

SINGLE units in the middle temporal area (MT), the middle superior temporal area (MST) and the upper part of the superior temporal polysensory area (STP_p) of the monkey's brain were recorded during the discrimination of direction of visual motion near contrast threshold. In addition to stimulus-related decisions the monkeys often made stimulus-independent decisions while stimuli were well below detection threshold (contrast <0.01%), or totally absent. During this condition MT neurones showed no systematic changes in their ongoing activity while in the MST and STP_p stimulus-independent decisions in the preferred direction of a given neurone were accompanied by the highest ongoing activity. We take this as evidence for internally generated representations of direction of motion in higher visual areas of the superior temporal sulcus. Neurones involved in the initiation of a decision or action are described for the first time in area STP_p.

Key Words: Middle temporal area (MT); Middle superior temporal area (MST); Superior temporal polysensory area (STP_p); Motion; Decision

Neuronal activity in MST and STP_p, but not MT changes systematically with stimulus-independent decisions

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Introduction

The visual system comprises several neuronal stages that extract information from physical stimulus parameters. In its final stage the extracted information leads to perception and appropriate behaviour. The so called dorsal pathway in the primates brain projects to the parietal cortex and is, in addition to other functions, specialized for motion analysis.^{1,2} Studies over the last years produced several lines of evidence that monkeys use directional information supplied by middle temporal (MT) and middle superior temporal (MST) neurones to form perceptual judgements during psychophysical motion discrimination of stochastic visual displays.³⁻⁹ The neural basis of behaviour which is not unequivocally linked to direct sensory input is much less understood. The activity of direction-selective neurones in MST (and MT) co-varies with the direction of a decision if visual noise with no correlated motion is presented to the monkey.⁷ Nevertheless a motion stimulus was presented to the neurone in their paradigm (though 0% correlation), which itself can elicit a strong response.¹⁰ In our paradigm the monkeys often indicated decisions for a certain direction, though visual motion stimuli were far below contrast threshold, or totally absent. This allowed us to investigate whether systematic neural activity differences occur even with stimulus-independent decisions. The areas investigated were MT, MST and the posterior part of the polysensory area of the superior temporal sulcus (STP_p), each of which belongs to a different hierarchical level of the visual cortex.¹

Materials and Methods

Two monkeys were trained in a direction discrimination task. During the experiment the animal sat in a primate chair with head restraint, facing a rear projection screen. Eye movements were monitored by scleral search coils.¹¹ Anaesthesia during surgery and animal care during experiments was according to the guidelines of the European Community (EUVD 86/609/EEC) and the American Physiological Society. When the monkey started a trial by touching a central touch bar in front of its chest, a fixation point was presented centrally on the screen. The maximum fixation window was between $\pm 1^\circ$ and $\pm 2^\circ$. After a randomly chosen time a stimulus moving in one of the four cardinal directions was presented in the receptive field of the recorded cell. The stimulus consisted of evenly spaced light bars (5-10 bars), all moving in the same direction. As each bar left the aperture on one side it was replaced by a new one on the other side. Stimulus size, speed and number of bars were matched to the receptive field size of the neurone under study. Stimuli were generated with an ELSA Winner 2000 graphics board (256 grey level, 800 × 600 pixel at 100 Hz), backprojected with an EPS 4000 Video projector (Electrohome) onto a screen 48 cm in front of the monkey. Screen size was $\pm 45^\circ$ of visual angle. A gaussian filtered static white noise was additionally projected onto the screen. Four different contrast levels were presented, two above threshold (53%, 24%), one close to threshold ($\sim 4\%$), and one well below threshold (0.003%, $< 0.0001 \text{ cd m}^{-2}$). Stimulus

and background intensity were measured with a photomultiplier (EMI, 14 dinodes, 20S, aperture 0.04° of visual angle). Linearity of measurements was ascertained with 50% transmission neutral grey filters (Schott). Due to the gaussian filtered static white noise the contrast of the stimulus varied within the visual field. Thus maximum, minimum, mean and s.d. were calculated for each contrast level. For subthreshold stimuli the maximum contrast was <0.01%. Even in a dark room these stimuli were totally invisible to a human observer after long periods of dark adaptation (>30 min).

