ELSEVIER

Behavioural Brain Research 76 (1996) 155–167

BEHAVIOURAL
BRAIN
RESEARCH

Motion sensitive cells in the macaque superior temporal polysensory area: response discrimination between self-generated and externally generated pattern motion

Jari K. Hietanen[1] and David I. Perrett *

School of Psychology, University of St. Andrews, St. Andrews, Scotland, KY16 9JU, UK

Received 11 July 1994; accepted 11 September 1994

Abstract

It was previously shown [17] that visual movement sensitive neurons lacking form selectivity in the anterior parts of the dorsal superior temporal sulcus (STP) of monkeys exhibited selective responses to externally moved objects and failed to respond to the sight of the animal's own limb movements. This paper describes a series of experiments in which a monkey was trained to operate an apparatus that produced visual motion of a projected two-dimensional patterned stimulus. Single unit responses from STP were recorded and responses to visual motion, produced externally by the experimenter, were compared to the responses to visual motion (of the same pattern) produced by the monkey itself. The majority of the movement sensitive cells giving reliable responses to the pattern motion responded statistically more strongly to the experimenter-induced motion than to the motion induced by the monkey itself. The cell responses were observed not to be affected by the motion velocity and the monkey's motor activity (handle rotation without any visual stimulation) did not affect the cell's spontaneous activity. The results indicate that the response discrimination of STP cells between externally and self-induced stimulus motion is not based on form sensitivity. Moreover, the mechanism which produces the described response selectivity is not only limited to naturally occurring visual consequences of the monkey's own motor activity but is plastic and can extend to arbitrary associations between the monkey's movements and consequent visual motion.

Keywords: Self-induced stimulation; Expectation; Visual motion; Superior temporal polysensory area; Macaque monkey

1. Introduction

Anatomical and physiological evidence suggests that the superior temporal polysensory area (STP) which is located in the dorsal bank of the anterior superior temporal sulcus in macaques is a part of the cortical motion processing pathway [3,4,20,29,12]. Motion information reaches STP through cortical areas V1, V2, the middle temporal area (MT), the medial superior temporal area (MST) and the fundus of the superior temporal sulcus (FST). A detailed investigation into the general physiological response properties and directional tuning of the motion sensitive cells in STP was made in our laboratory [29]. This study as well as the earlier ones showed that the majority of the motion sensitive units in STP do not show any selectivity for the form but respond equally well to moving bars, patterns and control objects [4,29,32].

An interesting response property of the motion sensitive cells lacking form selectivity in STP was described in a preceding paper [17]. It was shown that the responses of these units discriminated between the sight of external object movements and the movements of the monkey's own hand. The results were discussed in the context of 'cognitive expectations', suggesting that this discrimination might have resulted from the monkey's expectations about the visual appearance and motion of his own arm and hand. Another possibility was that this discriminative capacity might have resulted from the corollary discharge/kinaesthetic input to STP cells. It must be emphasized, however, that the contribution of corollary discharge/kinaesthetic input and 'expectation' in explaining the observed STP cell responses are not necessarily incompatible. On the contrary, in some cases

---

[1] Present address: Department of Psychology, P.O. Box 607, FIN_33101, University of Tampere, Tampere, Finland.

* Corresponding author.

SSDI 0166-4328(95)00193-X

corollary discharge/kinaesthetic feedback may be the physiological mechanism which accounts for some effects of 'expectation'.

The experiments that will be described in the present paper were aimed to clarify two issues raised by the previous experiments. First, is it possible to observe response discrimination between externally and self-induced stimulus motion when the visual appearance of the moving stimulus is identical in both conditions? Even though the (STP) cells were tested thoroughly for their apparent lack of selectivity for form, it was possible that the discriminative capacity previously reported was based on the dissimilarity in visual appearance between the two classes of studied objects (monkey's own arm vs. other objects). This type of 'pattern recognition' explanation is not implausible considering that STP has repeatedly been shown to contain units with high-level selectivity for visual features, e.g. hands and faces [4,6,16,19,30,31,33,35-37]. Second, the sight of one's moving limb is a natural self-produced motion stimulus but is it also possible to observe a similar type of response discrimination between externally and self-induced motion when the connection between actions and visual consequences are learned during a relatively short period of time and when they are based on an artificial association?

This paper investigates the extent to which STP cells discriminate against self-produced motion in more arbitrary associations between the monkey's movements and consequent visual motion. For this purpose a monkey was trained to operate a special apparatus that produced visual motion of a two-dimensional patterned stimulus. Single unit responses from STP were recorded and responses to visual motion produced externally, by the experimenter, were compared to visual motion that was produced by the monkey itself.

2. Materials and methods

The basic methods including extracellular single unit activity recording, horizontal and vertical eye movement recording and methods for cell localization were as described previously [17]. Techniques particularly relevant to the present experiments will be presented here.

2.1. Behavioural task and training

A monkey was first trained to perform a go/no go LED colour discrimination task involving a lick response for fruit juice reward [17]. The monkey was further trained to use an apparatus which was designed to generate motion under the control of the experimenter or the monkey itself.

The apparatus consisted of a vertically oriented handle within a wooden frame. The frame was fitted in front of the primate chair so that the monkey could easily extend its arm out from the chair and turn the handle (Fig. 1). The handle (height 20 cm) was situated at the level of the monkey's upper body and was occluded from the monkey's sight by the upper panel of the frame. The movements of the handle were transmitted through a belt to a turntable which was situated out of the monkey's sight, occluded by the side panels of the handle frame. A large diameter, patterned cylinder (see below) was fixed on the turntable and it was monitored by a close-circuit video system. Using a video projector (SONY VPH-1041QM) the video image of the cylinder surface was projected onto a display screen on which the LED lights were located (4 m in front of the monkey). By turning the handle the experimenter or the monkey could generate a leftward or rightward pattern movement on the projection screen. Because of the large diameter of the cylinder, the video camera (Panasonic NV-MS1B) could be used to produce a sharp focused video image of the cylinder pattern large enough to fill most of the projection screen (20 × 30 degrees of visual angle). When the cylinder rotated the video image of the pattern appeared to translate rather than rotate. The apparatus also allowed a disconnection between the handle and the cylinder. In this case the handle rotation did not result in any movement of the pattern on the screen.

The upper end of the handle was located within a closed compartment, inaccessible by the monkey. This compartment contained two wheels fitted to the end of the handle; one for transmitting the movements of the

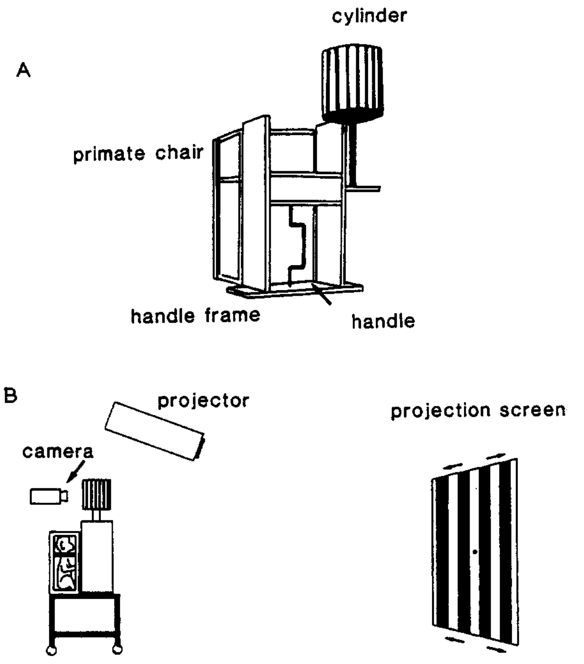

Fig. 1. (A) A schematic drawing of the apparatus used to generate the motion stimulation for the experiments. (B) The experimental set-up. For details, see text.

handle to the turntable and another used for detecting the rotation of the handle. The latter wheel was covered with 48 evenly distributed silver/black stripes. A light detector system positioned over the wheel detected the changes in light reflectance and was used to generate a short (1 ms) pulse every time a silver stripe was swept across the field of the detector. The minimum angle of handle rotation which could be detected was thus 7.5°. The first pulse in a train of pulses was used to trigger a computer. The rotation of the handle activated the onset of (a) a short (100 ms) tone signal, (b) the central LED light for 1.0 s and (c) data collection of cell activity and eye movements for 1.0 s time period.

