical hierarchy. We find that neuronal activity on error trials is equally reduced in all areas investigated. The activity difference between correct and error trials peaks shortly before the monkey's decision and wanes thereafter, indicative of attentional deficits on error trials. Moreover, the activity reduction on error trials varies with the direction of the decision. We therefore propose that stimulus expectation systematically modulates the activity levels in the dorsal visual pathway.

Correspondence: Professor Klaus-Peter Hoffmann, as above.
E-mail: kph@neurobiologie.ruhr-uni-bochum.de

**Current address*: The Salk Institute for Biological Studies, PO BOX 85800, San Diego, CA 92186, USA. E-mail: thiele@salk.edu

Received 30 November 1998, revised 1 February 1999, accepted 3 February 1999

Methods

Subjects

Two adult rhesus monkeys (Macaca mulatta; 1 male, 1 female) were used in this study. The animals were treated according to the published guidelines on the use of animals in research (European Communities Council Directive 86/609/ECC), and the

National Institute of Health guidelines for the use of laboratory animals.

Animal preparation

After initial direction-discrimination training, monkeys were surgically prepared for final training and physiological recording. Prior to surgery, the animals were pretreated with dexamethasone glucocorticoid (Voren, 1 mL i.m.), atropine (1 mL i.m.), and sedated with ketamine hydrochloride (10 mg/kg i.m.). All surgical procedures were performed under aseptic conditions using barbiturate anaesthesia (sodium pentobarbital, 10 mg/kg i.v. initially, followed by 5 mg/kg i.v. every 30 min). Two scleral search coils were implanted in each animal in order to monitor and control eye position, and were connected to plugs on top of the skull. A post for head restraint was affixed to the skull with dental acrylic and stainless steel screws. Two stainless steel recording chambers were implanted over a craniotomy. They were positioned bilaterally over occipital and parietal lobe regions in parasagittal stereotactic planes, tilted 60° backwards from vertical. The recording chambers, eye coil plugs and head restraint posts were all embedded in dental acrylic. Animals were given prophylactic postsurgical antibiotics (Sobeline, i.m. 0.1 mL/kg/d, for 5 days) and analgesics (Tomanol, 0.1 mL/kg/d, for 3–4 days). After healing, the cranial wound was treated daily by removal of hair and cleansing. When necessary, antibiotic powder (neomycinsulphate and bacitracin) was applied topically. The recording chambers were cleaned aseptically daily, and topical antibiotic powder was applied when necessary.

Paradigm

The monkeys were trained in a direction-discrimination task (Fig. 1a). During the experiments, each animal was seated comfortably in a primate chair with its head restrained. We monitored eye movements using scleral search coils. Monkeys started a trial by clutching a central touch bar in front of their chest upon which a fixation point (0.2° in diameter) was back-projected by a light-emitting diode onto a translucent tangent screen. The screen subtended 90° of the visual field along both the horizontal and the vertical axis. The viewing distance was 38 cm. The fixation point was always presented in the centre of the projection screen. The maximum fixation window was ± 1° for monkey A, and ± 2° for monkey H. Monkeys were required to fixate within 500 ms after the appearance of the fixation point.

Stimuli

During each experiment, the time of stimulus onset, contrast and direction of motion were varied randomly. The direction of motion was along one of the four cardinal directions. Stimuli were presented in the receptive field of the recorded neuron. When two or more single units were recorded simultaneously, the stimulus covered all of the units' receptive fields. Stimuli consisted of square wave gratings (0.3–0.5 cycles per degree) moving unidirectionally within a quadratic aperture. During the whole experiment, a stationary gaussian-filtered white noise stimulus was also back-projected onto the screen (by a slide projector). This added stationary noise made the task more difficult, causing a higher percentage of error trials (Hoffmann & von Seelen, 1980). Stimuli were presented 600–

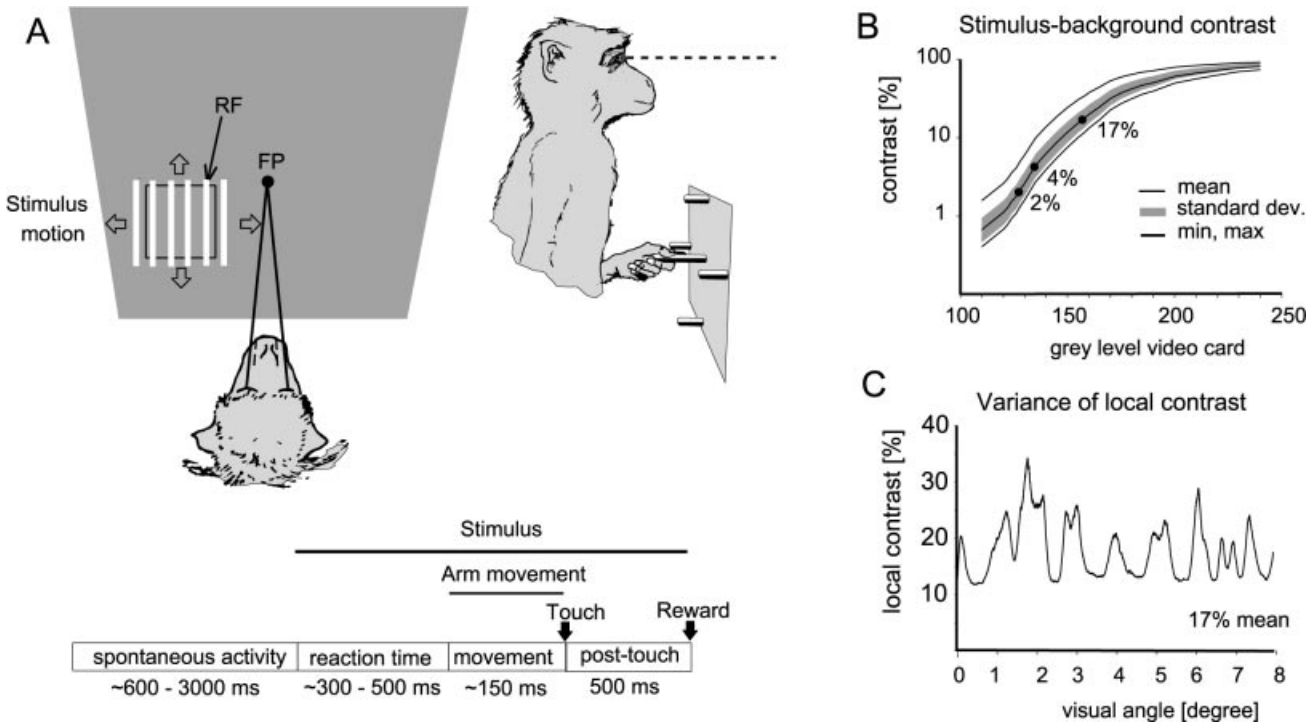


FIG. 1. (A) The animals were facing a rear projection screen, upon which a fixation point (FP, light emitting diode), the stimulus (VGA projector), and a static white noise background (slide projector) were back-projected. Boxes below illustrate the different time periods in a single trial. (B) Stimulus to background contrast (mean, standard deviation, and maximum and minimum) at a given stimulus intensity due to the structured background. Abscissa: relative grey level values as read out from the graphic board; Ordinate: stimulus contrast. (C) Variation of stimulus contrast within the visual field due to the static white noise background. Abscissa: visual angle in degrees. Ordinate: stimulus contrast.

3000 ms after the appearance of the fixation point (600 ms steps). The stimulus contrast was varied from high contrast levels to invisible contrast (0.003%, < 0.0001 cd/m^2, taken to be 0%). Typically, four contrast levels were tested for each neuron: 53, 24, 4 and 0% contrast in monkey H; and 17, 4, 2 and 0% in monkey A. These two different sets of contrast levels were used because of differences in each monkey's performance in the psychophysical task. In addition, different grey level resolutions were available using the graphic boards [VGA with ET4000 in monkey H: 64 grey level, 800*600 pixel at 72 Hz; ELSA Winner 2000 (S3, ELSA, Aachen, Germany) in monkey A: 256 grey level, 800*600 pixel at 100 Hz]. Stimuli were back-projected with an EPS 4000 video projector (Electrohome, USA) onto the translucent tangent screen.

The stimulus and background intensities were measured using a photo-multiplier (EMI, 14 dinodes, 20S, aperture 0.04° of visual angle), and the linearity of measurements was ensured with 50% transmission neutral grey filters (Schott, Mainz, Germany). As the gaussian-filtered white noise caused the stimulus contrast to vary within the visual field, the maximum, minimum, mean and standard deviation of the stimulus contrast were calculated for each contrast level (see Fig. 1B).

The variance of the stimulus contrast across the background is shown in Fig. 1C. The mean luminance of the background was 0.551 cd/m^2 and its standard deviation was 0.161 cd/m^2. The luminance of the stimulus was 0.011 cd/m^2 at 2% contrast, 0.023 cd/m^2 at 4% contrast, 0.11 cd/m^2 at 17% contrast, 0.16 cd/m^2 at 24% contrast, and 0.67 cd/m^2 at 53% contrast. The luminance of the grating changed with contrast because the grating was projected onto the stationary gaussian-filtered white noise background, which did not change throughout the experiments.

Whenever two units were recorded simultaneously from the same electrode in monkey H, we adjusted the stimulus speed to the preference of one of the two units. Six velocities were tested for the neurons (7.2–115 °/s), and the speed was set for the 'best response' which occurred in either of the neurons. However, in monkey A, as up to eight units could be recorded simultaneously from up to four electrodes, stimulus speed could not be optimized for all neurons. We therefore decided to fix the speed at 18.1 °/s for this monkey. This value is in the midrange of preferred speeds for MT neurons (Britten *et al*., 1993).

Behavioural paradigm

The monkeys performed a reaction-time task. As soon as they perceived (or believed they perceived) the direction of motion, they had to release the central bar and touch one of the four peripheral bars. These were positioned according to the directions of motion (see Fig. 1a). The time to release the central touch bar was taken as the reaction time. A 'go-signal' was never presented. After touching the peripheral touch bar, the monkey had to keep fixation for another 500 ms, during which the stimulus continued to move through the receptive field. These additional 500 ms were added for two reasons: (i) as the reaction time was variable, we wanted to avoid having to analyse variable neuronal response periods; and (ii) upon contacting the peripheral touch bar, the decision is indicated. As the monkey cannot change its decision, whatever the stimulus was, it might as well concentrate upon fixation, and redirect its attention from the stimulus presentation site to the fixation spot. If true, removal of attention from the stimulus site should result in decreased neuronal activity compared with what was found on error trials. If the monkey kept fixation throughout the trial and had indicated the correct direction of motion it was rewarded with a drop of apple juice after the trial ended. If the reaction time exceeded 2500 ms, the trial was stopped.