The monkey indicated its decision as soon as it perceived or believed that it perceived a direction of motion. A 'go signal' was never presented. Release of the central touch bar was taken as the decision time. At stimulus contrast <0.01% a decision was taken as stimulus-independent decision (SID). Whenever the stimulus contrast was larger, a decision was defined as stimulus-dependent decision. A SID in the correct time window was rewarded 50% of the time (mean). Response biases were minimized by storing the direction of the last 1000 SIDs. Thus the percentage of random reward as well as its quantity was adjusted automatically, based on the history of the monkeys behaviour.

Single neurones were recorded with glass insulated tungsten microelectrodes typically over a period of 200–300 trials including 80–150 SIDs. The preferred direction (PD) of each neurone was defined by its maximal response to one of the four directions of the visual stimulus in trials with correct decisions. The opposite direction was taken as null direction (Null). After subtraction of background activity the direction index (DI = 1 - (Null/PD)) was calculated. If the DI exceeded 0.5 the neurone was classified as direction-selective. For the following analysis only direction-selective neurones were taken into account. The mean activity during the last 500 ms before a SID was evaluated for each direction independently if at least five SIDs were performed in each of the four directions. From these values a normalized decision dependent activity vector was calculated according to the formula:

$$x = (A_{PD} - A_{NULL}) / (A_{PD} + A_{NULL} + A_{-90^\circ} + A_{+90^\circ})$$

$$y = (A_{-90^\circ} - A_{+90^\circ}) / (A_{PD} + A_{NULL} + A_{-90^\circ} + A_{+90^\circ})$$

$$R = \text{sqrt}(x^2 + y^2)$$

$$e_1 = x/R;$$

$$e_2 = y/R.$$

A_{PD} : activity with SIDs in preferred direction;
 A_{NULL} : activity with SIDs in null direction;

A_{-90° , A_{+90° : activity with SIDs to the left/right of the preferred direction, e_1 , e_2 : x and y vector components after normalization.

The vector represents the first trigonometrical moment of the decision dependent activity distribution. Neurones were excluded if the largest and second largest activity were along one axis, since this could easily lead to false direction estimations (maximum error: 90°).

At the end of the experiment Fast Blue was injected at identified recording sites in MT, two small electrolytical lesions were made in MST and horse-radish peroxidase was injected into the upper part of STP_p, close to Area 7a in one of the monkeys. As the second monkey is still involved in the experiment, we determined the recorded areas by their response properties, receptive field sizes, the penetration scheme and recording depths. A detailed description of how to locate areas MT and MST is given in Celebrini and Newsome.⁷ We employed a posterior approach to the superior temporal sulcus (STS). The electrode travelled in a parasagittal plane, tilted 30° with respect to the horizontal plane. Thus MT was the first visual area encountered upon arrival of the electrode at the posterior bank of the STS. MT is recognizable from its characteristic direction selectivity, the receptive field size of its neurones and its topographic map of the contralateral visual hemifield. After leaving MT, the electrode track crosses the lumen of the STS, recognizable by the absence of neuronal activity. The characteristic absence of neuronal activity, while traversing the lumen, helped to separate neurones from MT and MST. MT neurones can easily be separated from V4t neurones, since in contrast to MT, orientation, rather than direction selectivity is a dominant feature in V4t. For details how to locate neurones in MST see Ref.7. Neurones from STP_p can be separated from MST based on the response properties. Visual direction-selective neurones are less often found and are intermingled between neurones with seemingly premotor activity, activity that could be involved in action planning (see Results), somatosensory activity and sometimes auditory activity. The part of STP_p we recorded from corresponds to STP_c and the so-called 'mostly unresponsive area'.¹²

Results

Psychophysics: With suprathreshold stimuli the monkeys decisions were about 90% correct. Close to threshold (4% contrast) the performance fell to 50–70% correct (mean: 56%). With stimuli below detection threshold (SIDs) both monkeys performed the direction discrimination at chance level (24.7% and 25.3% correct). Reaction time increased with decreasing contrast (372 ± 96 ms with stimulus con-

