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Directional tuning of motion-sensitive cells in the anterior superior temporal polysensory area of the macaque

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Abstract. An investigation was made into the directional sensitivity of cells in the macaque anterior superior temporal polysensory region (STPa) to the motion of objects. The cells studied were sensitive to the presence of motion but showed little or no selectivity for the form of the stimulus. Directional tuning was not continuously distributed about all possible directions. The majority of cells were most responsive to motion in a direction within 15° of one of the three cartesian axes (up/down, left/right, towards/away). Tuning to direction varied in sharpness. For most (34/37) cells the angular change in direction required to reduce response to half maximal was between 45 and 70° (for 3/37 cells it was >90°). The estimates of the directionality (median $I_d = 0.97$) of STPa cells was similar to that reported for posterior motion processing areas (the middle temporal area, MT, and the medial superior temporal area, MST). The tuning for direction (sharpness, distribution and discrimination) of the motion-sensitive STPa cells were found to be similar to the tuning for perspective view of STPa cells selective for static form of the head and body. On average the STPa responses showed a 100- to 300-ms transient burst of activity followed by a tonic discharge maintained at approximately 20% of the peak firing rate for the duration of stimulation. The responses of motion-sensitive STPa cells occurred at an earlier latency (mean 91 ms) than responses of cells selective for static form (mean 119 ms), but the time course of responses of the two classes of cell were similar in many other respects. The early response latency and directional selectivity indicate that motion sensitivity in STPa cells derives from the dorsal visual pathway via MT/MST. The similarity of tuning for direction and perspective view within STPa may facilitate the integration of motion and form processing within this high-level brain area.

Key words: Movement direction – Form insensitive – Temporal cortex – Single unit – Macaque

Introduction

Visual information processing in the cerebral cortex of primates appears to have at least two major divisions, one analysing motion, the other analysing form. One stream runs ventrally from occipital cortex into the temporal lobe and is thought to be involved in the analysis of visual pattern and recognizing the form of objects (Ungerleider and Mishkin 1982). A second stream projects dorsally into the parietal cortex. This pathway has been postulated to be concerned with the spatial position of objects (Ungerleider and Mishkin 1982) and visuomotor coordination (Goodale and Milner 1992). Since this dorsal pathway involves areas in the posterior part of the superior temporal sulcus (STS) which contain cells almost invariably sensitive to motion, this stream of processing has also been dubbed the motion pathway (De Yoe and Van Essen 1988).

The upper bank of anterior sections of the STS contains an area, the anterior superior temporal polysensory region (STPa, also known as areas TPO and PGa, after Seltzer and Pandya 1978), which is a high-level visual processing area receiving input from both ventral (form) and dorsal (motion) processing streams (Felleman and Van Essen 1991; Young 1992). The majority of studies in this region have concerned the selectivity of cells to static pattern information and the analysis of complex biologically significant objects, e.g. the form of hands (Gross et al. 1972), faces and bodies (Bruce et al. 1981; Desimone et al. 1984; Perrett et al. 1982, 1984, 1992; Baylis et al. 1985; Young and Yamane 1992). Other studies in STPa have described cells selective for complex body movements including hand actions, patterns of walking, and head and limb articulation (Bruce et al. 1981; Perrett et al. 1985b, 1989, 1990a, 1990b; Hasselmo et al. 1989; Mistlin

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and Perrett 1990). These latter cells are interesting because they may indicate the integration of the form and motion streams of information at the cellular level.

Despite the preponderance of cells in STP with complex selectivity there are also large numbers of cells sensitive to motion but showing no apparent sensitivity to form in the same area (Bruce et al. 1981; Perrett et al. 1985b; Hikosaka et al. 1988; Mistlin and Perrett 1990). The functional significance of this cell population is unclear.

Bruce et al. (1981) distinguished three main types of direction selective cells in STPa: those sensitive to movement in the fronto-parallel plane, those sensitive to movement in depth, and those sensitive to radially symmetric movement about the centre of gaze. These types of cell responses are very similar to those found in the medial superior temporal area (MST) in the posterior section of the STS (Tanaka and Saito 1989; Tanaka et al. 1989; Duffy and Wurtz 1991a). Other STP cells exhibit less directional selectivity responding to multiple or all directions of motion, a property not reported for earlier visual motion areas. A variety of less common STPa cell types have also been reported which were sensitive to rotation, jerky motion, or appearance or disappearance from the visual field (Bruce et al. 1981; Perrett et al. 1985b). Bruce et al. (1981) reported that the majority of the STPa neurons displayed little or no form specificity. Perrett et al. (1985b) also found one-quarter (84/335) of the STP motion-sensitive cells lacked form selectivity.