Sometimes, the reaction-time task, in conjunction with the randomized stimulus onset and possible 0% contrast stimuli, forced the animals to indicate decisions even in the total absence of visual motion. Also, sometimes, the monkey indicated its decision prior to stimulus presentation period. In either case, the decisions were regarded as stimulus-independent decisions. In the latter case, the stimulus was omitted and therefore taken as a 0% contrast stimulus. Monkeys were never rewarded for early stimulus-independent decisions, which occurred prior to the stimulus presentation. If the stimulus contrast was 0% and the decision occurred after the stimulus presentation (though these stimuli were invisible), decisions were rewarded with 50% probability (mean). Response biases for stimulus-independent decisions were minimized by storing the direction of the last 1000 stimulus-independent decisions, allowing us to adjust the percentage of the reward as well as its quantity (the amount of apple juice per reward), based on the history of the monkey's behaviour.

Electrophysiological recording

In monkey H, glass-insulated tungsten microelectrodes (custom made, impedance: 1.5–3 MΩ at 1 kHz) were advanced using a hydraulic microdrive (Narishige, Japan), which was mounted on the recording chamber. The use of guidetubes guaranteed that the electrode tips were not damaged when traversing the dura and overlying tissue. Up to two units were recorded simultaneously from the electrode.

In monkey A, recordings were performed using the 'Eckhorn Matrix' (Uwe Thomas Recording, Marburg, Germany). Glass-insulated platinum-iridium electrodes (Uwe Thomas Recording, Marburg, impedance: 1.5–3 MΩ at 1 kHz) were advanced through guidetubes (outer diameter 305 µm) into the brain. Up to four guidetubes were inserted per recording session (outer overall diameter was 1220 × 305 µm). Each individual guidetube was sharpened, such that all inserted guidetubes together formed a single tip. This minimized damage to the underlying brain tissue. The guidetubes were not inserted deep into the animals' brains; only the dura was traversed. Prior to insertion, the position of the guidetubes within the recording chamber was manipulated using *x*- and *y*-coordinates perpendicular to the brain surface. The inner chamber diameter was 19 mm. The position of the chambers made all parts of MT and MST, as well as large parts of V3A and STPp accessible (details concerning the reconstruction of recording sites are described in the histological methods section). Amplified electrical activity from the cortex was band-pass filtered (0.3–10 kHz), and passed through oscilloscopes to spike-sorting devices [Alpha Omega (Nazareth, Israel) and Spectrum Scientific (Houston, Texas)]. The quality of spike separation was controlled online by displaying the interspike interval distribution for each spike channel on the monitor of a recording personal computer (486, 33 MHz). Behavioural control, data acquisition, and stimulus generation were accomplished by this recording personal computer, running software for real-time experiments ('Rec2', A. Thiele and A. Wachnowski). The monkey's reaction time was controlled online ('Psycho Master', custom made, time resolution 2 ms, connected to the personal computer), and the *x*- and *y*-eye positions were sampled and recorded at 500 Hz. Spike occurrences (TTL pulses generated by the spike-sorting devices) were sampled at 1 kHz.

Prior to the combined psychophysical test and neuronal recording, the receptive field location of each cell was mapped using a hand-held projector while the monkey fixated a central target on a dark background. Data were sampled only after the monkey had become well adapted to the background luminance (≈ 0.5 cd/m^2) for ≈ 20–30 min. In addition, the cell's spikes had to be well isolated for at least 5 min while the monkey performed the task. Each well-isolated

unit was recorded, regardless of its visual activation and possible participation in the task. In monkey H, we usually recorded 10–15 trials for each stimulus condition (160–240 trials in total), in order to record from many units every day. In monkey A, we tried to record as many trials as possible from each unit. As recording from many units simultaneously increased the probability of loosing a cell, data collection was discontinued whenever isolation of one of the units became poor, typically after 30–45 min of recording. This usually resulted in 15–25 trials per stimulus condition. In a few instances, up to 50 trials per stimulus condition were recorded.

Data analysis

Psychophysics

The monkey's performance (number of correct decisions) and reaction time (the period of time from stimulus onset until the monkey released the central touch bar) were assessed for each contrast level separately. The median reaction time and the distribution of reaction times were calculated separately for correct and error trials. A Kruskal–Wallis ANOVA on ranks revealed whether reaction times significantly differed with stimulus contrast.

Neuronal activity

Initially, the neuronal activity (spikes per second) was calculated for each single trial. This was done separately for each stimulus direction and contrast, and whenever the monkey had indicated a correct decision. However, the activity associated with correct decisions was only taken into account if the reaction time in the trial exceeded a certain minimum. This reaction-time minimum was derived from the rise in the distribution of all reaction times recorded at a given stimulus contrast. These reaction-time minima were 280 ms at $\geqslant 17\%$ contrast, 330 ms at 4% contrast, and 370 ms at 2% contrast in monkey A. For monkey H the corresponding values were: 260 ms (contrast $\geqslant 24\%$), and 320 ms at 4% contrast.

Neuronal activity was calculated within restricted time windows. Window widths and starting points depended on stimulus contrast. Different starting points for the analysis were chosen because cell latency was found to increase with decreasing contrast. The beginning of the window was varied with the population onset latency, which was assessed in a separate analysis according to a protocol described by Oram & Perrett (1992). At stimulus contrast $\geqslant 17\%$, the analysis started 40 ms after stimulus presentation (window width, 300 ms), at 4% contrast the analysis started 80 ms after stimulus presentation (window width, 400 ms), and at 2% contrast it started 150 ms after stimulus presentation (window width, 500 ms).

The spontaneous activity was calculated on trials in which the monkey indicated a correct decision after stimulus presentation, because this activity can be regarded as 'unbiased'. For a trial to be continued, fixation had to be reached within 500 ms of appearance of the fixation point. As only minimal eye movements occurred thereafter, we analysed the spontaneous activity in a time window starting 500 ms after the fixation point appeared, and ending at stimulus onset. To reveal whether significant cell responses ($P < 0.05$) occurred at a given contrast, a Kruskal–Wallis ANOVA was calculated (five groups, one group of trials with spontaneous activity, the other four groups with stimulus-related activity). To avoid false positives ($P < 0.05$ despite only random fluctuations in the firing rate), and to eliminate exclusively inhibitory responses, dot displays were also inspected visually. Only those neurons with a significant excitatory response are included in the present study. The stimulus direction that elicited the highest mean activity was defined as the preferred direction, the opposite direction was defined as the null direction. After subtraction of background activity, the direction index was calculated as follows.

$$\text{Direction index} = (1 - \text{null activity})/\text{preferred activity}.$$

If the direction index was > 0.5, the neuron was taken as direction selective.

Analysis of neuronal activity on correct and error trials

As error trials were rare at most of the contrast levels investigated, quantitative investigation of activity differences at the single cell level could only be performed in a few cases. We decided to test for significant differences (Mann–Whitney ranked-sum test, $P < 0.05$) if at least five correct and five error trials had occurred when the preferred direction was presented at a given contrast. For this test we used the same time windows as described in the previous paragraph.

In addition, we calculated the 'activity contrast' (AC) between the activity on correct and error trials for each neuron, if at least one correct and one error trial had occurred when the preferred direction was presented.

$$\text{AC} = (\text{activity}_{\text{correct}} - \text{activity}_{\text{error}})/(\text{activity}_{\text{correct}} + \text{activity}_{\text{error}})$$

In addition to the single cell analysis, the population activity on correct and error trials was calculated. The population activity was calculated from the single cell activity means, using the time windows described above. In addition, a 'time-resolved population activity' was calculated. This was applied to determine the onset and time course of significant activity differences on correct and error trials. Therefore, the normalized and raw population activity was averaged from 250 ms before stimulus onset to 1000 ms afterwards (5-ms bins). A bin-wise ANOVA was calculated on the normalized population activity to find periods of significant differences (for a detailed description of the procedure, see Oram & Perrett, 1992). To calculate the population activity, the preferred directions of direction-selective units were aligned.

Histology

During the recording experiments MT and MST were identified on the basis of physiological response properties (Celebrini & Newsome, 1994; Britten *et al*., 1996). In addition, we injected different tracers into the brain and/or made electrolytic lesions at physiologically defined recording sites (positive current, 10 μA, 10 s). After the final experiment, the animals were killed with an overdose of pentobarbital and perfused transcardially with 0.9% NaCl and 0.1% procainhydrochloride followed by paraformaldehyde (4%) lysine-perjodate. The brains were removed, blocked and cryoprotected in glycerol (10% followed by 20%). Frozen sections were cut in the sagittal plane at 50 μm thickness and stained, in part, with cresyl violet, for myelinated fibers (Gallyas, 1979; Hess & Merker, 1983), and for SMI-32 and parvalbumin immunohistochemistry. Recording sites were reconstructed from the location of the injections and lesions, relative to the *x*-, *y*-positions of the penetrations, and their respective recording depth and mapped on two-dimensional maps of the cortical hemispheres (Ungerleider & Desimone, 1986). Areal borders were largely determined based on myeloarchitecture. Unfortunately, we were unable to replicate the characteristic staining pattern for parvalbumin and SMI-32 published by Cusick *et al*. (1995) for frontal sections in our sagittal material.

TABLE 1. Reaction time as a function of contrast and performance

Monkey	Contrast (%)	Decision	Decisions (*n*)	(too early)	Reaction time (median)	Reaction time (mean)
H	4	Correct	4737	–	499	636 ± 371
H	4	Error	2911	(457)	844	1013 ± 557
H	24	Correct	5952	–	371	391 ± 137
H	24	Error	723	(245)	416	584 ± 439
H	53	Correct	6223	–	355	364 ± 92
H	53	Error	675	(280)	371	460 ± 323
A	2	Correct	9375	–	637	823 ± 494
A	2	Error	4024	(1109)	1064	1230 ± 725
A	4	Correct	13187	–	445	494 ± 215
A	4	Error	670	(624)	654	971 ± 686
A	17	Correct	12363	–	355	361 ± 61
A	17	Error	157	(358)	377	467 ± 363

Reaction time increased with decreasing contrast. Reaction times at all contrasts were significantly longer on error trials, compared with correct trials. The incidence of error trials decreased with increasing contrast. 'Too early' decisions (in brackets) were excluded from the data shown in the last two columns.