As the monkey was already trained in a red/green LED colour discrimination task, it learnt relatively quickly to rotate the handle in order to activate the LEDs and access reward. The red and green LED lights were presented in random order on different trials under computer control. The monkey performed the go/no go LED colour discrimination task at a high level of accuracy (> 90%) despite the concomitant pattern movements on the screen. Before the neurophysiological recordings were started, the monkey was trained in this task for 2 months (on average 2–3 training sessions/week), during which time it generated approx. 10 000 trials of pattern motion with concomitant LED fixation light presentation. The training and some early recordings were performed by using a vertically striped white/black pattern on the cylinder. Perhaps because of its high spatial and temporal frequency, this pattern was often found ineffective in eliciting reliable responses in the recorded STP cells and, therefore, it was replaced by an irregular low-frequency colour pattern for the majority of the recording sessions.

2.2. Testing procedures

After a cell was isolated its responsivity to various visual moving stimuli was initially tested using a shutter as described previously [17]. Cells studied here were to sensitive to motion but unselective for the form of the moving stimulus. Cells were selected for further testing on the basis of whether or not they responded to leftward or rightward movement at the projecting distance of 4 m from the monkey. Further testing comprised of recording cell responses to the sight of the projected pattern motion generated by the experimental apparatus and controlled by the experimenter. If the cell gave reliable and consistent responses to this motion, trials were collected when the pattern was (a) moved by the monkey, (b) moved by the experimenter and (c) stationary while the monkey moved the handle. In order to measure the cell's spontaneous activity (sa) in the absence of any motion or motor responses, responses to the sight of the static pattern were collected with a stationary image pattern on the screen and the presentation of the tone and LED light signals triggered externally. Different conditions were interleaved in counterbalanced order.

2.3. Recording procedures and data analysis

Extracellular single unit activity together with horizontal and vertical eye movements were recorded from one female (J) rhesus monkey (*Macaca mulatta*). In some experiments the filtered cell activity, together with the horizontal and vertical eye position signals and handle rotation signals, were additionally recorded on audio tape using a four-channel FM tape recorder (RACAL) for off-line analysis. This method also provided the most convenient way for inspecting pre-stimulus cell activity for self-initiated trials.

The train of 1 ms pulses generated by the handle rotation was used to assess the velocity of the pattern movement during rotation. For this the pulse train was fed from the audio tape back to the computer and was analysed with the same program for neuronal spikes analysis. The displacement of the projected pattern while the handle was rotated between adjacent pulses was used to convert the recorded pulse frequency into a pattern velocity.

Quantitative measurements of cell responses to self-induced and externally induced pattern motion were obtained by calculating the neuronal spike activity during 250 ms after the stimulus (movement) onset. Cell responsivity to the sight of the static pattern was obtained similarly and was used as a reference level (spontaneous activity) against which the responses to motion stimuli were compared. These data were analysed by using 1-way ANOVA and post-hoc tests (protected least significant difference, PLSD [41]).

3. Results

3.1. General response properties

Fifty-one movement sensitive cells lacking selectivity for form were tested for their response to the projected 2D image of the patterned cylinder. Despite the responsivity of these cells to moving 3D objects during the initial movement sensitivity testing, 33 cells did not exhibit consistent responses to the projected 2D pattern motion. One reason for this lack of responsivity was possibly due to the high-frequency stimulus pattern used during the early recordings. Even after replacing this pattern by a colourful low-frequency pattern, many of the tested units failed to respond to this kind of motion stimulation. Possible reasons for this might have been the relatively large size of the moving stimulus (approx. 20 × 30 degrees of visual angle) or its two-dimensionality.

Eighteen cells responded consistently to the pattern movement and these cells were further subjected to testing, comparing the responsivity between externally induced and self-induced pattern motion conditions. These cells form the basis for the results presented here.

In the initial movement sensitivity testing 9 cells responded to every direction of object movement in the frontoparallel plane. 3 cells were classified as bidirectional responding to the object movement directed left or right. 6 cells exhibited unidirectional responses, 4 of those to the right, 1 up and 1 down. Even though the apparatus had been designed to produce only leftward and rightward movement, two cells which gave unidirectional responses to object movement along the vertical axis were tested and found to be responsive to the projected pattern movement when the video camera was rotated through 90° to induce vertical (up or down) motion on the screen. The directional preferences of the cell responses during projected pattern movement always matched that observed during initial testing using 3D objects.

Fig. 2 shows responses of one unit that responded to the large-field pattern movement projected on the wall. The upper part of the figure shows the responsivity in 8 different directions of object movement during the initial directionality testing. The cell was more responsive to motion directed downwards than to other directions of motion or static stimuli. The responses to the projected pattern movement showed the same directional selectivity (lower part of the figure).

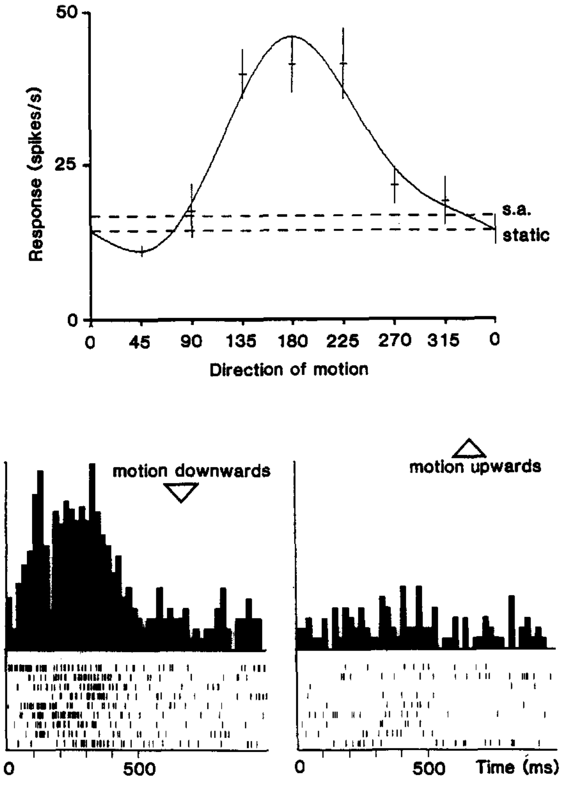

Fig. 2. Directionally selective responses of one cell to object movement and projected large-field pattern movement. Upper part: The cell was tested with 8 directions of object movement in the fronto-parallel plane (0 = up, 180 = down). The cell responded (mean ± 1 SE) to three directions of object movement (180, 225 and 135, $P<0.001$) significantly more (PLSD, each comparison $P<0.001$), than to motion at angles of 0, 45, 90, 315 and 270 or to the static control object or spontaneous activity (s.a.). [Overall effect of condition, one-way ANOVA; $F_{8,36}=18.7$, $P<0.001$, number of trials in each conditions, $n=5$]. The curve is the best fit cardioid function, relating response to direction of movement [$r^2=0.68$; $F_{4,35}=18.2$, $P<0.001$]. Lower part: cell responses to the projected video image of the cylinder used in the experiments. The rasterograms show individual neuronal spikes (short vertical dashes) during post-stimulus time period collected from nine different trials. Poststimulus time histograms (PSTH) show averaged response from nine trials (bin width = 20 ms). The cell responded strongly to the pattern movement directed downwards but failed to respond to similar movement directed upwards (stimulus onset at time 0). The ordinate of the PSTHs denote the cell responsivity for 100 spikes/s.

3.2. Response discrimination between externally induced and self-induced pattern motion

Eleven out of the 18 cells responding to the motion generated by the apparatus gave statistically stronger responses when the movement was generated by the experimenter as opposed to the self-generated pattern motion. 5 cells of these failed completely to respond to the self-induced pattern motion above spontaneous activity. 6 cells exhibited responses to the self-induced motion that were above spontaneous activity, even though statistically weaker than responses to experimenter-induced motion.