One possible function of these motion-sensitive STPa cells lacking form selectivity might be to contribute to the properties of cells conjointly sensitive to form and motion. Intuitively, these could be created by combining the outputs of cells sensitive to the static form with the outputs of cells sensitive to direction of motion. In order to evaluate this scheme more information is needed about the motion-sensitive STPa cells lacking form selectivity. Such information could also clarify their relation to motion processing in regions within the dorsal pathway.

Motion pathways

In order to understand the motion-sensitive properties of cells in STPa it is useful to review motion processing in earlier cortical regions of the motion pathway. In the macaque monkey the cortical processing of motion information involves a hierarchical series of steps through magnocellular layers of the lateral geniculate nucleus, the upper and lower portions of layer 4Cα of V1, the thick stripes of area V2, the middle temporal area (MT or V5), area MST, an area on the floor of STS (FST) and posterior sections of STP (STPp).

Whilst areas V1 and V2 contain neurons selective for both static and moving visual stimuli in roughly equal proportions, areas in the posterior sections of STS (MT, MST, FST and STPp) contain a very high proportion of motion-selective cells (Zeki 1974; Maunsell and Van Essen 1983; Albright et al. 1984; Movshon et al. 1985; Hikosaka et al. 1988; Rodman and Albright 1989; Duffy and Wurtz 1991a).

In V1, V2 and MT there is clear retinotopic mapping but, in MST, FST and STPp this mapping does not appear to be present (Gattass and Gross 1981). Further, in MT and MST, receptive fields show little or no relationship between eccentricity and receptive field size (Tanaka et al. 1986; Komatsu and Wurtz 1988a). Like V1 and V2, both MT and MST do show evidence of a columnar organization with cells displaying similar motion sensitivity occurring in close proximity (Albright et al. 1984; Saito et al. 1989). Proximity of similar cell types has also been reported in STPa (Harries and Perrett 1991; Perrett et al. 1984, 1985b).

Receptive field size increases going up the motion processing stream. For instance, cells in MT have receptive fields approximately 5 times the size of those in V1 (Mikami et al. 1986b). In the next cortical area of the motion processing hierarchy, MST, the receptive field size increases again, typically extending into the ipsilateral hemispace (mean square-root size range 45–53°, Tanaka and Saito 1989; 62–64°, Duffy and Wurtz 1991a). From MST to STPa there is again an increase, with receptive field size of some 80% of the neurons in STPa covering nearly all of the visual field (median size 150° horizontal, 105° vertical; Bruce et al. 1981).

Cells of V1 and V2 with directional selectivity show a preferred direction of motion that is perpendicular to the orientation of bar stimuli. In area MT some 30% of cells show selectivity for a direction of motion parallel to the preferred bar orientation, allowing the area to code the global direction of an object's motion independent of its local contour orientations (Albright 1984; Snowden et al. 1991). MST neurons, particularly those in the dorsal region (MSTd), prefer motion over a wide field (Tanaka et al. 1986, 1989; Komatsu and Wurtz 1988a, b; Tanaka and Saito 1989; Duffy and Wurtz 1991a, b). Further, most neurons in MST show no response to self-induced retinal motion resulting from eye movement, a property not observed as frequently in neurons of V4 and MT (Duffy and Wurtz 1991b; Erickson and Thier 1991; cf. Galletti et al. 1990), are relatively insensitive to speed or dot density of moving patterns (Duffy and Wurtz 1991b), but are sensitive to disparity (Roy and Wurtz 1990; Roy et al. 1992).

Tanaka and Saito (1989) have suggested that the sensitivity to wide field motion in MST has a role in maintaining visual stability during self-motion and hence to control of posture. Despite the size of their receptive fields, STP cells do not require large field stimuli. Thus as the hierarchy of motion-processing areas is ascended towards the STP, receptive fields increase in size and cells become less responsive to self-induced motion (Hietanen and Perrett 1993). The functional role of motion processing within the STP, however, remains unclear, particularly for those cells lacking form selectivity.