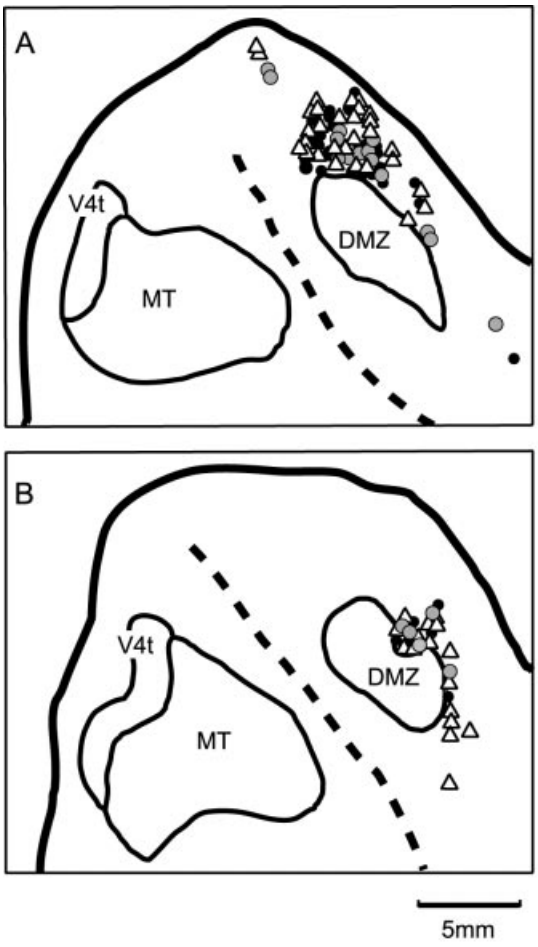


FIG. 2. Two-dimensional maps of the posterior part of the left STS in two monkeys. (A) monkey H and (B) monkey A (to allow for better comparison, the left hemisphere of monkey A is displayed as a right hemisphere). Posterior is to the left, anterior to the right. Thick lines indicate the lip, dashed lines the fundus of the sulcus. Myeloarchitectonic borders of areas V4t, MT and the densely myelinated zone (DMZ) of MST are indicated by thin lines. Open triangles, grey-filled circles and black-filled circles indicate unresponsive, visual and visual direction-selective neuronal recording sites, respectively. Scale bar, 5 mm.

TABLE 2. Number of directionally selective units recorded from the areas recorded

Area	*n* cells (total)	*n* cells (monkey H)	*n* cells (monkey A)
V3A	37	14	23
MT	371	185	186
MST	145	60	85
STPp	83	66	17

Results

Psychophysics

Reaction times and performance

Both monkeys worked reliably and performed consistently. Their decisions were subdivided into three categories: too early; stimulus-related error; and correct trials. Too early decisions were defined in terms of the timing relative to the distribution of all correct responses (see Methods section for details). The psychometric data were calculated from correct and error trials. Too early decisions were excluded from the data set. Both monkeys performed at threshold level when subthreshold stimuli were presented (contrast < 0.003%). Performance increased as stimulus contrast increased and reached a plateau once stimulus contrast was > 4%. The overall performances of the two monkeys, however, differed. Monkey A performed at 69.9% at 2% contrast, and at 95.1 and 98.7% at 4 and 17% contrasts, respectively. Monkey H did not perform as well (4% contrast, 61.3% correct; 24% contrast, 89.2% correct; 53% contrast, 90.2% correct). Reaction time varied significantly (ANOVA on ranks, $P < 0.05$) as a function of luminance contrast and as a function of correct and error trials (see Table 1).

Histology

As the exact definition of area STPp is still somewhat controversial we show our presumed STPp recording sites on two-dimensional maps of the posterior part of the superior temporal sulcus of the hemispheres included in this study (Fig. 2). The myeloarchitectonic borders of area V4t, area MT, and the densely myelinated zone of MST (DMZ) are indicated. Because DMZ is considered to be the most lateral part of MST, only recording sites lateral to the DMZ border were included in

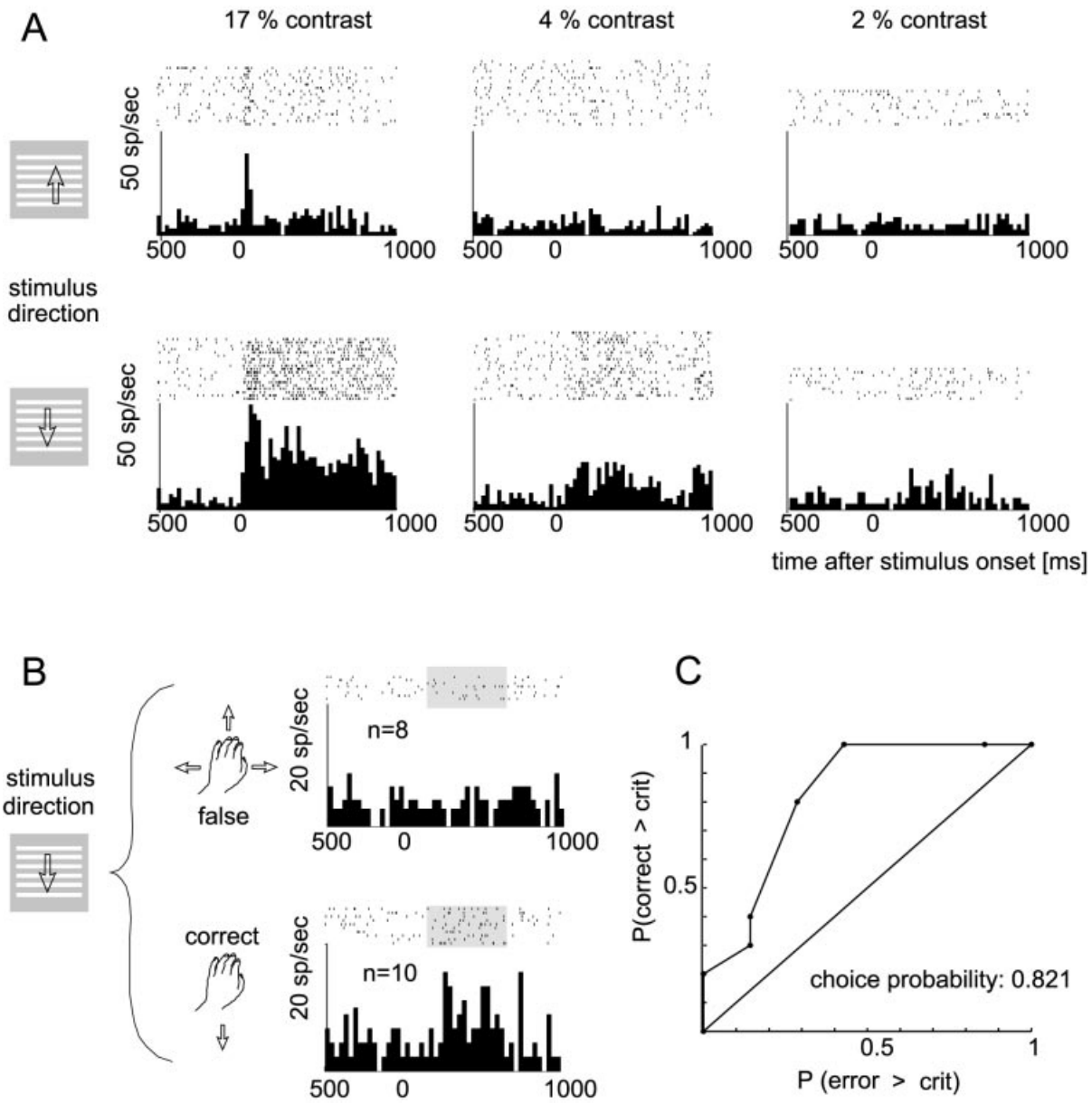


FIG. 3. (A) Single unit activity from V3A dependent on direction of motion and stimulus contrast. The monkey indicated correct decisions in all of the trials shown. The *upper* histograms display the neuron's activity when stimulus motion was upward (the neuron's null direction). The *lower* histograms display the corresponding activity when stimulus motion was downward (the neuron's preferred direction). (B) The activity of the same neuron as in A on correct (*lower* histogram) vs. error trials (*upper* histogram). The stimulus moved in the neuron's preferred direction (downward) in all of the trials. The stimulus contrast was 2%. The time period taken to compare the activity on correct and error trials is indicated by the grey squares behind the dot displays. We selected this time period because the response latency with 2% contrast stimuli was ≈ 150 ms in all four areas. We used this latency to determine the onset of our response window. The median reaction time (the release of the central touch bar) with correct decisions was ≈ 650 ms at 2% contrast. Therefore the response window ended 650 ms after stimulus onset. (A and B) Hand symbols: direction of the decisions; bar symbols: direction of stimulus motion. Rasters and histograms are aligned with stimulus onset. (C) Choice probability (CP), a measure which captures the overlap in the neuron's response distributions for error and correct trials (as shown in the grey shaded area in B). Each point on the CP curve depicts the proportion of trials on which the correct decision response exceeded a criterion firing level (plotted along the *y*-axis) against the proportion of trials on which the error response exceeded a criterion firing level (plotted along the *x*-axis). The area under this curve corresponds to the CP value, an indication of how well an ideal observer can predict the monkey's choice given the activity on a single trial. In the example shown here the ideal observer would be correct on 82% of the trials.

the STPp sample. Our presumed STPp recording sites largely coincide with area TPOc (Cusick *et al*., 1995) and the posterior parietal polysensory area (Ungerleider & Desimone, 1986) and possibly overlap, in part, with TPOi. In our sample, no segregation of visually responsive and unresponsive regions was evident. Interestingly, many of our effective recording sites seemed to lie in the 'mostly unresponsive' zone (Hikosaka *et al*., 1988).