Three of the cells which discriminated between externally induced and self-induced motion were classified as exhibiting directional responses. For one of these cells the only condition which was able to activate the cell above its spontaneous activity was the externally induced pattern motion in the cell's preferred direction. The two other cells exhibited response discrimination in the cell's preferred direction of movement for the stimulation induced by the experimenter compared to self-induced stimulation. The weaker responses in the cells' non-preferred direction were equivalent for self-induced and externally induced motion (e.g., Fig. 3).

Motion velocity. The experimenter tried to match the velocity of the handle rotation with that generated by the monkey. The velocity between individual rotations naturally varied in both cases but, within the range of velocities generated by the experimenter or the monkey, no effect of velocity on the cell responses was observed. Fig. 4 depicts the results of testing with one cell which responded selectively to the externally induced motion. The figure also shows the average velocity profile of the pattern motion across the collected trials.

Fig. 5 depicts the responses of the same cell together with stimulus velocity from four selected individual trials. The figure shows comparable response to one of the slowest and one of the fastest externally induced pattern motion. Self-induced pattern motion with com-

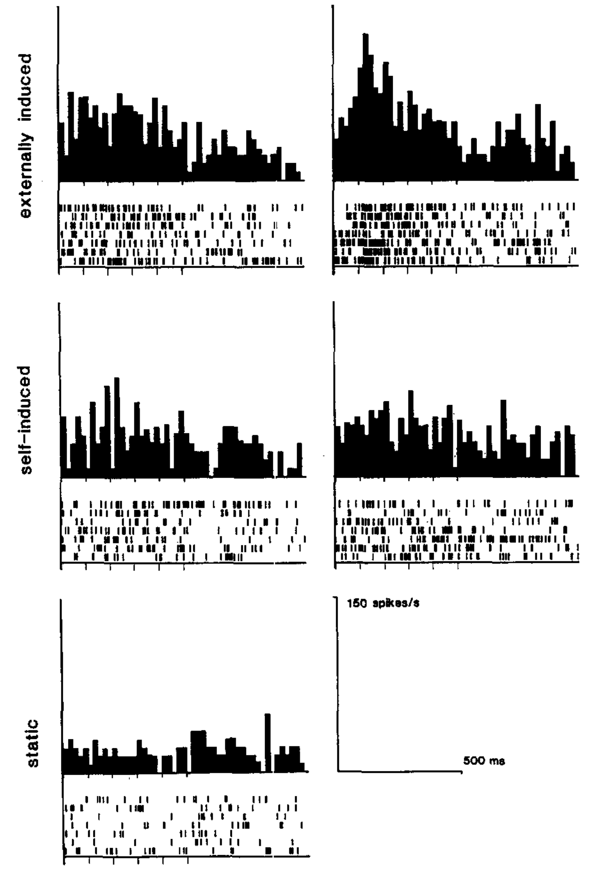

Fig. 3. Directionally selectively responses of one cell to externally induced pattern movement. Upper row: response to the externally induced motion to the left and right; middle row: self-induced motion to the left and right; bottom left: response to the static pattern. Externally induced pattern motion to the right elicited statistically stronger responses than any other stimulus condition ($P<0.005$ each comparison). The cell responded above the spontaneous activity (= static pattern) to the externally induced motion directed to the left and to both self-produced directions of motion ($P<0.02$ each comparison). These responses, however, were graded so that the externally induced motion to the left did not exceed the self-induced motion to the right ($P>0.1$), but was stronger than the self-produced motion to the left ($P<0.02$). There was no difference in responses between the self-induced conditions ($P>0.3$). [ANOVA, $F_{4,30}=17.7$, $P<0.0005$, $n=7$ in each condition.] Stimulus motion onset occurs at the beginning of the rasterograms and PSTHs (bin width = 20 ms). Calibration marks on the right bottom corner give the scale of the responsivity and time.

parable high and low stimulus velocities did not activate the cell.

The effects of motor activity on the cell's spontaneous activity. The testing of 6 of the cells which discriminated between self-induced and experimenter-induced motion included also a condition where the monkey rotated the handle but the handle was disconnected from the turntable and did not, therefore, result in any visual motion. Neuronal data were collected in an otherwise similar way to the testing during motion stimulation. The cells' responsivity during the handle rotation did not differ significantly from the cells' spontaneous activity.

Motor vs. kinaesthetic inhibition. A test was conducted in order to provide insight into the physiological mechanisms resulting in discriminative responses to self-induced and externally induced motion stimulation. The monkey was encouraged to maintain a grasp of the handle while the experimenter held the handle stationary. When the experimenter felt that the monkey was holding the handle and had its arm in an otherwise relaxed state (without attempting to rotate the handle by itself), the experimenter rotated the handle. Collecting such trials while the monkey held the handle during the externally generated rotation and was not put off by the experimenter's intrusion was not easy but, from one cell, a sufficient number of uncontaminated trials was collected. The results (Fig. 6) showed that the cell did not respond in this externally induced condition and indicated that the kinaesthetic feed-back provided sufficient information to cancel the visual response to the pattern motion.

Laterality of the hand used for handle rotation. The monkey was observed to prefer using its right hand in performing the handle rotation, though occasionally it used its left hand as well. During the testing of one cell which was recorded from the right hemisphere the monkey was encouraged to use both hands one at a time. An equal number of trials was collected for self-produced stimuli generated using the left and right hand. The cell (Fig. 7) responded significantly more strongly to the externally induced motion than to the pattern motion generated by the monkey and the visual responses to self-induced motion were unaffected by the hand that the monkey used for the rotation.

3.3. Cells responding equally to self-induced and externally induced motion

Seven out of the 18 cells tested for responsivity to self-induced and externally induced pattern motion exhibited comparable responses in these two stimulus conditions. Fig. 8 shows an example of the responses of one such cell. During the first half second after motion onset the visual motion stimulation triggered a response that was very similar and independent of the origin of the motion-generation. The cell activity during the self-generated trials seems to be slightly attenuated as compared to experimenter-induced trials after the first 500 ms but this probably reflects slight differences in the duration of the handle rotation. Such differences in the duration of motion could not, however, explain the observed discriminative responses for other cells as the statistical analysis of the cell responsiveness was always based on the first 250 ms after the motion onset. When selectivity for direction of motion was present (3 cells), the cell responses showed similar directional preference independent of the generator of the movement (experimenter or monkey).