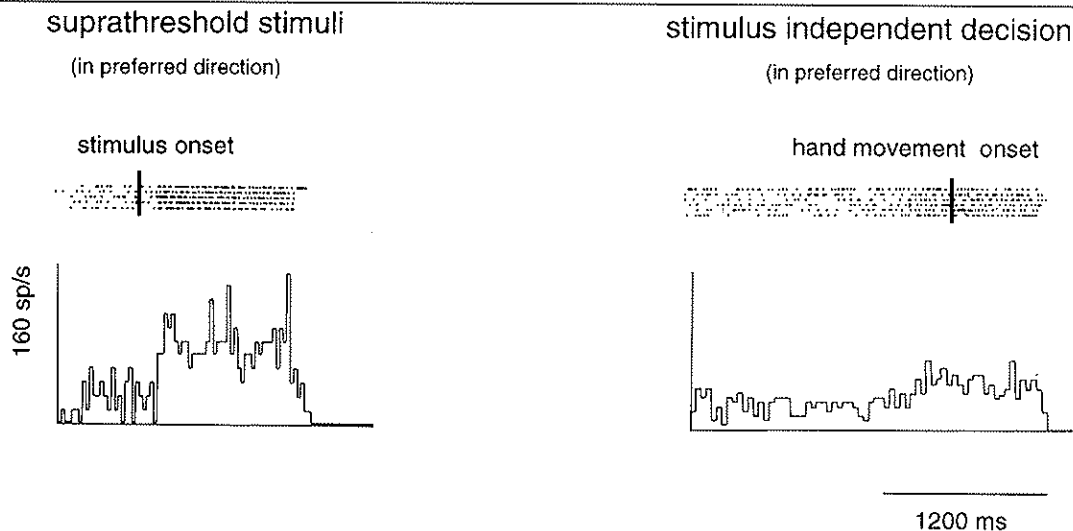


FIG. 1. Single neurone from area STP_p. The left histogram indicates the neuronal activity during visual stimulation in the preferred direction and correct decisions. If the monkey indicated a decision although stimuli were absent, the neurone nonetheless elevated its activity before a decision in the preferred direction (right histogram).

trast >10%, 582 ± 374 ms with 4% contrast, 1108 ± 619 ms with contrast <0.01%). No peak in the distribution of reaction time with subthreshold stimuli was found. Reaction time was evenly distributed around the largest probability for receiving a random reward (2500–3500 ms).

Electrophysiology: A total of 241 visual neurones were recorded from MT, 201 from MST and 84 from STP_p. An example of a single direction-selective visual neurone from STP_p, which additionally exhibited higher activity during SIDs in the preferred direction is shown in Figure 1.

From the total sample the activity of 74 direction-selective neurones from MT, 63 from MST and 32 from STP_p was examined when the monkey had indicated at least five SIDs in all four possible directions. Sixty of the 74 cells from MT had a directed activity distribution during the last 500 ms prior to a SID. The decision-dependent activity (as defined in methods) had a vector component in the preferred direction in 30 of these cells and in the null direction in the other 30 cells (Fig. 2A). The population vector, calculated from the single cell vector distribution, was very small (0.04), but had a slight component in preferred direction. A V' -test was applied to test whether any significant accumulation of vectors in preferred direction could be found.¹³ No significant accumulation of vectors along the preferred direction occurred for MT ($\mu = 0.5307$, $p > 0.05$). From 57 MST cells, 34 had a vector component in the preferred direction (Fig. 2A). The resulting population vector had its main component in the preferred direction.

Its length was 0.164 ($\mu = 1.649$, $p < 0.05$). Thus even in the absence of visual stimuli a significant proportion of MST neurones exhibited a higher activity if the

monkey indicated a decision in the direction of preferred visual motion than in the null direction. This was even more profound for direction-selective cells in STP_p. Most STP_p cells had a vector component in the preferred direction with SIDs (20 out of 29 cells, Fig. 2A). The population vector pointed in the preferred direction, its length was 0.41 ($\mu = 2.44$, $p < 0.01$). Furthermore for each single neurone an activity difference index ($ADI = (A_{PD} - A_{NULL}) / (A_{PD} + A_{NULL})$) between the preferred and null direction was calculated. The median for MT was 0.04 (range: -0.68 to 0.71), for MST 0.11 (range: -0.48 to 0.64) and the STP_p even higher at 0.17 (range: 0.45–0.66). Thus the median, the mean and the distribution of the ADI increase from MT to MST to STP_p.