Electrophysiology

We recorded from a total of 1512 cells from the areas described in this paper (V3A, $n = 177$; MT, $n = 733$; MST, $n = 306$; STPp, $n = 296$), with a minimum of seven trials per stimulus condition. We recorded a cell's activity whether or not it participated in the task. However, in this paper we selectively describe directionally selective cells. Table 2 gives a survey of the numbers of directionally selective units

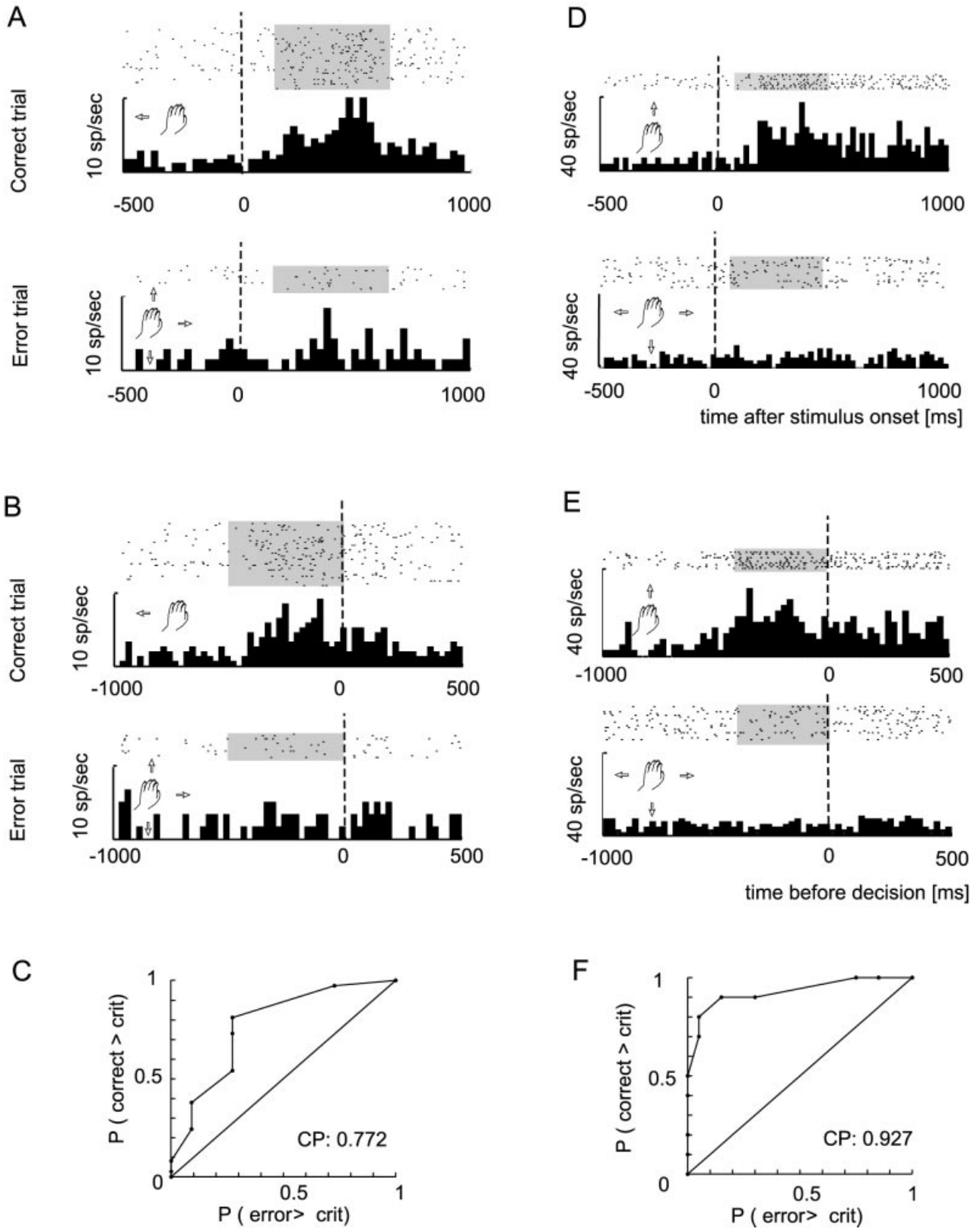


FIG. 4. Neuronal activity in MT and MST on correct and error trials with stimulus motion in the preferred direction. (A) Neuron recorded in MT at 2% stimulus contrast. The activity is aligned to stimulus onset. (B) The activity of the same MT neuron re-plotted relative to the reaction time of the monkey. (C) ROC calculated from the activity of the MT neuron during correct and error trials when the activity is aligned to the reaction time of the monkey. (D) Neuron recorded in MST at 4% stimulus contrast. The activity is aligned to stimulus onset. (E) The activity of the same MST neuron re-plotted relative to the reaction time of the monkey. (F) ROC calculated from the activity of the MST neuron during correct and error trials when the activity is aligned to the reaction time of the monkey. Gray shaded areas: time window used to calculate the mean single trial activity on correct and error trials. The activity was significantly reduced on error trials in both cells (Mann–Whitney ranked-sum test, $P < 0.05$). The ROCs were calculated from the activity displayed in the grey windows in B and E.

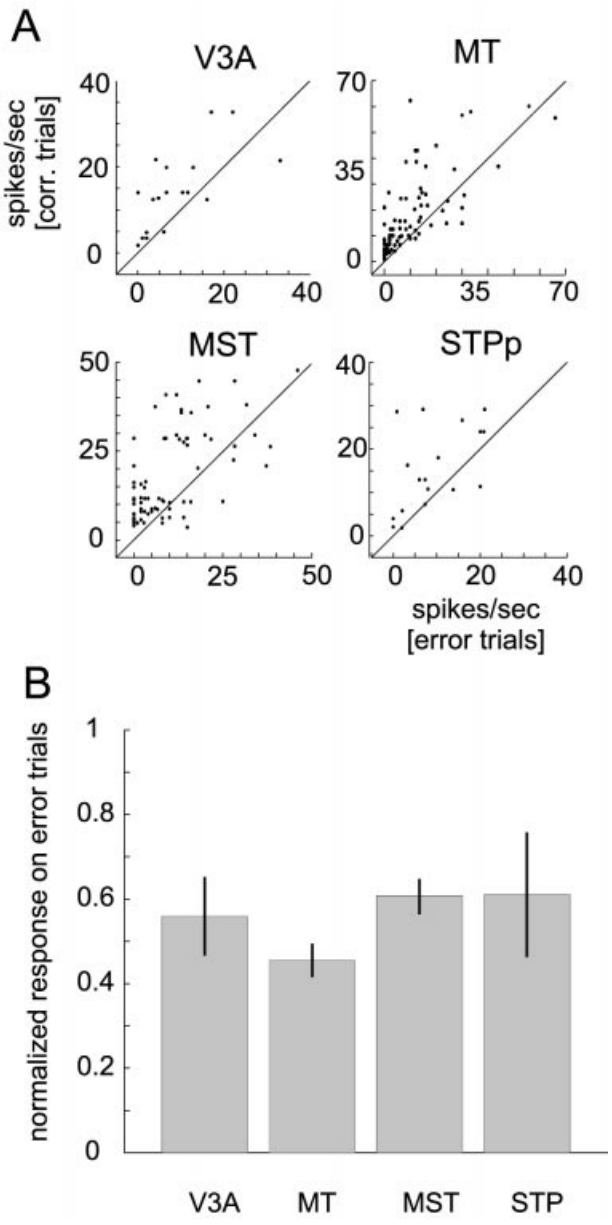


FIG. 5. (A) Distribution of neuronal activity on correct vs. error trials for area V3A, MT, MST and STPp. The stimulus contrast was either 2 or 4% for a given cell. A Mann–Whitney ranked-sum test revealed that the activity was significantly lower on error trials than on correct trials in all of the areas. To avoid data points lying on the *x*- or *y*-axis, the axes cross at (–5, –5). (B) Normalized population activity on error trials in areas V3A (18 neurons), MT (92 neurons), MST (72 neurons) and STPp (18 neurons). Neurons recorded on error trials at 2 and 4% were pooled after normalization, as their normalized responses were not significantly different (Mann–Whitney ranked-sum test). Stimulus motion was in the preferred direction of the neurons. Error bars: standard error of the mean.

recorded from the different areas. The percentage of directionally selective cells from our study is relatively small for, e.g. area MT when compared with previous studies (Dubner & Zeki, 1971; Maunsell & Van Essen, 1983; Albright, 1984). This discrepancy can be reconciled by our observation that a large number of cells that responded to visual stimuli presented on a dark background during receptive field mapping became less responsive or unresponsive when the structured gaussian background noise was turned on. Under the latter conditions the visual stimulus activates the receptive field centre, while the structured background activates the inhibitory surround, thereby diminishing responsiveness. Similar findings have been reported previously (Olavarria *et al*., 1992), demonstrating that structured surrounds can significantly decrease the response strength and direction selectivity of otherwise direction-selective units.

Figure 3 shows data typical of those found in direction-selective neurons from all four areas. This neuron was recorded in V3A and preferred downward visual motion (Fig. 3A, lower histograms). The neuron's responses associated with correct decisions and errors for 2% contrast stimuli moving in the preferred direction are shown in Fig. 3B. Stimulus-evoked activity was significantly reduced on error trials (Mann–Whitney ranked-sum test, $P < 0.05$). Figure 3C shows a nonparametric measure (receiver operating characteristics: ROC, Green & Swets, 1966) which allows quantification of the amount of overlap in the activity distributions associated with correct and error trials, respectively. This measure has been used previously to describe neuronal responses (Tolhurst *et al*., 1983; Vogels & Orban, 1990; Britten *et al*., 1992; Celebrini & Newsome, 1994) or to test whether a relationship existed between behavioural choice and neuronal response (Britten *et al*., 1996). The latter was termed 'choice probability' (CP), which indicates how well an ideal observer can predict the monkey's choice based on the overlap in the neuronal activity distributions (e.g. if the distributions overlap entirely, CP = 0.5, indicating that the ideal observer can perform no better than chance level, and if he performs at 100% correct, then CP = 1.0). In the example presented here an ideal observer could correctly predict the monkey's choice on 82% of the trials.