As mentioned above, two cells exhibited directional

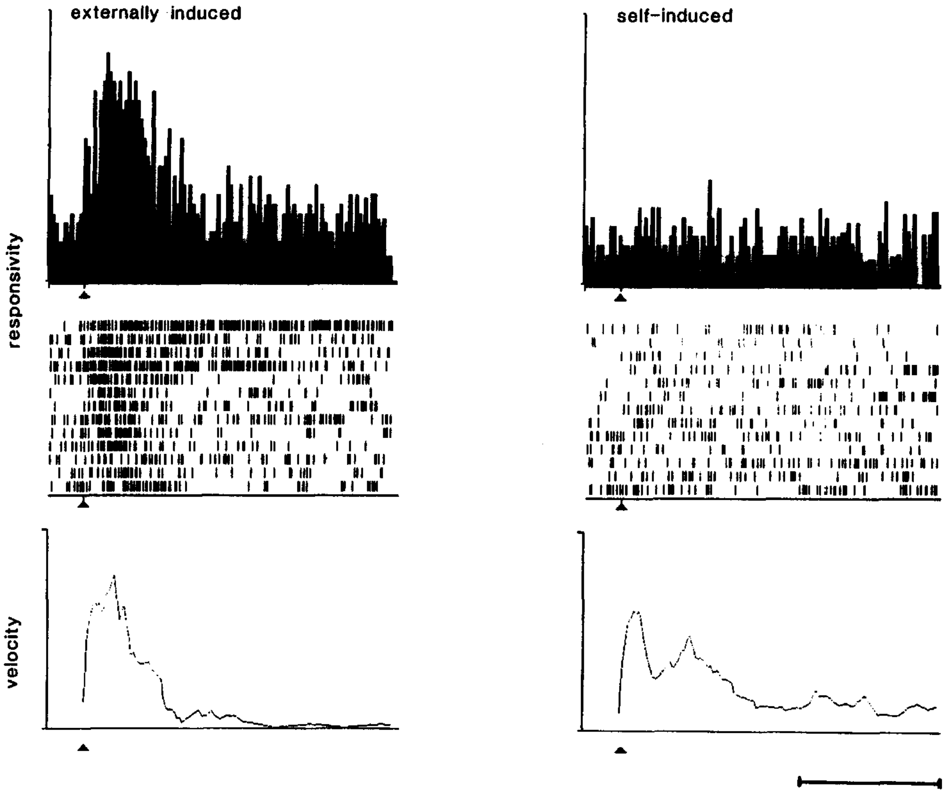

Fig. 4. One cell exhibiting discriminative responses to externally induced motion. The responses were not directionally selective and the directions of movement are combined for the data analysis. The cell responded to externally induced motion above the spontaneous activity and above self-induced motion ($P < 0.0005$ each comparison). [ANOVA, $F_{2.60} = 20.0$, $P < 0.0005$, $n = 18, 28, 17$]. The peri-stimulus time rastrograms show neuronal spikes from 13 individual trials and the histograms above them depict the averaged response of these trials (bin width = 20 ms). The curves below the rasterograms depict the average velocity (in degrees of visual angle per second) of the pattern motion across the collected trials. The pattern motion velocity is comparable for both types of stimulation, especially during the first 300 ms where the difference in strength of cell responses was maximal. The ordinate of the PSTHs denotes the cell responsivity for a range of 0–100 spikes/s. The ordinate of the velocity curves denotes the velocity for a range of 0–150 degree/s. Arrow heads below the time axes denote the stimulus onset. Time scale (1.0 s) is shown at the bottom.

selectivity along the vertical axis and were examined with self-induced and externally induced pattern motion by rotating the video camera monitoring the cylinder through 90° to produce upward and downward motion on the screen. This testing condition was totally unfamiliar to the monkey (for the first of these cells) as the horizontal handle rotation produced now vertical motion on the screen. Both of these cells failed to show discrimination in responses between self-induced and externally induced stimulus conditions and gave equally strong responses independent of the origin of the motion.

3.4. Relative strength of responses in self-induced and externally induced stimulus conditions

A response modulation index (M), indicating the relative responsivity to self-induced (R_{self}) and externally induced (R_{ext}) stimuli was calculated for the studied cells [$M = 1 - (R_{\text{self}-\text{sa}}/\text{R}_{\text{t}-\text{sa}})$]. Value 0 of the index M would indicate no difference in responses between self-produced and externally produced stimulus conditions. Values greater than 0 indicate progressively stronger responses to externally produced pattern motion than to self-produced motion and indices less than 0 indicate increasingly stronger responses to self-produced stimulation than to externally produced stimulation.

The distribution of the calculated M values for the 18 tested cells is depicted in Fig. 9. The cells which gave statistically stronger responses to externally produced stimulation turned out to have index values > 0.3, whereas the values of M for the cells failing to show this discrimination are scattered around 0.

3.5. Eye movements during self-induced and externally induced pattern motion

Eye movement recordings showed (for an example, see Fig. 10) that despite the pattern motion being projected on the screen, the monkey continued fixating on the LED fixation light and generally the eye movement pattern was similar across all stimulus conditions. Cell responses were never found to be linked in time with saccades or fixation onset but depended on the stimulus condition. For example, in Fig. 10 the eye movement

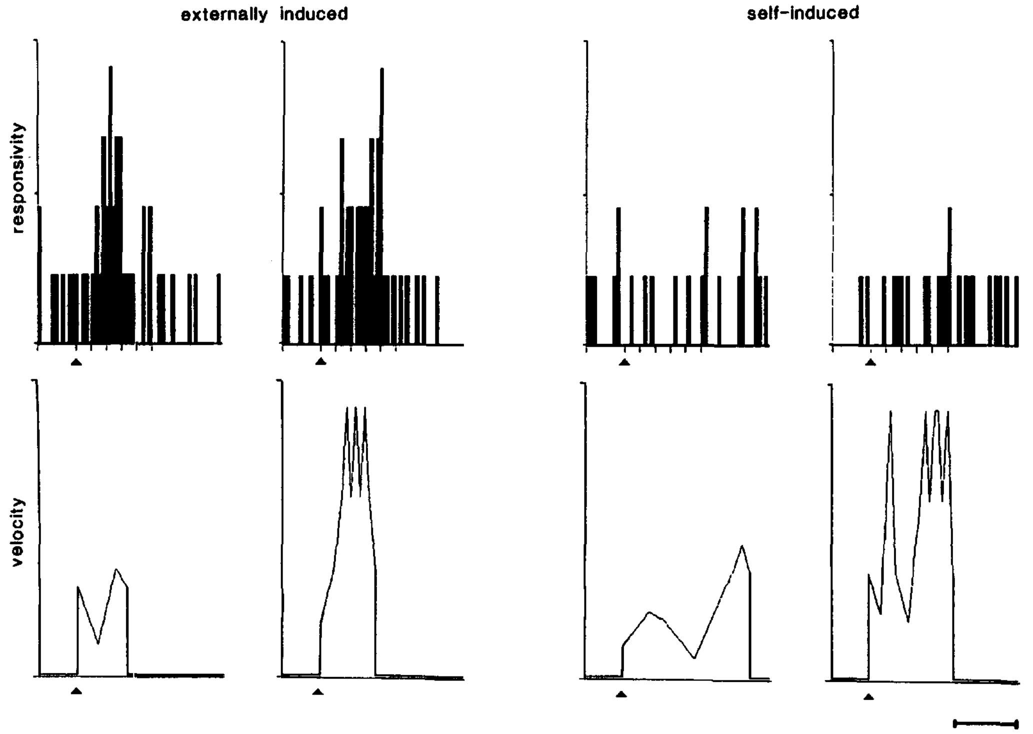

Fig. 5. PSTHs and stimulus velocity curves from four individual trials in externally and self-induced stimulus conditions. The cell (same as in Fig. 4) responded to externally induced motion over a wide range of stimulus velocities but failed responding to self-induced stimulation having comparable motion velocities. The ordinate of the PSTHs denotes the cell responsivity for a range of 0–200 spikes/s (bin width = 20 ms). The ordinate of the velocity curves denotes the velocity for a range of 0–150 degrees/s. Arrow heads below the time axes denote stimulus motion onset. Time scale (0.5 s) is shown at the bottom.

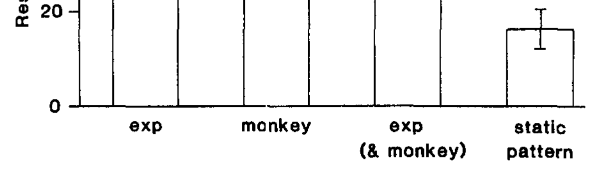

Fig. 6. Histogram presentation of the mean responses (±1 SE) of one cell to different stimulus conditions. The cell responded to externally induced pattern motion (exp) stronger than any other stimulus conditions ($P < 0.0005$ each comparison). The responses to the self-induced motion (monkey) or to the externally induced motion by the experimenter when the monkey passively held from the handle (exp & monkey) did not differ from the cell's spontaneous activity (sight of static pattern, $P > 0.09$). [ANOVA, $F_{3,52} = 23.5$, $P < 0.0005$, $n = 14$, each condition].