This tendency for higher activity with SIDs in preferred than with SIDs in the null direction in MST and STP_p was also supported by the calculation of the normalized as well as absolute population activity for the period 500 ms before the monkey's decision (Fig. 2B). While hardly any difference occurs for MT, a slight difference is visible for MST, and this difference is even more compelling in STP_p. The absolute activity difference at the population level between preferred direction and null direction was 0.45 spikes s^{-1} in MT (5.4%, not significant: $p > 0.05$, Kolmogorov–Smirnov test), 1.41 spikes s^{-1} in MST (19.1%), and 2.27 spikes s^{-1} in STP_p (27.5%) (both significant: $p < 0.05$, Kolmogorov–Smirnov test).

In STP_p a number of neurones ($\approx 4\%$) seemed to be involved in timing of action planning. These neurones showed a steady increase of activity during the period the monkey waited for the stimulus. When the stimulus was presented they either exhibited a short activity burst (30 ms), with a total lack of activity afterwards (Fig. 3, left histogram), or they reduced their activity without a burst. If, however, no stimulus

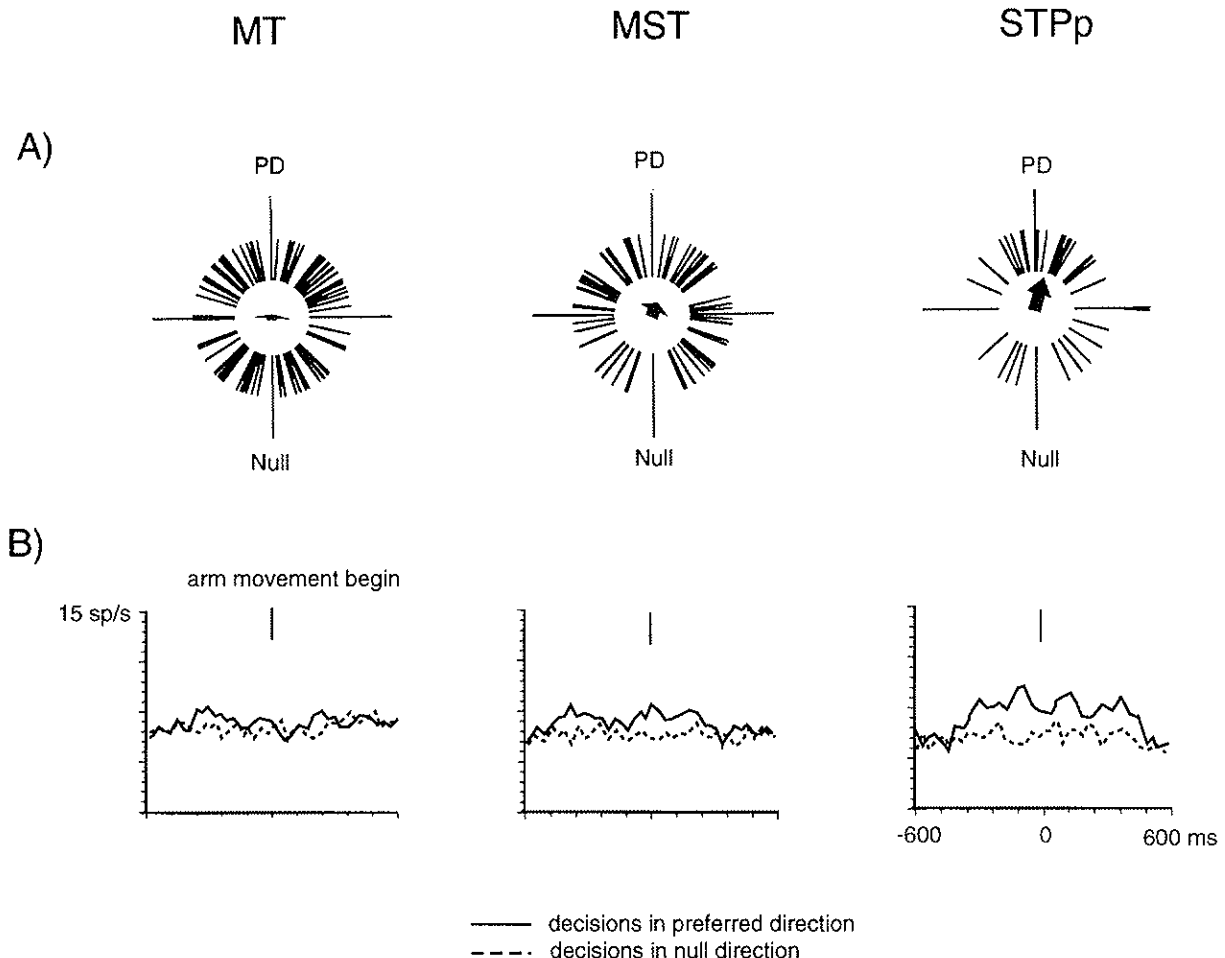


FIG. 2. (A) Distribution of normalized decision-dependent activity vectors for neurones in area MT, MST and STP_p. The preferred direction for visual stimulation (PD) is presented upwards, the null direction (Null) downwards. Each vector can be regarded as the direction in which the maximum activity with stimulus independent decisions can be expected. For MT no accumulation of vectors in a particular direction was found. For MST and even more for STP_p an accumulation along the preferred direction occurred. For both areas these accumulations were significant (MST: $p < 0.05$, STP_p: $p < 0.01$). The arrows in the centre represent the calculated population vector for each area. This population vector successively increased from MT to MST to STP_p. (B) Population activity histograms for the neurones recorded from area MT, MST and STP_p. The two curves indicate the activity level in spikes per second (Y-axis) over a