Additional examples of activity reduction on error trials for single units are shown in Fig. 4. For both cells the activity is displayed when stimulus motion was in the preferred direction. Figure 4A displays the activity of a neuron recorded in area MT at 2% contrast. The upper panel displays the activity on correct trials, the lower panel the activity on error trials, aligned to stimulus onset. The mean single trial activity was assessed during a 500-ms period, starting 150 ms after stimulus onset [150 ms corresponds to the onset latency of the population of directionally selective units for 2% stimulus contrast; a 500-ms window was taken because the end of this window corresponds largely to the median reaction time for 2% contrast stimuli (637 ms)]. A Mann–Whitney ranked-sum test revealed that the activity level was significantly higher during correct trials than during error trials ($P < 0.01$). The activity of this neuron is re-plotted in Fig. 4B, but now the activity is aligned to the reaction time (the moment the monkey released the central touch bar). This plot demonstrates that the activity difference is the same regardless of which of the two events it is aligned. Figure 4C shows the ROC calculated from the activity displayed in the grey shaded area of Fig. 4B. An example of a single unit recorded in area MST at 4% contrast is shown in Fig. 4D. The upper panel shows the activity during correct trials, the lower the respective activity during error trials, aligned to stimulus onset. The mean single trial activity was assessed in a 400-ms window starting 80 ms after stimulus onset [the population onset latency was 80 ms at 4% stimulus contrast, and the median reaction times were 445 ms (monkey A) and 499 ms (monkey H)]. Different analysis windows were used for the neuron shown in Fig. 4A–C vs. the neuron in Fig. 4D–F, because the neuronal activity was recorded at different contrast levels (2 and 4%, respectively) , not because they were recorded from different areas. The activity was significantly reduced on error trials in this cell (Mann–Whitney ranked-sum test, $P < 0.05$). As for the MT neuron, we re-plotted the activity of the MST neuron aligned to the reaction time (Fig. 4E), and calculated the ROC from the activity shown in the grey shaded areas (Fig. 4F). As for the MT cell,

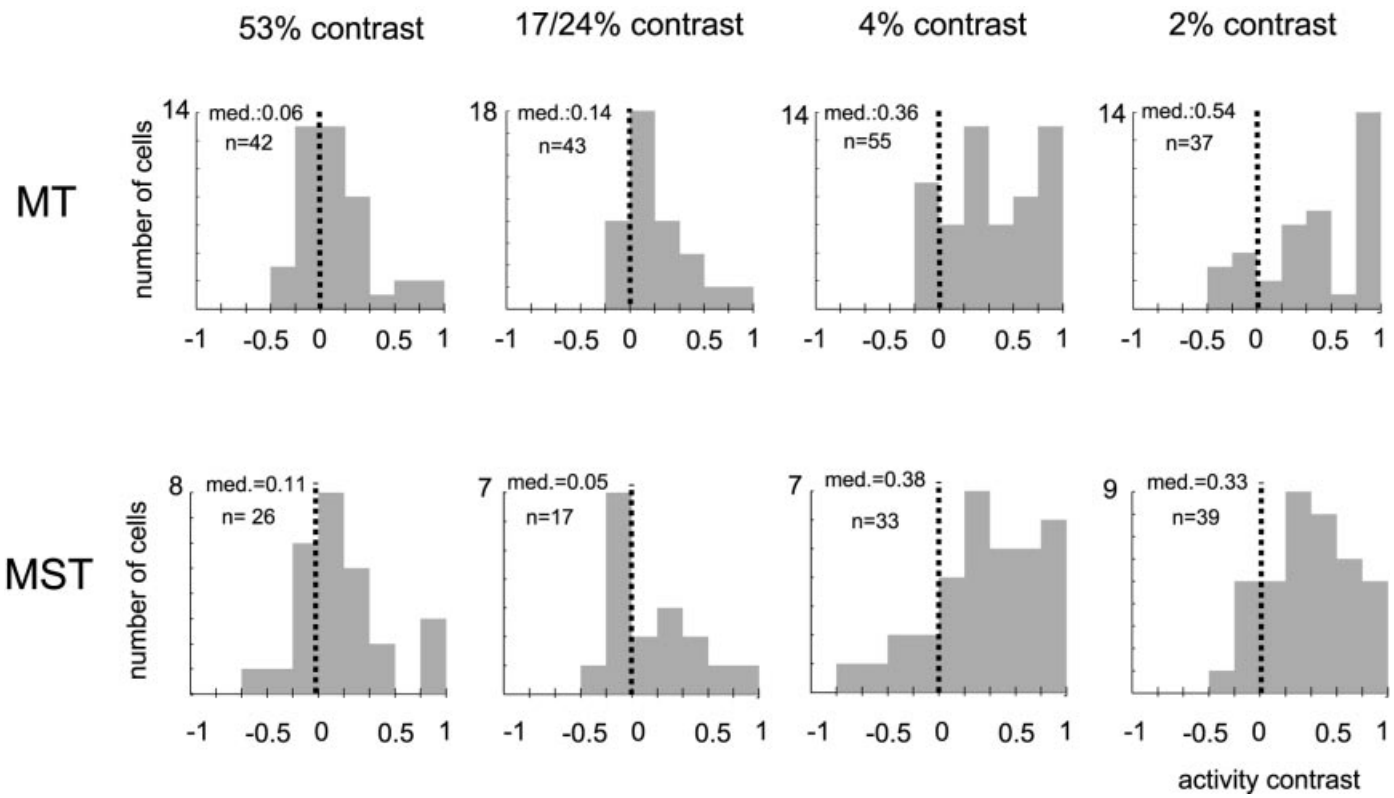


FIG. 6. Distribution of 'activity contrast' for single MT and MST units. The stimulus always moved in the preferred direction of the cells. The activity on correct vs. error trials was compared. Negative values indicate that the activity was higher on error trials and positive values that they were higher on correct trials. A value of 1 indicates that the activity was zero on error trials, a value of –1 indicates that the activity was zero on correct trials. The distribution median was calculated separately for each contrast from the unbinned values; it is given as an inset in each figure. In addition, the total number of cells that were analysed are shown.

the activity difference was significant, regardless to which of the two events the neuronal activity was aligned.

We encountered two limiting factors in the context of the analysis of correct and error trial activity at the single cell basis. (i) Error trials were relatively rare even at low stimulus contrast, and (ii) the number of cells that exhibited significant responses with stimuli moving in the preferred direction decreased as a function of stimulus contrast. As a result we were able to test for significant activity differences in two single cells from V3A, six cells from MT, four cells from MST and two cells from STPp at 2% contrast. The activity was significantly reduced on error trials in all of these cells. At 4% contrast we were able to test for significant activity differences in one cell from V3A ($P < 0.05$), in five cells from MT (4/5 $P < 0.05$), in four cells from MST (3/4 $P < 0.05$) and in one cell from STPp ($P < 0.05$). At 17/24 and 53% contrast we were able to test for significant activity differences in two cells from MT (nonsignificant, $P > 0.05$) and in two cells from MST (nonsignificant, $P > 0.05$).

However, the relatively low number of comparisons that could be performed at the single cell level does not jeopardize our analysis. In any given situation a decision has to be based on a single trial only, and this is presumably done by averaging the response of large cell populations, rather than averaging over large number of trials. Thus, the population response is crucial, and we assessed it by calculating how many cells showed a response reduction as opposed to a response increase (or no change) on error trials. We did this by calculating the mean response of each cell to a stimulus moving in the preferred direction associated with a correct decision and comparing it with the mean response associated with an error. At low stimulus contrast (2 and 4%) the overwhelming majority of cells exhibited lower responses on error trials, and this effect was significant at the population level in all four areas ($P < 0.05$, Mann–Whitney ranked-sum test). The distribution of this relation is shown for each area in Fig. 5A.

According to proposed hierarchical schemes, V3A resides lowest, followed by MT, followed by MST, while STPp resides highest in the visual hierarchy. If these areas were differentially affected by decisions, the least pronounced effects would be expected for area V3A, while neurons from STPp should exhibit the largest response reduction on error trials. To compare the response reduction across areas, we normalized the data from each cell by dividing the response on error trials by the response on correct trials (when stimulus motion was in the preferred direction). To increase our data-set we pooled each area's normalized responses for 2 and 4% contrast stimuli (a Mann–Whitney ranked-sum test did not reveal significant differences between these 2 groups). To avoid counting neurons twice, we initially eliminated neurons which yielded data points at both luminance contrast (these amounted to five out of 92 from MT, two out of 72 from MST, one out of 18 from V3A and none out of 18 from STPp. This small number of neurons is due to: (i) no data at 2% contrast were obtained from monkey H; (ii) many neurons that gave visual responses at 4% were not active at 2% contrast; and (iii) when a neuron was active at 2 and 4% contrast, errors were rare at both contrast levels when the preferred direction was presented, because of monkey A's high performance at 4% luminance contrast). As the results with and without these neurons were not different, we decided to present our whole data set. We applied a two-factor ANOVA to the pooled data with factor 1 being 'cortical area' and factor 2 being 'decision'. The difference in the mean values for the different decisions was significant ($P < 0.0001$). However, no significant effect was found for the different areas ($P = 0.314$). The normalized activity reduction for the four areas is shown in Fig. 5B. The response

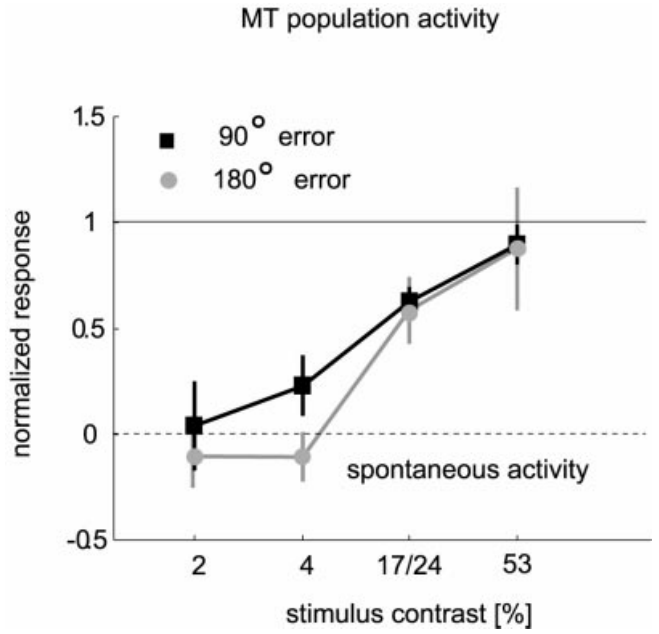


FIG. 7. Population activity dependent on contrast and the direction of a decision on error trials in area MT. Stimulus motion was in the preferred direction of the cells. Solid lines and squares indicate activity differences with decisions orthogonal to the preferred direction. Dashed lines and circles indicate activity differences with decisions opposite to the preferred direction. Grey symbols: activity differences on correct and error trials were not significant (Mann–Whitney ranked-sum test). Black symbols: differences were significant. Data recorded at 17% (monkey A) and 24% (monkey H) contrast were pooled. The upper horizontal line indicates the normalized activity on correct trials, the lower horizontal line represents the background activity level.

reduction amounts to ≈50% in all four areas. The largest reduction was found for area MT, followed by V3A, followed by MST, with the smallest activity reduction in area STPp. Thus the neuronal response reduction associated with errors does not increase with position along the cortical visual hierarchy.