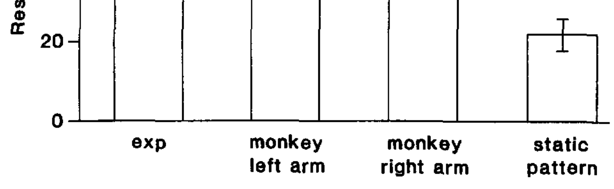

Fig. 7. Responses (mean ± 1 SE) of one cell that responded significantly stronger to the externally induced motion than to the pattern motion generated by the monkey ($P < 0.0005$). The cell responded also above spontaneous activity ($P < 0.03$ to the pattern motion generated by the monkey itself, and the responses were almost identical independent of the hand the monkey used for the rotation [ANOVA, $F_{3,43} = 18.3$, $P < 0.0005$, $n = 13, 16, 11, 7$].

recordings indicate that in the externally induced conditions the monkey fixated the LED light on each trial, usually before the trial onset but occasionally 50–150 ms after the stimulus onset. In the self-initiated trials, the monkey knew when the LED light would become lit and tended to fixate the LED light before stimulus onset. The responsivity in the externally induced stimulus conditions was not related to the eye movements, as the stronger responses on these trials continued during

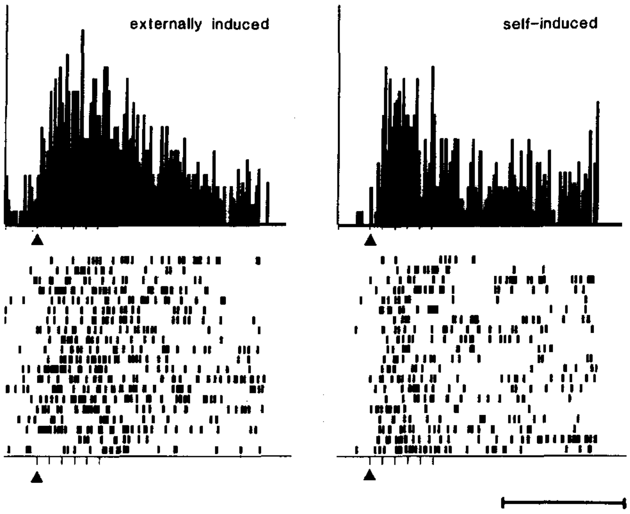

Fig. 8. An example of the cell which responded equally to externally induced and self-induced pattern motion. Analysis of the cell activity based on the number of neuronal spikes during 250 ms after the stimulus onset revealed that the responsivity was the same independent of the origin of the motion-generation ($P>0.5$) and that the responses were significantly stronger ($P<0.0005$) than the cell's spontaneous activity (not shown). [ANOVA, $F_{2.49}=11.0$, $P<0.0005$, $n=20$, 20, 12]. The peristimulus time rasterograms show neuronal spikes from 20 individual trials and the PSTHs above them depict the average response of these trials (bin width = 20 ms). The ordinate of the PSTHs denotes the cell responsivity for a range of 0–50 spikes/s. Arrow heads below the time axes denote the stimulus onset. Time scale (1.0 s) is shown at the bottom.

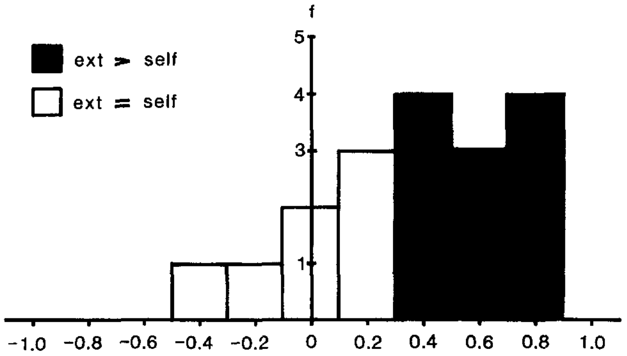

Fig. 9. Frequency histrogram showing the distribution of the M values (see text for explanation) calculated for the 18 recorded cells responding to the projected pattern movement. Black bars indicate the values for the cells which exhibited statistically stronger responses to externally than to self-induced motion, whereas clear bars indicate values for the cells which failed to show such discrimination.

the period of steady fixation. On the other hand, the eye movements after the fixation periods were not correlated with enhanced neuronal activity. Moreover, during the stationary pattern presentation, when the LED was also externally triggered, there were eye movements present before the fixation (in the period 0–150 ms post LED onset) but, again, they were not accompanied by neuronal response.

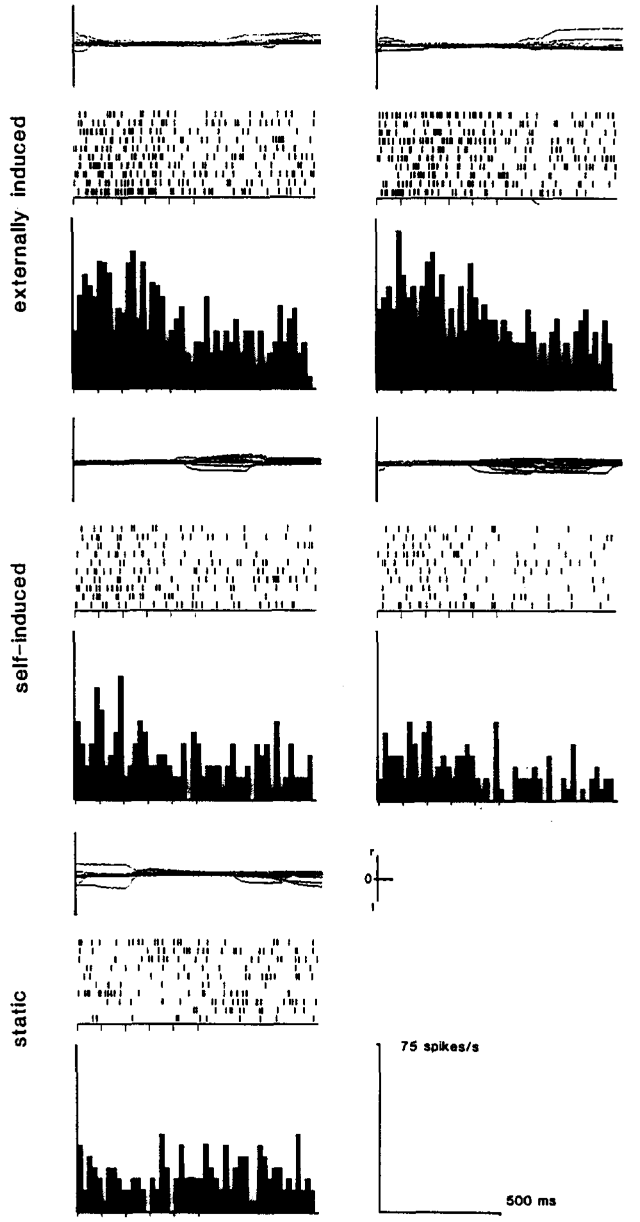

Fig. 10. Horizontal eye position, poststimulus time rasterograms and PSTHs for a cell that responded significantly more strongly to externally induced pattern motion to the left and right than the cell's spontaneous activity (sight of the static pattern, $P<0.003$). Self-induced pattern motion in either direction did not activate the cell above its spontaneous activity ($P>0.05$). [ANOVA, $F_{4.43}=12.1$, $P<0.0005$, $n=10$, each condition]. The LED fixation light was activated by the handle rotation at time 0 (the beginning of the time scale) and remained on for 1 s during which time spike activity and eye movement data was collected. Calibration marks on the right bottom corner give the scale of the eye position (±30°), responsivity and time.

3.6. Location of cells

Histological reconstruction indicated that 15 of the 18 tested cells were located in the cortex of the dorsal bank of the superior temporal sulcus (STP after Ref. [4]. or areas TPO and PGa after Ref. [40]). 9 cells (60%)

exhibited selective responses for externally induced motion. Six cells which gave indiscriminate responses to self-induced and externally induced pattern motion were also located within this same area.

Histological reconstruction indicated that 2 of the studied cells were in the fundus and ventral bank of the STS (areas IPa and TEa after Ref. [40]). Both of these cells also showed selective responses to the externally induced motion. One of the tested cells which responded to projected pattern motion but failed to discriminate between externally and self-induced stimulation was also located in the ventral convexity of the inferotemporal cortex. Fig. 11 shows the results of the histological reconstruction.