Form processing

The manner in which static form is processed within the STPa has been more fully characterized and may provide insight into motion processing in the same area. The vast

majority of STPa cells sensitive to the static form of objects display selectivity for perspective view (Desimone et al. 1984; Perrett et al. 1991, 1992). The distribution of view tuning displayed an interesting inhomogeneity; namely in the horizontal plane of rotation, statistically more STPa cells were found with optimal views of the head and body close to the front and side views of the head than to intermediate views (Perrett et al. 1991, 1992). This uneven distribution of optimal views amongst STPa neurons supports theoretical models of recognition whereby a small number of "characteristic" views of the object are selectively represented in the nervous system (Koenderink and van Doorn 1979).

One of the main aims of the present study was to examine the directional selectivity of STPa cells and to determine whether the distribution of directions preferred by cells was continuous, or whether particular directions were preferentially represented. Since other classes of STP cell are selective to head or body view *and* direction of motion, the preferential analysis of particular directions might facilitate the integration of the two types of information. Studies of V1 indicate a slight bias for coding horizontal and vertical directions of motion (Mansfield and Ronner 1978; DeValois et al. 1982). Studies of MT and MST have not noted any strong bias in the distribution of optimal directions of motion (e.g. Albright 1984). Despite this apparent absence of preferential tuning to particular directions there is some evidence for its appearance in STPa. In a preliminary report optimal direction of STPa motion-sensitive cells appeared to coincide with cartesian axes (up/down, left/right and towards/away; Perrett et al. 1985b, 1990a, b), but no systematic study has yet been made of direction tuning in STPa. Thus there is a need for quantitative study of tuning to determine whether processing of direction of movement is similar to the processing of static view.

A second aim of the study was to define the breadth of tuning for direction. This is likely to be related to the distribution of preferred directions. With broad tuning (45°, half-width at half-height), four populations of cells tuned to directions 90° apart could represent all directions of motion in a plane; with narrower tuning of, say 22.5°, eight populations would be needed. Of course, finding broad tuning for direction in the STP does not itself guarantee an uneven distribution of directions preferred by cells. For example cells in MT are found tuned to a continuous range of directions, yet tuning appears relatively broad (Albright 1984). Knowledge of the breadth of tuning is also important for comparison with motion processing in other areas.

The time course of neuronal responses to movement was also examined in the present study, since this information can help specify the likely source of visual input to the motion-sensitive STP cells.

Materials and methods

Subjects

Two female (4 kg) and three male (5–10 kg) rhesus macaque monkeys were used. The monkeys are referred to as F, J, B, D and H.

Fixation task

Before recording began, the subjects were trained to discriminate between the red or green colour of a light-emitting diode (LED). The LED was situated level with the monkey's line of sight on a blank white wall at a distance of 4 m. The LED and test visual stimuli were presented from behind a large-aperture (6.5 cm diameter) electromechanical shutter (Compur) or an alternative (20 cm square) liquid crystal shutter (Screen Print Technology). Both types of shutter had rise times of less than 15 ms. On each trial the shutter was opened under computer control (after a 0.5-s signal tone) to reveal the stimulus and remained open for a period of 1 s. The LED light became visible at the time of shutter opening (stimulus presentation) and was randomly red or green on different trials. When open the shutter allowed the monkey to view only the central 30° (Compur) or 100° (liquid crystal shutter) of visual space. The monkeys were trained to lick for fruit juice reward on trials with a green LED. On trials with a red LED they were trained to withhold response to avoid saline solution. Subjects were deprived of water for periods of up to 24 h before training and recording sessions, to motivate task performance.

Although the subjects did not have to fixate the LED throughout the trial period, the monkeys attended to the LED at the beginning of trials in order to lick several times for multiple juice rewards in the 1.0-s trial period. Once they had judged the colour of the LED they were then free to move their eye. The two-dimensional (2D) test stimuli were projected onto the wall on which the LED was located; three-dimensional (3D) test stimuli were presented in front or to either side of the LED. The monkeys performed the task at a high level of accuracy during the recording sessions, independent of simultaneously presented test stimuli. On trials where the monkey licked for fruit juice, normally two and occasionally three licks were completed in the 1-s period available.

Recording techniques

Each monkey was sedated with a weight-dependent dose of ketamine i.m. and anaesthetized with barbiturate i.v. (Sagatal). Full sterile precautions were then employed to implant two stainless steel recording wells (16 mm internal diameter, ID) 10 mm anterior to the interaural plane and 12 mm to the left and right of midline. Plastic tubes (5 mm ID) were fixed horizontally with dental acrylic in front of and behind the wells. Metal rods could be passed through these tubes to restrain the monkey's head during recording sessions.