Activity reduction as a function of luminance contrast

To obtain a better impression of the distribution of activity reduction on error trials as a function of contrast we calculated the activity contrast (see Methods section for details). This was done for each MT and MST cell when the preferred direction was presented and at least one correct and error trial occurred. Though it is not possible to calculate a statistic for most of these single cell data, the distribution derived from the AC sheds light on whether a systematic trend exists in the cell responses associated with correct and error trials. The distributions of the ACs are shown in Fig. 6. Values larger than zero indicate that the activity was higher on correct than on error trials, while values smaller than zero indicate the reverse. The medians of the distributions are larger than zero for all contrast levels investigated. However, a systematic increase of the median occurs with decreasing contrast. An ANOVA on ranks revealed that ACs significantly depended on luminance contrast in both areas ($P<0.001$). *Post hoc* testing using Dunn's method showed that ACs determined at 2 and 4% were significantly different from those determined at 17/24 and 53% in both areas. ACs determined at 2% were not different from those determined at 4%, and the same applies for the comparison of ACs determined at 17/24 and 53% contrast. Our data set from the other areas (V3A and STPp) was not sufficient to calculate the distribution of activity contrast for different stimulus contrasts. Thus in area MT and MST the activity reduction on error trials depends largely on stimulus contrast. It is profound at low contrast, and basically absent at high contrast.

The previous test compared the AC values as a function of luminance contrast, and showed that the activity reduction on error trials significantly increases with decreasing contrast. However, this analysis does not address whether, at high contrast level, the activity on correct and error trials is the same or different. To test this we applied a Mann–Whitney ranked-sum test in order to determine whether the activity on error trials was significantly reduced at all contrast levels, or only at low contrast. The activity in MT and MST was significantly reduced on error trials at 2 and 4% contrast, while at 17/24 and 53% contrast it was not significantly different from the activity on correct trials.

Activity reduction as a function of the direction of the decision

As our monkeys were engaged in a four-alternative forced-choice task, it is reasonable to ask if the direction of the decision on error trials is systematically reflected in the neuronal activity. Our MT data set allowed us to differentiate between decision that were orthogonal and those that were opposite to the presented preferred stimulus direction. Figure 7 shows the normalized population activities on error trials as a function of luminance contrast and as a function of the direction of the decision. Normalization was achieved by calculating, for each cell, the mean neuronal activity on error trials divided by the mean activity on correct trials, after subtraction of background activity. The time windows used were the same as described in the previous sections. A Mann–Whitney ranked-sum test revealed that the activity was significantly reduced ($P<0.05$) on error trials at low and intermediate contrasts and that this reduction was most profound on error trials opposite to the stimulus direction.

These findings suggest that there could be some sort of paradoxical enhancement of neuronal activity with a nonoptimal direction of stimulus motion when the monkey concomitantly indicates an error in favour of the preferred direction. The corresponding results, however, are somewhat unequivocal, and they were different for the two monkeys. In monkey A, the median activity was not affected by an inaccurate decision in favour of the preferred direction at any contrast level ($P>0.1$, signed rank test). However, in monkey H, we found a trend towards higher activity on error trials in favour of the preferred direction when the stimulus moved orthogonal to the preferred direction, but not when the null direction was presented. This trend was significant at high luminance contrast (24 and 53%, $P<0.05$, signed rank test).

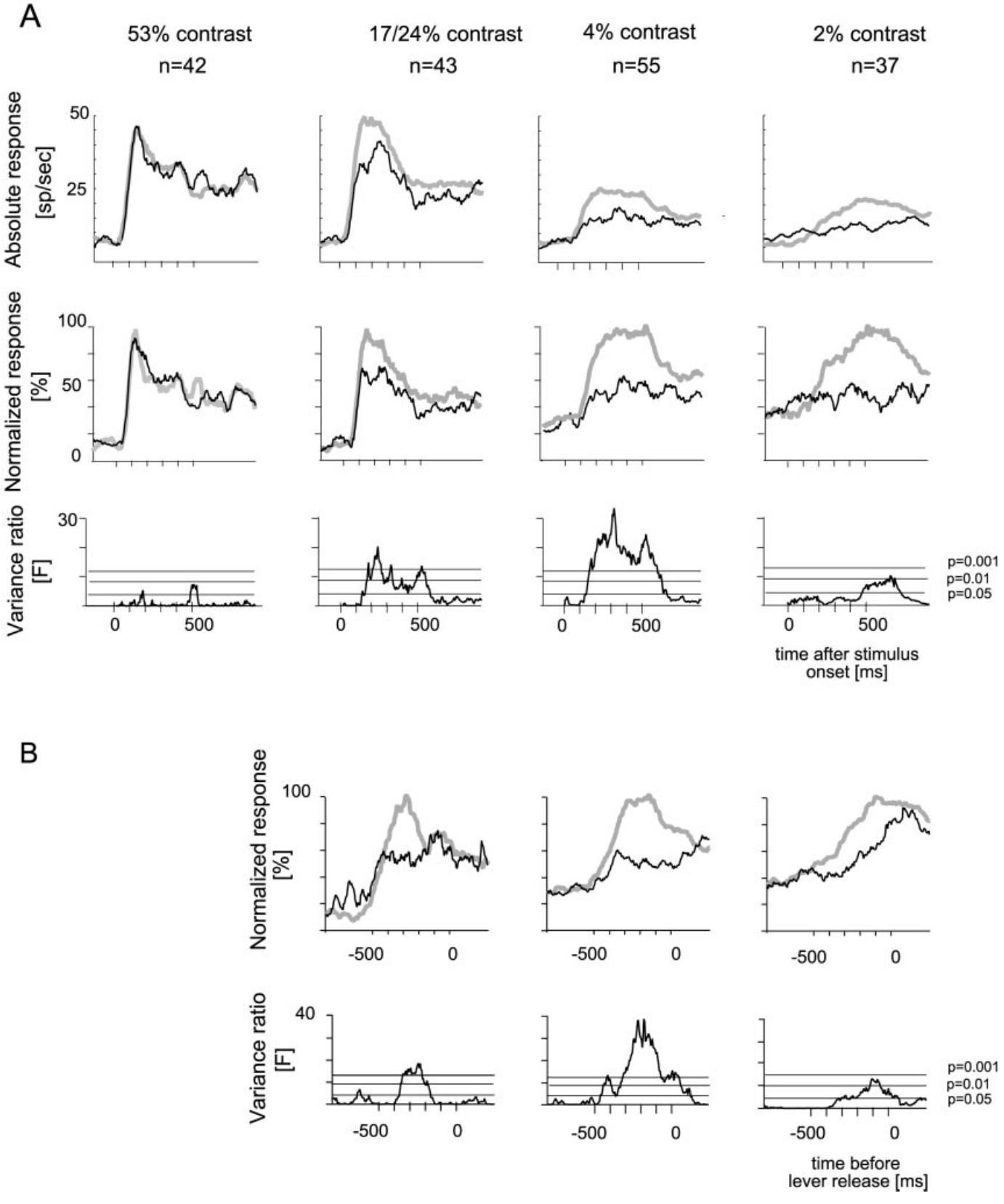
Thus, the direction of the decision is systematically reflected in the neuronal activity of MT on error trials when the preferred direction was presented, but less so when a nonoptimal stimulus was presented.

Activity differences as a function of time

We assume that the activity differences were partially due to attentional lapses on error trials. If true, we would expect the activity differences to increase until shortly before the decision, and to decrease rapidly at around the time the decision has been indicated.

To test this hypothesis we analysed the time course of activity differences on correct and error trials. Therefore we normalized the single cell MT activity when stimulus motion was in the preferred direction. From this normalized activity we calculated the population activity in bins of 5 ms and applied an ANOVA to each of these bins to test for significant differences. The resulting *F*-values (and the related *P*-values) are measures of distance between the two population activities. The larger the *F*-value the larger the activity reduction on error trials. If attentional lapses explained our data on error trials, we

would expect the largest *F*-values (*P*-values) to be related to the timing of the monkey's decision. The normalized MT population activity aligned to stimulus onset and the respective time-resolved statistic for activity differences on correct and error trials as a function of luminance contrast is shown in Fig. 8A. As predicted, we found that the maximum divergence between activity on error and correct trials always occurred 130–150 ms before the median RT for correct decisions; the relationship between the population response



onset and the timing of significant activity differences related to the monkey's reaction time as a function of luminance contrast is summarized in Table 3. Moreover, we found a decline of activity differences at about the time the monkey had indicated the decision (Table 3, column 6), defined by the time when the monkey touched the peripheral touch bar. This moment marks the end of the behavioural part of the task (referred to as 'decision end'), when the monkey was likely to withdraw attention from the stimulus location, because he was only required to keep fixating for the remaining 500 ms, while the visual stimulation remained identical.

Reaction time varies from trial to trial and reaction time on error trials is generally longer than on correct trials (see Table 2). It might therefore be argued that the neuronal activity should be aligned to the monkey's decision rather than to stimulus onset in order to see whether activity differences peak shortly before the decision. The population activity on correct and error trials aligned to the monkey's decision and the respective time-resolved statistics are plotted in Fig. 8B. In accordance with the previous analysis, the activity difference reached its maximum shortly before the monkey indicated the decision (peak difference: 125 ms before the reaction time at 2%; 195 ms before the reaction time at 4%; and 235 ms before the reaction time at 17/24% contrast). Note that the *F*-value peaks (corresponding to *P*-value peaks) are considerably sharper when aligned to the reaction time compared with the condition when aligned to stimulus onset.

In conclusion, both analyses provide clear evidence for an increase in activity differences until shortly before the decision, and a rapid decrease of activity differences after the decision, although the visual stimulation before and after the decision was the same.