4. Discussion

The experiments described in the present paper followed a previous study in which motion sensitive STP cells were found unresponsive to the sight of the monkey's own hand moving [17]. In that study it was argued that the difference in neuronal response to the movements of the monkey's hand and other objects could not be attributed to differences in the monkey's attention to the two types of stimuli. The results of the present experiments provide two further pieces of evidence against the suggestion that the lack of responsiveness to the self-induced pattern motion condition results from factors related to the differences in the animal's attention. First, it should be noticed that the moving pattern occupied a considerable portion of the visual field (approx. 30 x 20 degrees) and the receptive field size of the STP cells is known to be very large, often covering the whole visual field [4]. Hence it is unlikely that the motion stimulus could have fallen completely outside the cells' receptive fields. Second, the animal was performing the LED colour discrimination task which was designed to secure that the monkey directed its gaze straight ahead. The small size and low contrast of the LED light spot (0.07° of visual angle) necessitated accurate fixation in the middle of the moving pattern for both stimulus conditions. As the monkey was observed to perform the discrimination task accurately during both self-initiated and externally initiated trials, the eye position must have been similar in both cases, particularly during the initial period of fixation. The behavioral task accompanying both types of motion stimulation may have directed the monkey's attention away from the motion stimulation as such and further ensured that

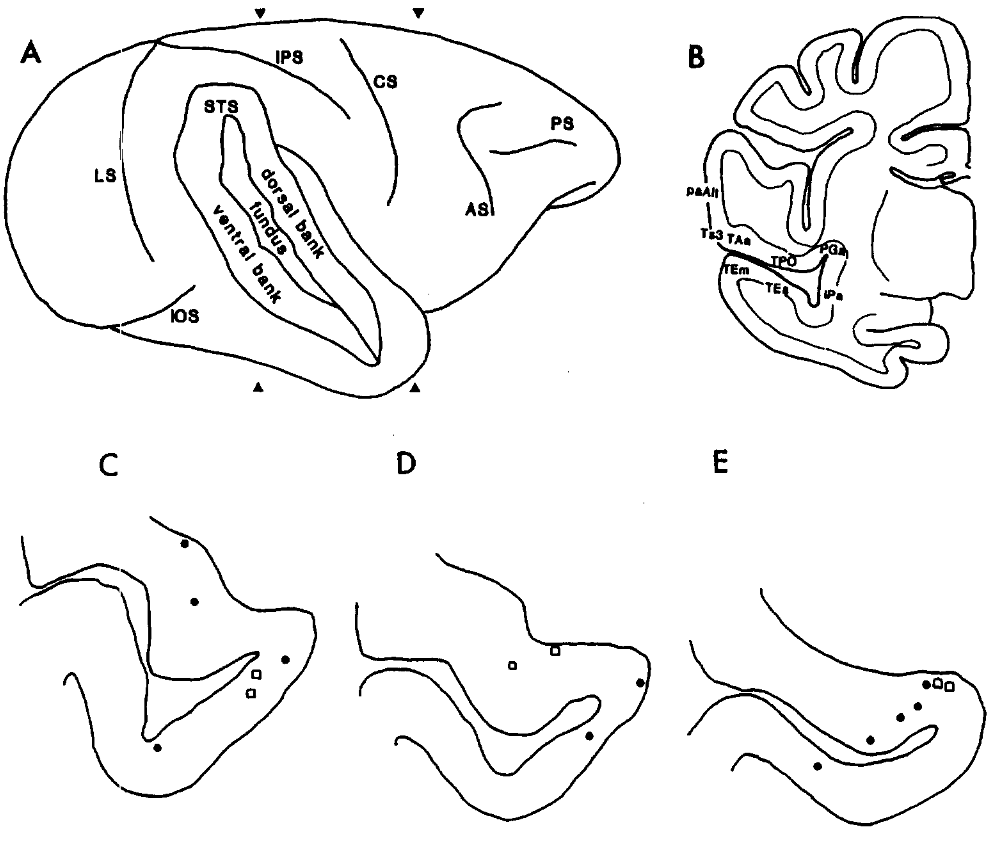

Fig. 11. Three enlarged coronal sections of the STS taken at the levels of +6.5 mm, +9.5 mm and +12.5 mm. The position of the recorded cells located between +5 mm and +14 mm along the rostro-caudal extent of the STS. For the illustration, the studied cells from both hemispheres which were located between 5–8, 8–11 and 11–14 are shown in A, B and C, respectively. The filled circles mark the location of cells responding selectively to externally induced pattern movement, and the open squares show the location of cells failing to show this discrimination.

the discriminative cell responses were not just results of differential attention to externally and self-induced stimuli.

The STP cell responses to motion have been found to be tolerant of variation in the stimulus speed [29]. This was also apparent in the present study as illustrated in Fig. 5. The cell illustrated in Fig. 5 exhibited comparable responses to externally-induced motion irrespective of variation in the stimulus speed. By contrast, self-generated motion did not evoke responses in the cells despite comparable variation in the stimulus speed. Thus it is difficult to argue that the differential responses to self-induced vs. externally induced motion reflect differences in the stimulus velocity between these conditions.

If eye movements accompanying self-induced condition were different in some systematic way from those in the externally induced condition then conceivably the direction of motion on the retina could change between the two conditions. This potential artefact cannot explain the selectivity observed, since nine of the motion sensitive cells tested were classified as lacking directional selectivity in the frontoparallel plane. For these cells, the lack of response in the self-generated stimulus condition cannot be attributed to any potential differences in direction of the retinal motion between self-generated and externally generated movement conditions since these cells responded to externally induced motion in any direction.

More generally, it is implausible that differences in eye movements can account for the difference in STP responses to self-generated and externally generated movement. It was shown in our preceding paper (Fig. 6. in [17]) that the STP cells continue responding consistently to externally induced motion stimulation despite variation in the pattern of concomitant eye movements. With the grating pattern and LED colour discrimination task used in the present study, the monkey's pattern of eye movements was more consistent across trials than in our previous study [17]. The monkey tended to maintain a period of steady fixation on each trial in both self-generated and externally generated stimulus conditions (Fig. 10). Thus the retinal velocity of the grating pattern would vary between individual trials (due to variation in the speed of stimulus motion) but the range of velocities was matched across self and externally induced movement conditions during the trial period in which response magnitudes were assessed.

The results of the present experiments were based on recordings from 18 cells in the left and right hemisphere of one monkey subject. One might question the extent it is possible to generalise from neurophysiological findings in one subject, though we note that other investigators have reported neurophysiological phenomena based on single-unit recordings in one monkey [7,8,14]. As others have argued, even if phenomena were to reflect individual experience or cognitive strategy and hence were to be observed in some but not all subjects, this would not make the physiological findings any less interesting for an account of the neural mechanisms underlying the psychological processes investigated.

Earlier studies have shown that STP cell responses discriminate between self-generated and externally generated stimulation for other classes of visual motion (and stimulation in other modalities) [17,18,27]. In these studies, the discrimination between self-generated and externally generated stimulation was observed in several monkeys (including the present subject) [17,18]. The present example of discrimination between self-externally generated stimulation appears to reflect a more general property of processing in the anterior STP. We believe therefore that the phenomenon described in this preliminary report is likely to occur in other suitably experienced subjects, since it is important to discriminate self-from externally generated sensory signals in many contexts [17,18,27].

5. The effects of experience in modifying the STP cell responses

A possible physiological mechanisms responsible for the observed response discrimination could involve motor/kinaesthetic signals originating in posterior parietal cortex and used in the STP to inhibit the responses to the visual consequences of the monkey's actions. The sight of an animal's own limb movements is a natural type of self-produced motion stimulation and it has been suggested that reactions to the animal's own movements might be innate and 'hard-wired' to the neuronal structure [5].

Considerations about whether the observed response properties are based on pre-programmed connectivity or whether they result from plastic processes are relevant for the speculations as to the function of the STP cells. One could argue that the lack of STP cell responses to the sight of the monkey's own limb movements is based on hard-wired connections between the parietal and STP cortex. On the other hand, it should be remembered that monkeys (as well as humans) undergo extensive practice in visually guided hand movements and have enormous experience in observing their own movements. Moreover, even if the rudiments of a neuronal wiring were innate, they must show considerable plasticity as the signals used for the necessary computations would need to be changed during the growth process. Finally, if STP has a role in the processing of externally produced and 'unexpected' information as suggested elsewhere [27]. it would be functionally more useful if the system was capable of plasticity in the adult state and susceptible to relatively short-time experiences.