period of 600 ms before and after (X-axis) stimulus-independent decisions (at time 0) in the preferred direction (solid line) and null direction (broken line). In MT no significant activity difference was found between these conditions. In MST and STP_p the activity before and during decisions in the preferred direction was significantly higher than the activity before and during decisions in the null direction.

was presented, the monkey indicated a SID when a certain activity level was reached (Fig. 3, right histogram) and activity decreased with onset of hand movement. During the intertrial interval these neurones showed very low activity levels. The period of increasing activity varied from 500 ms to 4500 ms. No evidence of direction selectivity was found in these neurones with either SIDs or stimulus presentations. Neurones active before hand movements were also found in STP_p (response onset preceded the hand movement by up to 200 ms). With one exception such neurones were not recorded in MST or MT.

Discussion

We were able to localize visually responsive neurones in area MST and STP_p whose activity at the population level was significantly higher during

stimulus-independent decisions in the cell's preferred direction than in the cell's null direction. Even though in MT a significant difference at the population level was not found, the activity before and during SIDs was also slightly higher if the monkey indicated the preferred direction. It is unclear whether these activity differences in MST and STP_p themselves lead to the decisions or whether they are merely a reflection of activity in higher areas projected back to MST and STP_p. A systematic activity difference with the monkey's decision has been reported for MT and MST neurones when a 0% correlated motion stimulus is presented.⁷ This systematic trial to trial variability in MT and MST is suggested to directly influence the outcome of the decision process:⁷ the higher the activity in a given cell, the more likely it is that the monkey will indicate the decision according to the preferred direction of the neurone. In our paradigm