Discussion

Our results are significant for three reasons. (i) They provide a comparison of decision-dependent activity reduction on error trials in four areas assumed to reside at different hierarchical levels of the dorsal visual pathway. At low luminance contrast the activity reduction is profound in all areas investigated (V3a, MT, MST and STPp), and the reduction is independent of the hierarchical position a given area occupies. (ii) The activity reduction depends on luminance contrast, at least for area MT and MST. It increases with decreasing stimulus contrast, i.e. it increases with decreasing driving power of the stimulus. (iii) In area MT the activity reduction on error trials also depends on the direction of the decision. The activity reduction on erroneous decisions 90° to a stimulus moving in the preferred direction is less profound compared with erroneous decisions in the direction opposite to the stimulus.

Before discussing these results, we first evaluate potential confounding factors and attempt to discount the possibility that they have contributed to the observed effects.

Potential artifacts

Eye movements

We must consider the possibility that the activity differences in the areas investigated were due to eye movements rather than deficient stimulus processing. In monkey A, the eye position was restricted to a region of ± 1°; in monkey H, it was restricted to ± 2°. Even within these restricted areas, eye movements occurred. Fixational accuracy, however, was much better at low contrast compared with high contrast, where the activity reduction on error trials was less profound. It might still be argued that the monkey tracked the stimulus in one condition, and did not in the other. Tracking leads to a reduction of the motion signal on the retina, resulting in decreased cell activity in visual MT cells (Erickson & Dow, 1989). Thus, the argument could be made that the monkey tracked the stimulus on error trials. This appears highly unlikely to us, because the monkey must then track a stimulus that it apparently does not perceive. Additionally, tracking was absent on most trials when low luminance contrast stimuli were presented (2 and 4%). Nevertheless, we grouped error trials that were accompanied by eye movements of $< 0.4°$ and

TABLE 3. Relation of MT population response onset, time course of activity difference on correct vs. error trials and the monkey's median reaction time as a function of luminance contrast

Luminance contrast (%)	Population response onset (ms)	Time when activity difference became significant (ms)	Time when activity difference peaked (ms)	Time difference (ms) [median reaction time minus time of maximum activity difference]	Time difference (ms) [decision end minus start of difference decrease]
2%	140	475	500	137	–35
4%	80	145	320	≈ 150	–10
17/24%	40	125	225	≈ 1	60

The population response onset decreased as luminance contrast increased (column 2). The time when the activity difference first reached significance ($P \leqslant 0.05$, column 3, time-resolved statistic of 5-ms bins) increased to a larger extent than the increase in population activity onset (compare columns 2 and 3). The time from stimulus onset until the activity difference reached its maximum (the largest *P*-value) also increased to a larger extent compared with the population response onset (column 2 vs. 4). Interestingly, the time difference, between the median reaction time and the time when the maximum activity difference occurred, remained fairly constant across different luminance contrasts (column 5). Moreover, at around the time the monkeys indicated their decision, activity difference waned sharply [column 6: difference between the median 'decision end' (touch of peripheral bar) and the start of activity differences decrease].

FIG. 8. Time course of the firing rate differences for the MT population aligned to stimulus onset (A) and aligned to the monkey's decision (B). Direction of motion was in the preferred direction. The number of cells included in the different histograms is indicated above the subplots. Each cell gave a pair of averaged response histograms (5-ms binwidth, smoothed with a half gaussian of 30 ms) corresponding to correct and error trials. (A) *Upper* panels: absolute MT population activity dependent on stimulus contrast on correct (grey line) and error trials (broken black line). Middle panels: normalized MT population activity dependent on stimulus contrast on correct (grey line) and error trials (dashed black line). *Lower* panels: time-resolved statistics for the activity difference on correct and error trials. (B) Time course of the firing rate differences for the MT population relative to the monkey's decision (lever release = reaction time). *Upper* panels: normalized MT population activity dependent on stimulus contrast on correct (grey line) and error trials (broken black line). *Lower* panels: time-resolved statistics for the activity difference on correct and error trials. (A and B) Cell activity was normalized to the peak activity that occurred on either error or correct trials. Dashed horizontal lines in the time-resolved statistics denote the significance of activity differences.

those that were accompanied with eye movements of $>0.4°$ (occurring from stimulus onset until the monkey indicated the decision**).** A position threshold was used which detects drifts, pursuit and saccadic eye movements. This analysis was restricted to the MT data, because a sufficient number of error trial activities could be compared for this data set (at 2 and 4% luminance contrast). The neuronal activity was not significantly different (Mann–Whitney ranked-sum test, $P>0.05$) on trials with larger eye movements compared with trials with small (or no) eye movements. We therefore conclude that residual eye movements cannot account for the activity differences found on correct and error trials.

Adaptation

Adaptation could be another reason for the correlation between neuronal and behavioural performance. Because the high contrast stimuli were also higher luminance, there might be luminance (or contrast) adaptation arising from these trials. Low contrast stimuli that immediately followed high contrast stimuli might be expected to be less perceptible, and to generate weaker responses, simply from adaptation at earlier levels, perhaps the retina. We investigated this possibility on the basis of the monkey's psychophysics (because this leaves us with a larger data base). If adaptation is the reason for our findings, we would also expect to find a larger number of error trials following high contrast stimuli, and we would expect to find longer reaction times following high contrast stimuli. We therefore sorted all trials according to whether the preceding trial had higher luminance contrast or lower/equal luminance contrast. The performance of the monkey was independent of whether the preceding trial had higher luminance contrast or not (to within 0.4% of the monkeys performance for all luminance contrasts). Additionally the reaction time was unaffected of whether the preceding trial had higher luminance contrast or not (Mann–Whitney ranked-sum test, $P>0.05$) for all luminance contrasts tested. Surprisingly it was even slightly shorter ($\approx$ 10–20 ms) if the preceding trial had higher luminance contrast. We therefore conclude that our results are not due to luminance or contrast adaptation.

Hand movements

What if activity differences at low luminance contrast were due to directionally selective hand movement related neuronal responses? Though we think it is pretty unlikely to find directionally selective hand movement related activity in areas like MT or V3a (and even MST) this argument cannot be excluded unless controls show otherwise. We used stimulus-independent decisions as controls. These were recorded in the absence of visual stimuli when the monkeys nevertheless indicated a directional decision. We determined the activity preceding these decisions using a 500-ms time window that started 500 ms before the monkey released the central touch bar. A Mann–Whitney ranked-sum test revealed whether a significant activity difference existed between decisions in favour of the neuron's visual preferred direction (which was determined using high contrast visual stimuli) and decisions in favour of the other directions. Such activity differences are not necessarily related to hand movement itself, but could as well be interpreted as '*a statistical signature of the contribution that MT* [and other visual areas involved in motion processing] *neurons make to perceptual judgements*' (Britten *et al*., 1996). Though we favour the explanation of Britten *et al*. (1996) for such effects, we nevertheless excluded neurons that showed significant differences on stimulus-independent decisions, in the preferred direction vs. stimulus-independent decisions in the other directions, from the data set presented previously in the Results section. Therefore we are confident that the activity reduction on error trials is not due to directionally selective hand movement neurons.

Decision-related activity and its relation to dorsal visual hierarchy

Neuronal response reduction associated with errors did not increase with progression along the cortical visual hierarchy. It was largest for area MT, followed by V3A, followed by MST, with the smallest activity reduction in area STPp. This result contradicts, somewhat, most other studies of decision-related activity differences in the primate dorsal pathway (Ferrera *et al*., 1994; Thiele & Hoffmann, 1996; Treue & Maunsell, 1996). When monkeys indicate directional decisions in the absence of moving visual stimuli, neuronal activity in areas MT, MST and STPp is correlated with the direction of the decision, and this correlation increases with increasing hierarchical position (Thiele & Hoffmann, 1996). A similar conclusion can be drawn from the studies of Britten *et al*. (1996) and Celebrini & Newsome (1994). In both these papers, their figure 5 suggests that the correlation between neuronal activity and the decision direction is slightly larger in area MST compared with MT. Congruent with these reports Ferrera *et al*. (1994) report increasing contributions of 'extraretinal' signals from MT to MST to area 7a. The amount of modulation in all of these studies was in the range of 10–33%. A similar amount of modulation occurs when monkeys attend to a moving stimulus either inside or outside the cell's receptive field (Treue & Maunsell, 1996). If, however, attention was allocated to one of two oppositely moving dots, both located within the cell's receptive field, the neuronal activity increased by 86% in MT and by 112% in MST (Treue & Maunsell, 1996). The latter study nicely shows that the activity difference depends critically on stimulus parameters and the behavioural conditions. These activity differences are similar to our data. If the monkeys made a correct decision instead of an error the median activity increase was 85% in V3A (mean increase, 78%), 222% in MT (mean increase, 119%), 108% in MST (mean increase, 64%), and 78% in STPp (mean increase, 63%). Though the differences among the areas appear profound, they were not significant in our study, which is an important difference from that in the report of Treue & Maunsell (1996). We can only speculate on the reason of this difference. It could be argued that different tasks were exploited: a task that explicitly aimed to reveal the influence of attention on neuronal responses in MT and MST in the study of Treue & Maunsell (1996), as opposed to a direction-discrimination task in which we sought to determine a possible neural basis for errors which, including attention, may be manifold.

Despite our finding that the areas show equally reduced activity on error trials we do not reject the notion that they are part of different hierarchical levels in the brain. In principle 'top-down' influences (from, e.g. parietal or prefrontal cortex) could enhance feedback projections in MT, MST and/or STPp, which are important for adaptive filtering and increase salience of stimuli in lower areas (e.g. the influence of MT feedback on V1, V2 and V3; Hupé *et al*., 1998). Failure to enhance these feedback projections would decrease the representation of the stimulus in lower areas and higher areas, because the latter would, in turn, receive weaker input.

Underlying mechanisms: lack of attention and/or stimulus expectation?

Our finding that a decrease in neuronal activity on error trials occurs mostly at low levels of luminance contrast, could suggest that decision errors at high and low luminance contrast have different origin. Though this cannot entirely be ruled out, we think that lack of

attention in combination with stimulus expectation contribute to the effects reported at all luminance contrasts.