For each recording session, topical anaesthetic (lignocaine hydrochloride, Xylocaine 40 mg/ml) was applied to the dura and a David Kopf micro-positioner fixed to the recording well. A transdural guide tube was inserted 3–5 mm through the dura and a glass-coated tungsten microelectrode (Merrill and Ainsworth 1972) advanced with a hydraulic micro-drive to the temporal cortex. The target area for recording was area STPa in the anterior part of the upper bank of the STS (which includes areas TPO and PGa of Seltzer and Pandya 1978).

Localization of recording

Following the last recording session, a sedating dose of ketamine was administered, followed by a lethal dose of barbiturate anaesthetic. The monkey was then perfused transcardially with phosphate-buffered saline and 4% gluteraldehyde/paraformaldehyde fixative. The brain was removed and sunk in successively higher concentrations (10, 20 and 30%) of sucrose solution or 2% dimethylsulphoxide (DMSO) and 20% glycerol (Rosene et al. 1986).

Frontal and lateral X-radiographs were taken of the position of microelectrodes at the end of each recording session. Reconstruction of electrode position was achieved by reference to the positions of

micro-lesions (10 μA DC for 30 s) made at the end of some electrode tracks, which were subsequently identified using standard histological techniques. In three monkeys additional markers used in calibration of electrode position were provided by micro-injection of anatomical tracers (horseradish peroxidase and fluorescent dyes true blue and diamadino yellow) at the site of cell recording on three recording tracks. For these markers the position of injection, recorded in X-radiographs could be compared with the anatomical location of injection revealed through normal or fluorescence microscopy.

Test procedure

Each cell recorded was first subjected to exploratory testing involving the presentation of a variety of static and moving objects. Testing associated with other experiments involved presenting tactile, auditory stimuli and up to eight views of static and walking human bodies. Trials were initiated by the experimenter but thereafter under computer control and consisted of a 0.5-s warning tone, followed by the shutter opening for 1 s to reveal the stimulus. Any hand-held stimulus motion was started before the shutter opened and continued until after the shutter closed. Videodisc images of moving stimuli were under the control of the computer and were therefore exactly repeatable. Speed sensitivity was assessed with hand-held stimuli using three broad categories: fast ($>30°$/s), medium (10–30°/s) and slow ($<10°$/s). This ensured that directional tuning was assessed for each cell at an effective stimulus speed. The accuracy of live 3D presentation was assessed by analysis of video recordings of movements of a typical testing protocol. The analysis took the form of marking the object in each frame of the video sequence and storing the x–y co-ordinates using a Pluto Graphics system (IO Research). Position and velocity profiles could then be calculated for each of the directions tested. It was found that the variation of the mean speed of motion between directions was within $\pm 15\%$, and the overall range of speeds was within $\pm 30\%$. Directional accuracy of hand-held stimuli was better than $\pm 10°$.

A cell which exhibited consistent responses only to moving stimuli or gave preferential responses to stimulus motion was tested for possible selectivity for direction of movement. The cells were routinely tested for six different directions of movement along three orthogonal axes (towards, away, up, down, right, left). This testing included moving 3D stimuli in front of the monkey in the preferred direction(s) under strong diffuse room lighting (>800 W total). The stimuli included human faces and bodies and various hand-held laboratory objects of different shape, size (subtending 1 to >20°), colour and texture (fruit, tools, boxes, curtains, fur, bodies, etc.). Cells were also tested with moving 2D stimuli from a videodisc library, which included simple geometrical images (e.g. bars, spots, gratings) as well as complex images of moving bodies. These video stimuli moved in eight directions in a given plane and allowed precise repetition of stimulus trajectory, etc.

If the cell was observed to respond equally to all stimuli tested in the preferred direction(s) it was classified as a non-form, motion-sensitive cell (e.g. see Fig. 1). In some cases the size of the object was found to have an effect on the responses but, as no other selectivity for features could be established, these cells were also classified as non-form selective. Cells which were found selective for both motion and stimulus form will be reported elsewhere. Speed of stimulus motion was also regularly tested (5–100°/s) and when found to have an effect the preferred speed was used for all subsequent testing. The effect of the position of motion within the visual space was also examined and again if there was found to be an effect of the position of stimulus presentation the most effective position was used for subsequent testing.

Cells lacking form sensitivity but which showed a tendency to discriminate between moving and static objects were tested with five trials of four or eight directions of movement, presented in a computer-controlled and randomized order. Testing was performed in one mode using either real 3D, projected 2D slides or videodisc stimuli. Computer-controlled testing protocols enabled data to be subjected to ANOVA and regression analysis on-line.