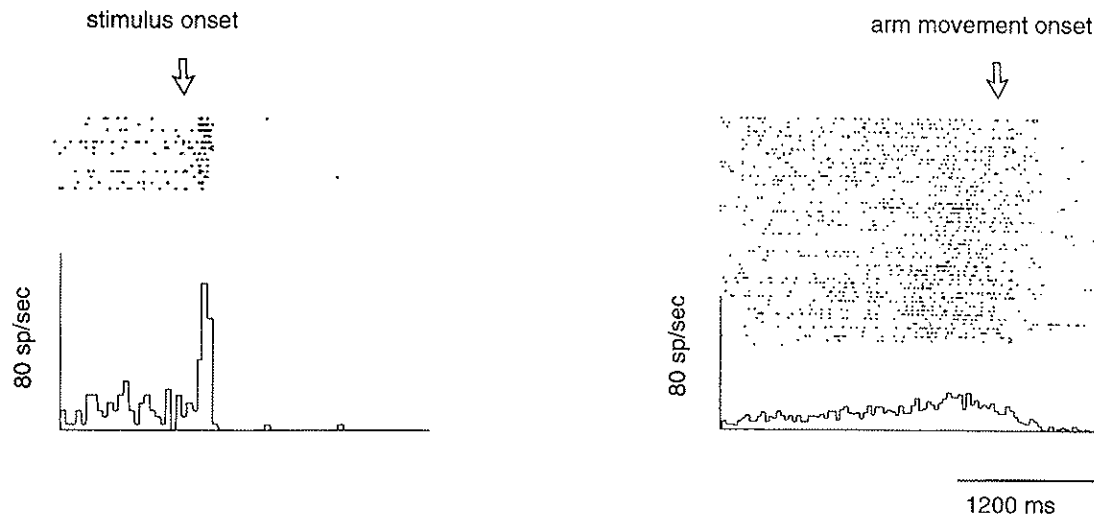


FIG. 3. Example of a neurone from area STP_p that could be involved in the initiation of action showing a short activity burst when a visual stimulus was presented. Activity ceased after this burst (left histogram). This response was independent of the direction of motion (only one direction is shown here). In the right histogram the neurone steadily increased its firing rate while the monkey waited for a stimulus. If a certain activity level was reached the monkey indicated a decision. This activity was seen with subthreshold stimuli or decisions that were indicated prior to stimulus presentation.

we did not find these systematic activity differences in MT. One major difference is the total absence of visible motion in our study compared with random noise motion (0% correlation) in the study of Britten *et al.*⁶ and Celebrini and Newsome.⁷ Moreover in their study the monkey was always given a 'go signal'.^{6,7} Prior to this the monkey could direct its attention to one of the motion components in the random noise. This attention for a certain direction could bias the neuronal response. Dots with motion components in the attended direction could have a larger influence than dots with motion components in the opposite direction. On the other hand our data from MST and STP_p are very similar to the findings of Celebrini and Newsome.⁷ In contrast to their interpretations we do not suggest pure feedforward mechanisms that trigger the outcome of the decision process. The build up of the activity differences in MST seems too slow for such a conclusion. Both feedforward and feedback projections could be used instead to establish the activity differences, as well as the decision making. Simultaneous multi-electrode recordings from 'lower' and 'higher' areas are needed to clarify this point. Synchronous activity in specific neuronal networks, in addition to small spike rate differences, could be important for decision making in the absence of visual stimuli.

The activity difference index for each area is rather small, increasing from MT to MST to STP_p. The values for MT and MST are smaller than those found in the literature.⁹ This might be due to different paradigms. Ferrera *et al.*⁹ used a match to sample paradigm, where the actual activity difference was calculated, if identical stimuli were either matching or non-matching a sample stimulus. No stimulus was present in our paradigm, however; we simply

compared the activity with SIDs in preferred and null directions.

From the distribution of the activity difference indices it is clear that individual cells from one area behave in different ways. It is only at the MST and STP_p population level that systematic activity differences with the direction of a decision are established. Higher activity occurs in the population coding for the direction of visual motion that the monkey will indicate. Whether the differences at the single cell level reflect different functional cell groups remains a subject of speculation.

Our data are similar to results reported by Assad and Maunsell¹⁴ which showed that neurones from 7a exhibit specific activity during inferred motion. Talking in human psychological terms, the monkeys in our study were guessing or imagining a direction of motion. If the monkeys were really imagining a direction of motion, our data would support the idea that only higher visual areas are active during mental imagery.¹⁵ Specific activity differences were not found in MT, they occur in MST and are larger in higher areas like STP_p. This would go against the notion of significant activity increase during mental imagery in early visual areas such as V1.¹⁶ To interpret the action of the monkey as imagery remains highly speculative, but it is tempting to compare the results from positron emission tomography studies in humans and data from single neurones in behaving monkeys.

Conclusions

Systematic variations of ongoing activity related to the direction of a decision were found at the population level in areas MST and STP_p. However, little evidence for such activity differences was found

in MT. These results may reflect the different hierarchical levels of the areas investigated. In addition to a steady increase in the activity difference from area MT to MST to STP_p, the number of neurones that reflect action planning also increase within this hierarchy. No such neurones were found in MT, they were extremely rare in MST, and constitute a significant proportion in STP_p.

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