Though our experiment was not specifically designed to manipulate attention (unlike that of Treue & Maunsell, 1996), we propose that monkeys suffered from attentional lapses on error trials. This proposal is based on three grounds. (i) It has previously been demonstrated that allocation and dislocation of attention can significantly alter the neuronal responses of MT and MST neurons (Treue & Maunsell, 1996), and the response reduction found in that study is roughly similar to what we report at low stimulus contrast. (ii) A contrast-dependent response reduction related to allocation and dislocation of attention, similar to ours, has been described for neurons in area V4 (Reynolds *et al*., 1996). These authors found activity changes due to allocation of attention mainly for nonsalient stimuli (low contrast). Salient stimuli may cause neurons to fire near their maximum rate in the presence and absence of attention. Therefore, we expected strong activity reductions on error trials at low luminance contrast, and almost no activity reduction at high luminance contrast, as was the case in our study. (iii) Activity differences increased and peaked as a function of the median reaction time. The activity differences were largest shortly before the decision for luminance contrasts of 2, 4 and 17/24% (at 53% no differences were found). After the decision was indicated, the monkey did not need to attend to the stimulus any more, and it was then that the activity differences decreased. These data support the hypothesis of attentional lapses on error trials. This finding is different from that of Britten *et al*. (1996), that response differences occured early in a trial and remained largely constant throughout the trial. However, their monkeys were not engaged in a reaction-time task, but rather had a fixed viewing period of 2 s. Therefore the monkey may form its decision anytime in this period. If the activity difference was largest shortly before the decision (which may vary in time from trial to trial) the activity difference would be smeared, and the 'real' difference cannot be recovered because of the fixed viewing period. However, dislocation of attention is not sufficient to explain our data. If the monkeys simply attended elsewhere we would expect to get modulation in the range of 20–40% (see Treue & Maunsell, 1996). In addition to attentional lapses, we assume that monkeys also had a certain stimulus expectation on error trials. These expectations could explain why the neuronal activity on error trials depended on the direction of the decision. A stimulus expectation could bias response properties of competing local feature detectors through 'top-down' processes. If the expectation is sufficiently strong, neurons tuned to the presented direction of stimulus motion are suppressed while those tuned to the expected direction of motion may be enhanced (Buračas *et al*., 1996). Such a scenario could explain the result that activity reduction on error trials varies as a function of the direction of the decision.

Conclusions

Response reduction on error trials is equally strong in several areas of the dorsal visual pathway. This indicates that all four areas tested are modulated by 'top down' processes in a similar manner. However, the failure to report differences due to hierarchical position may well be limited to the areas investigated. It remains to be tested whether the same effects occur in area V1 or V2. Also, decision-related areas in the prefrontal cortex have been shown to reflect the monkey's choice in an unequivocal manner (Goldman-Rakic, 1995). Increasing neuronal response differences due to the monkey's choice may therefore occur along the cortical hierarchy once areas are more involved in behavioural planning (Shadlen & Newsome, 1996) rather than in the analysis of visual features.

Acknowledgements

We thank S. Cardoso de Oliveira for inspiring discussions; L. Croner for providing valuable suggestions for the manuscript; and E. Brockmann for help in histology. Supported by the German Science Foundation DFG: 'Neurovision'.

Abbreviations

AC, activity contrast; CP, choice probability; DMZ, densely myelinated zone; MT, middle temporal area; MST, middle superior temporal area; ROC, receiver operating characteristics; STPp, polysensory area of the superior temporal sulcus.

References

Albright, T.D. (1984) Direction and orientation selectivity of neurons in visual area MT of the macaque. *J. Neurophysiol.*, **52**, 1106–1130.

Bremmer, F., Ilg, U.J., Distler, C., Thiele, A. & Hoffmann, K.-P. (1997) Eye position effects in monkey cortex. 1. Visual and pursuit-related activity in extrastriate areas MT and MST. *J. Neurophysiol.*, **77**, 944–961.

Britten, K.H., Newsome, W.T., Shadlen, M.N., Celebrini, S. & Movshon, J.A. (1996) A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Vis. Neurosci.*, **13**, 87–100.

Britten, K.H., Shadlen, M.N., Newsome, W.T. & Movshon, J.A. (1992) The analysis of visual motion: a comparison of neuronal and psychophysical performance. *J. Neurosci.*, **12**, 4745–4765.

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.

Buračas, G.T., Albright, T.D. & Sejnowski, T.J. (1996) Varieties of attention: a model of visual search. *Inst Neural Computation. Proc. 3rd Joint Symp Neural Computation, Pasadena.*, **6**, 11–25.

Celebrini, S. & Newsome, W.T. (1994) Neuronal and psychophysical sensitivity to motion signals in extrastriate area MST of the macaque monkey. *J. Neurosci.*, **14**, 4109–4124.

Cusick, C.G., Seltzer, B., Cola, M. & Griggs, E. (1995) Chemoarchitectonics and corticocortical terminations within the superior temporal sulcus of the rhesus monkey: Evidence for subdivisions of superior temporal polysensory cortex. *J. Comp. Neurol.*, **360**, 513–535.

Dubner, R. & Zeki, S.M. (1971) Response properties and receptive fields in an anatomically defined region of the superior temporal sulcus in the monkey. *Brain Res.*, **35**, 528–532.

Erickson, R.G. & Dow, B.M. (1989) Foveal tracking cells in the superior temporal sulcus of the macaque monkey. *Exp. Brain Res.*, **78**, 113–131.

Felleman, D.J. & Van Essen, D.C. (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cerebr. Cortex*, **1**, 1–47.

Ferrera, V.P., Rudolph, K.K. & Maunsell, J.H.R. (1994) Responses of neurons in the parietal and temporal visual pathways during a motion task. *J. Neurosci.*, **14**, 6171–6186.

Galletti, C. & Battaglini, P. (1989) Gaze-dependent visual neurons in area V3A of monkey prestriate cortex. *J. Neurosci.*, **9**, 1112–1125.

Galletti, C., Battaglini, P. & Fattori, P. (1990) Real-motion cells in area V3A of macaque visual cortex. *Exp. Brain Res.*, **82**, 67–76.

Gallyas, F. (1979) Silver staining of myelin by means of physical development. *Neurol. Res.*, **1**, 203–209.

Girard, P., Salin, P.A. & Bullier, J. (1991) Visual activity in areas V3A and, **3**: during reversible inactivation of area V1 in the macaque monkey. *J. Neurophysiol.*, **66**, 1493–1503.

Goldman-Rakic, P.S. (1995) Cellular basis of working memory. *Neuron*, **14**, 477–485.

Green, D.M. & Swets, J.A. (1966) *Signal Detection Theory and Psychophysics.* John Wiley and Sons, New York.

Hess, D.T. & Merker, B.H. (1983) Technical modifications of Gallyas' silver stain for myelin. *J. Neurosci. Meth.*, **8**, 95–97.

Hikosaka, K., Iwai, E., Saito, H.A. & Tanaka, K. (1988) Polysensory properties of neurons in the anterior bank of the caudal superior temporal sulcus of the macaque monkey. *J. Neurophysiol.*, **60**, 1615–1637.

Hilgetag, C.-C., O'Neill, M.A. & Young, M.P. (1996) Indeterminate organization of the visual system. *Science*, **271**, 776–777.

Hoffmann, K.-P. & von Seelen, W. (1980) Performance in the cat's visual system: a behavioral and neurophysiological analysis. *Behav. Brain Res.*, **16**, 101–120.

Hupé, J.M., James, A.C., Payne, B.R., Lomber, S.G., Girard, P. & Bullier, J. (1998) Cortical feedback between figure and background by V1, V2 and V3 neurons. *Nature*, **394**,784–787.

Maunsell, J.H.R. & Van Essen, D.C. (1983) Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed and orientation. *J. Neurophysiol.*, **49**, 1127–1147.

Mishkin, M., Ungerleider, L.G. & Macko, K.A. (1983) Object vision and spatial vision: two cortical pathways. *Trends Neurosci.*, **6**, 414–417.

Olavarria, J.F., DeYoe, E.A., Knierim, J.J., Fox, J.M. & Van Essen, D.C. (1992) Neural responses to visual texture patterns in middle temporal area of the macaque monkey. *J. Neurophysiol.*, **68**, 164–181.

Oram, M.W. & Perrett, D.I. (1992) Time course of neural responses discriminating different views of the face and head. *J. Neurophysiol.*, **68**, 70–84.

Reynolds, J., Pasternak, T. & Desimone, R. (1996) Attention increases contrast sensitivity in macaque area V4. *Soc. Neurosci. Abstr.*, **22**, 475.3.

Rodman, H.R., Gross, C.G. & Albright, T.D. (1989) Afferent basis of visual response properties in area MT of the macaque. I. Effects of striate cortex removal. *J. Neurosci.*, **9**, 2033–2050.

Scalaidhe, S.P.O., Albright, T.D., Rodman, H.R. & Gross, C.G. (1995) Effects of superior temporal polysensory area lesion on eye movements in the macaque monkey. *J. Neurophysiol.*, **73**, 1–19.

Shadlen, M.N. & Newsome, W.T. (1996) Motion perception. Seeing Deciding. *Proc. Natl Acad. Sci. USA*, **93**, 628–633.

Thiele, A. & Hoffmann, K.-P. (1996) Neuronal activity in MST and STPp, but not MT changes systematically with stimulus-independent decisions. *Neuroreport*, **7**, 971–976.

Tolhurst, D., Movshon, J. & Dean, A.F. (1983) The statistical reliability of signals in single neurons in cat and monkey visual cortex. *Vis. Res.*, **23**, 775–785.

Tootell, R., Mendola, J., Hadjikhani, N., Ledden, P., Liu, A., Reppas, J., Sereno, M. & Dale, A. (1997) Functional analysis of V3A and related areas in human visual cortex. *J. Neurosci.*, **17**, 7060–7078.

Treue, S. & Maunsell, J.H.R. (1996) Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature*, **382**, 539–541.

Ungerleider, L.G. & Desimone, R. (1986) Cortical connections of visual area MT in the macaque. *J. Comp. Neurol.*, **248**, 190–222.

Vogels, R. & Orban, G.A. (1990) How well do response changes of striate neurons signal differences in orientation: a study in the discriminating monkey. *J. Neurosci.*, **10**, 3543–3558.

Young, M.P. (1992) Objective analysis of the topological organization of the primate cortical visual system. *Nature*, **358**, 152–155.

Zeki, S. (1978) The third visual complex of rhesus monkey prestriate cortex. *J. Physiol. (Lond.)*, **277**, 245–272.