The results of the present experiments clearly indicate that the mechanisms producing differential cell responses to self-induced and externally induced stimulus motion in the STP cells are modifiable by experience. The monkey was trained to perform a task where the connection between its actions and the following visual consequences was arbitrary. Over half of the cells that responded to the visual motion stimulation produced by the apparatus used gave statistically stronger responses when the motion was generated by the experimenter as opposed to similar motion generated by the monkey itself. Some cells failed completely to respond to the self-induced pattern motion, whereas others exhibited weak responses to the self-induced motion. Approximately a third of the cells gave comparable responses to self-induced and externally induced motion.

The results with the two cells that were tested by projecting the image of the cylinder so that it was moving along the vertical axis rather than along the horizontal one together with the handle, were potentially revealing. Both of these cells failed to show discrimination in responses to the self-induced and externally induced conditions. Now, it could be speculated that the discriminative capacity is based on experience in the experimental situation. To produce such response properties as those described here, the signal that inhibits responses to self-induced motion may need to be associated with the specific visual input that has repeatedly accompanied a particular motor act. An interesting experiment would be to study how quickly these types of associative changes take place.

5.1. Physiological mechanisms of the response discrimination

The results indicated that the spontaneous activity of all the cells which discriminated between self-induced and experimenter-induced motion was not affected by the monkey's motor activity during the handle rotation when there was not any visual motion present. The lack of inhibition shows that the mechanism causing the lack of responsiveness to self-induced motion stimulation is working on the ascending visual input signal reaching the recorded cell. The same conclusion was drawn from previous experiments which showed a lack of responsiveness to the sight of the monkey's own hand movements was based on the finding that the cells continued responding normally to external movement even when the monkey's own hand was present in view. The idea of presynaptic inhibition is also compatible with the findings of other studies of the visual cells which discriminate between object motion and motion caused by the animal's own eye movements. For these cells the spontaneous activity is not affected by eye movements in darkness [9,11,13].

The distribution of the response modulation indices presented in Fig. 9 shows that the majority of the cells responded more to the externally produced pattern motion. The negatively skewed distribution may reflect the model suggested above, namely that the mechanism which produces weaker responses to self-produced stimulation works presynaptically on the visual input signal. All that the mechanism can do is to suppress the self-produced motion signal (a total suppression would result in an index value of 1.0) but it cannot suppress the cell discharges below the cell's spontaneous activity level (there were no index values greater than 1.0 which would result if responsivity in the self-induced condition was less than the spontaneous activity).

An important question concerns the nature of the mechanism that produces attenuated responses to self-induced visual motion in STP. Two alternatives were considered previously in explaining the discrimination in responses to the sight of movement of external objects and the animal's own limb [17]. One possibility was that the motion sensitive cells were provided with a signal carrying information about the form, position and direction of the animal's own limb movements and that this signal was used to inhibit the visual responses to the sight of own limb movements. This type of inhibitory signal was suggested to reflect motor (corollary discharge) and kinaesthetic output from other brain areas. Another alternative presented was that the response discrimination was based on the monkey's cognitive-mnemonic 'expectations' about the appearance of its own limb. This model would probably include a signal-match mechanism which compares 'expectations' with actual sensory stimulation. The existence of this type of matching mechanisms in other sensory modalities has been suggested previously [10,22].

It was shown that when the monkey held the handle while the experimenter performed the actual rotation (and generation of the pattern movement), one cell that was tested this way did not respond in this externally induced stimulus condition. In this case, as the monkey's arm moved passively, a corollary discharge should not have been emitted either. This would indicate that the corollary discharge is not, or at least not the only, source of input necessary for the described response discrimination and that the recorded cell might have relied on the kinaesthetic feed-back. One of the neurons tested in the present experiments was also subjected to the experiments described previously [17]. This neuron exhibited a lack of response both to the sight of monkey's own hand movements and to the self-generated pattern motion. These observations seem to suggest that the neuronal systems within STP use multiple mechanisms to produce the observed response selectivity. The type of 'expectation' signal as postulated above could derive its contents from corollary discharge, kinaesthetic, pattern matching as well as other, yet undefined, types of modulatory signals.

Response properties of single units in the anterior parts of the nucleus caudatus that are similar to those reported here have been described elsewhere [38]. Generally, the responses of neurons in the anterior striatum are not tightly linked with specific sensory inputs or motor outputs but rather reflect the significance of external events in preparing the animal to initiate behavioural responses. Many of the response properties are present only in a behavioural testing paradigm where the animal has had the possibility to form 'expectations' of the sequence of external events based on its extensive previous experience in performing in a particular task. For example, it has been reported that in a task where the animal was required to perform a visual discrimination for stimuli presented from behind a shutter, the shutter opening was observed to elicit a clear response from the striatal cells [38]. This response was not, however, a visuosensory response to the discriminanda. This conclusion was based on the observations that an additional visual or auditory cue prior to the shutter opening reduced the response latencies radically. Instead, it was suggested that the response was elicited by the opening of the shutter that worked as a cue for the animal to prepare itself for the visual discrimination task. Particularly interesting were the results from the tests where the animal was able to initiate the trials itself. In this condition there was no response to the opening of the shutter, even though the sensory event was exactly the same. There is, however, one essential difference between these caudate responses and the reported STP cell responses that should be considered. The occurrence of the STP neuronal response was dependent on the special type of visual stimulation (i.e. motion in a certain direction) and reflected, hence, strictly sensory processing of the visual input.

Several brain areas have been shown to exhibit neuronal signals that have been suggested to reflect 'anticipatory' responses to external events. Such responses have been found in prefrontal [28,23,39], premotor [26], parietal [25] and cingulate [28] cortices and in the striatum (nucleus caudatus and putamen [2,21,18]. In these cases the anticipatory responses are dependent on the specific context of experimental behavioural paradigms used and they have been suggested to prepare the animals for the next stages in sequential behaviour.

It has been shown that the supplementary motor area (SMA), motor cortex (MC) and putamen contain relatively high numbers of neurons (36–40%) that exhibit directionally selective preparatory activity prior to movements of an external stimulus (a cursor on a computer screen) also when the movement is controlled by the monkey itself [1]. A minor proportion of the neurons in these areas (16% in SMA, 14% in MC and 6% in putamen) also discharge during the self-produced motion of the external stimulus in a certain direction independent of the direction of the concomitant limb movement of the monkey. These types of cell responses in the motor areas were considered to reflect a 'high-level' neural representation of the target or goal of the movement rather than the animal's limb movement itself. Similar types of neural representation could access STP as well but, whereas the above-mentioned motor structures use it for the planning and execution of motor acts in STP, it is used to cancel the processing of self-induced, expected, sensory information.

It has been suggested that the function of the striatum is to mediate the results of sensory (or 'cognitive') processing to the motor systems [38]. This hypothesis offers appealing explanations as to the functions of STP cortex. It can be postulated that one of the functions of STP is to separate externally caused and 'unexpected' sensory inputs from those that result from the individual's own actions and to relay the information from the external events to the striatum, for example, in order to prepare the animal for necessary behavioural responses. Anatomical connections exist between STP and the striatum [42]. Even though the motion stimulation did not have any behavioural significance to the monkey in the present experiments, unexpected motion probably would in the natural environment. The present results further strengthen the hypothesis proposed by several studies that STP monitors the visual environment for unexpected events [4,15,24,27,34].

Acknowledgment

We acknowledge the considerable help of M.W. Oram in the physiological recordings and data analysis. M.H. Harries and P.J. Benson also participated in some of the experiments. This research was funded by grants from the SERC (GR/F 96723) and ONR (United States) and NEDO (Japan). J.H. was supported by the Pirkanmaan Kulttuurirahasto, Kordelinin Säätiö, Aaltosen Säätiö, and Tampereen Kaupungin Tiederahasto (Finland).

References

[1] Alexander, G.E. and Crutcher, M.D., Neural representations of the target (goal) of visually guided arm movements in three motor areas of the monkey, *J. Neurophysiol.*, 64 (1990) 164–178.

[2] Apicella, P., Scarnati, E., Ljunberg, T. and Schultz, W., Neuronal activity in monkey striatum related to the expectation of predictable environmental events, *J. Neurophysiol.*, 68 (1992) 945–960.

[3] Boussaoud, D., Ungerleider, L.G. and Desimone, R., Pathways for motion analysis: Cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque, *J. Comp. Neurol.*, 296 (1990) 462–495.

[4] Bruce, C., Desimone, R. and Gross, C.G., Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque, *J. Neurophysiol.*, 46 (1981) 369–484.

[5] Bullock, T.H., The comparative neurology of expectation: Stimulus acquisition and neurobiology of anticipated and unanticipated input. In J. Atema, R.R. Fay, A.N. Popper and W.N. Tavolga

(Eds.), *Sensory Biology of Acquatic Animals.* Springer-Verlag, New York, 1988, pp. 269–284.

[6] Desimone, R., Albright, T.D., Gross, C.G. and Bruce, C., Stimulus-selective properties of inferior temporal neurons in the macaque, *J. Neurosci.*, 8 (1984) 2051–2062.

[7] di Pellegrino, G. and Wise, S.P., Effects of attention on visuomotor activity in the premotor and prefrontal cortex of a primate, *Somatosens. Motor Res.*, 10 (1993) 245–262.

[8] di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. and Rizzolatti, G., Understanding motor events: a neurophysiological study, *Exp. Brain Res.*, 91 (1992) 176–180.

[9] Erickson, R.G. and Thier, P., A neuronal correlate of spatial stability during periods of self-induced visual motion, *Exp. Brain Res.*, 86 (1991) 608–616.

[10] Freeman, W.J., EEG analysis gives model of neuronal template-matching mechanism for sensory search with olfactory bulb. *Biol. Cybern.*, 35 (1979) 221–234.

[11] Galletti, C., Battaglini, P.P. and Aicardi, G., 'Real-motion' cells in visual area V2 of behaving macaque monkeys, *Exp. Brain Res.*, 69 (1988) 279–288.

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

[13] Galletti, C., Squatrito, S., Battaglini, P.P. and Maioli, M.G., 'Real-motion' cells in the primary visual cortex of macaque monkeys. *Brain Res.*, 301 (1984) 95–110.

[14] Georgopoulos, A.P., Lurito, J.T., Petrides, M., Schwartz, A.B. and Massey, J.T., Mental rotation of the neuronal population vector. *Science*, 243 (1989) 234–236.

[15] Gross, C.G., Contribution of striate cortex and the superior colliculus to visual function in area MT, the superior temporal polysensory area and inferior temporal cortex. *Neuropsychologia*, 29 (1991) 497–515.

[16] Hasselmo, M.E., Rolls, E.T., Baylis, G.C. and Nalwa, V., Object centred encoding by face selective neurons in the cortex in the superior temporal sulcus of the monkey, *Exp. Brain Res.*, 75 (1989) 417–429.

[17] Hietanen, J.K. and Perrett, D.I., Motion sensitive cells in the macaque superior temporal polysensory area. I. Lack of response to the sight of the animal's own limb movement, *Exp. Brain Res.*, 93 (1993) 117–128.

[18] Hietanen, J.K. and Perrett, D.I., A comparison of visual responses to object- and ego-motion in the macaque superior temporal polysensory area, *Exp. Brain Res.*, (1996) (in press).

[19] Hietanen, J.K., Perrett, D.I., Oram, M.W., Benson, P.J. and Dittrich, W.H., The effects of lighting conditions on responses of cells selective for face views in the macaque temporal cortex, *Exp. Brain Res.*, 89 (1992) 157–171.

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

[21] Hikosaka, O., Sakamoto, M. and Usui, S., Functional properties of monkey caudate neurons. III. Activities related to expectation of target and reward, *J. Neurophysiol.*, 61 (1989) 814–832.

[22] Hocherman, S., Itzhaki, A. and Gilat, E., The response of single units in the auditory cortex of rhesus monkeys to predicted and to unpredicted sound stimuli, *Brain Res.*, 230 (1981) 65–86.

[23] Joseph, J.P. and Barone, P., Prefrontal unit activity during a delayed oculomotor task in the monkey, *Exp. Brain Res.*, 67 (1987) 460–468.

[24] Luh, K.E., Butler, C.M. and Buchtel, H.A., Impairments in orienting to visual stimuli following unilateral lesions of the superior sulcul polysensory cortex, *Neuropsychologia*, 24 (1986) 461–471.

[25] Mackay, W.A. and Crammond, D.J., Neuronal correlates in posterior parietal lobe of the expectation of events, *Behav. Brain Res.*, 24 (1987) 167–179.

[26] Mauritz, K.-H. and Wise, S.P., Premotor cortex of the rhesus monkey: Neuronal activity in anticipation of predictable environmental events, *Exp. Brain Res.*, 61 (1986) 229–244.

[27] Mistlin, A.J. and Perrett, D.I., Visual and somatosensory processing in the macaque temporal cortex: The role of expectation, *Exp. Brain Res.*, 82 (1990) 437–450.

[28] Niki, H. and Watanabe, M., Prefrontal and cingulate unit activity during timing behaviour in the monkey, *Brain Res.*, 171 (1979) 213–224.

[29] Oram, M.W., Perrett, D.I. and Hietanen, J.K., Directional tuning of motion-sensitive cells in the anterior superior temporal polysensory area of the macaque, *Exp. Brain Res.*, 97 (1993) 274–294.

[30] Perrett, D.I., Rolls, E.T. and Caan, W., Visual neurons responsive to faces in the monkey temporal cortex, *Exp. Brain Res.*, 47 (1982) 329–342.

[31] Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D. and Jeeves, M.A., Neurons responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception, *Hum. Neurobiol.*, 3 (1984) 197–208.

[32] Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D. and Jeeves, M.A., Visual cells in the temporal cortex sensitive to face view and gaze direction, *Proc. R. Soc. Lond. B*, 223 (1985) 293–317.

[33] Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., Mistlin, A.J., Chitty, A.J., Hietanen, J.K. and Ortega, J.E., Frameworks of analysis for the neural representation of animate objects and actions, *J. Exp. Biol.*, 146 (1989) 87–113.

[34] Perrett, D.I., Harries, M.H., Mistlin, A.J., Hietanen, J.K., Benson, P.J., Bevan, R., Thomas, S., Oram, M.W., Ortega, J.E. and Brierley, K., Social signals analyzed at the single cell level: Someone is looking at me, something touched me, something moved!, *Int. J. Comp. Psychol.*, 4 (1990) 25–55.

[35] Perrett, D.I., Oram, M.O., Harries, M.H., Bevan, R., Hietanen, J.K., Benson, P.J. and Thomas, S., Viewer-centred and object-centred encoding of heads by cells in the superior temporal sulcus of the rhesus monkey, *Exp. Brain Res.*, 86 (1991) 159–173.

[36] Perrett, D.I., Hietanen, J.K., Oram, M.W. and Benson, P.J., Organization and functions of cells responsive to faces in the temporal cortex, *Phil. Trans. R. Soc. Lond. B*, 335 (1992) 23–30.

[37] Rolls, E.T. and Baylis, C.G., Size and contrast have only small effects on the responses to faces of neurons in the cortex of the superior temporal sulcus of the macaque monkey, *Exp. Brain Res.*, 65 (1986) 38–48.

[38] Rolls, E.T., Thorpe, S.J. and Maddison, S.P., Responses of striatal neurons in the behaving monkey. 1. Head of the caudate nucleus, *Behav. Brain Res.*, 7 (1983) 179–210.

[39] Sakai, M., Prefrontal unit activity during visually guided lever pressing reaction in the monkey, *Brain Res.*, 81 (1974) 297–309.

[40] Seltzer, B. and Pandya, D.N., Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey, *Brain Res.*, 149 (1978) 1–24.

[41] Snedecor, G.W. and Cochran, W.G., *Statistical Methods*, 7th Edn., Iowa State University Press, Iowa, 1980.

[42] Van Hoesen, G.W., Yeterian, E.H. and Lavizzo-Mourey, R., Widespread corticostriate projections from temporal cortex of the rhesus monkey, *J. Comp. Neurol.*, 199 (1981) 205–219.