Measurement of cell responses

Subjects were restrained in a primate chair for periods of 2–4 h. Various types of visual stimuli were presented while the monkeys performed the fixation task (see above). Neuronal firing rates were measured using standard techniques for a period of 250 ms beginning 100 ms after stimulus presentation. This short period was selected as during this period the monkey would have to attend (and therefore fixate) the LED to be able to obtain multiple rewards during the 1-s availability period. (A 500-ms sample period was occasionally used for cells with small or late responses.) These data were analysed on-line by a microcomputer (Cromemco System 3 or AT compatible PC; Hyundai, Del.). Horizontal and vertical eye movements were monitored using an infra-red corneal reflection system (ACS, modified to allow recording of the two signals from one eye) to determine whether any response differences reflected differential patterns of fixation. Differentiating the position information allowed assessment of whether speed of eye movements affected response magnitudes.

Data analysis

Assessment of response magnitude. Cell responses to four or eight directions, static controls and spontaneous activity (SA) were compared on-line using one-way ANOVA and post-hoc tests (protected least-significant difference, PLSD; Snedecor and Cochran 1980). For cells tested with eight directions, multiple linear regression analysis was used to estimate the best relationship between response and 2nd order cardioid function of direction. In effect this calculates the values of the coefficients β_{1-5} of the equation below which produce the highest correlation between response and the angle of motion.

$$R = \beta_1 + \beta_2 \cos\theta + \beta_3 \sin\theta + \beta_4 \cos 2\theta + \beta_5 \sin 2\theta \quad (1)$$

where R is the response, θ is the directional angle and β_{1-5} are coefficients.

This equation was chosen because it makes very few assumptions about the nature of direction tuning. It also provides a good estimate of tuning of cells with a single preferred direction and cells with two preferred directions approximately 180° apart (e.g. movement left and right). See Perrett et al. (1991) for a detailed discussion.

Where the regression analysis produced a significant ($P<0.05$) relation between predicted and observed values, the regression equation was used to define: (a) the optimal direction (θ_{max}), (b) the maximum response at this direction (R_{max}), (c) the sharpness of tuning (average angle of rotation required to reduce the response to half R_{max}) and (d) the angle and magnitude of any second peak in the direction tuning.

Assessment of response time course. The criteria for the onset of cell responses was set at the upper limit of the 95% confidence interval of the pre-stimulus period. The latency was assessed for the responses to the most effective direction(s) and taken as the first of three consecutive (5.0 or 5.2 ms) bins exceeding the onset criteria (Oram and Perrett 1992). For these same cells, the responses in each time bin were normalized so the spontaneous activity was set to 0 and

peak response set to 1.0. Averaging responses across cells gave the population response profile.

Once the latency estimate had been made, firing rates were calculated for each cell for the 1st, 2nd and 5th 100-ms periods after response onset. The firing rate during the final 100 ms of the data collection period was also calculated for each cell (800–900 ms after response onset). The peak firing rate was taken as the maximum value of a 3-bin running average of firing rate. The rise time was calculated as the time from response onset to the peak firing rate. The half fall time was calculated as the time from peak to the time when the 3-bin running average fell below (peak − SA)/2. The decay time was calculated as the time from peak to the time when the 3-bin running average fell below the threshold criteria used for the latency estimate. Finally, the duration was taken as the time from response onset to the first time when the 3-bin running average fell below threshold level. Note that for some cells this was before peak firing rate had been reached.

Results

Cell classification

Of the visually responsive cells, 553 were classified as lacking selectivity for stimulus form but having sensitivity for motion. It should be pointed out that few of these cells showed selectivity for speed or position in the visual space of the motion. Where such selectivity was noted, optimal conditions were used for further testing. Figure 1 shows an example of a cell which was selective for the speed of motion (top) but not the form of the stimulus (bottom). Shown above each of the peri-stimulus time histograms (PSTHs) is a schematic representation of the stimulus motion within the area revealed from the open shutter. The LED was situated in the centre of this area. The stimulus was moved by hand at speeds corresponding to 0, 7, 13 and 40°/s (±15%). As can be seen for all motions there was at least a slight response, and above 10°/s the cell produced a clear response. In contrast for static stimuli there was slight inhibition. The lower section shows the mean response (spikes per second) of three objects (a simple bar, grating and a body) moving at approximately 20°/s. As can be seen, the response magnitudes are all equivalent ($P > 0.2$) but substantially greater than the spontaneous activity or during the presentation of static stimuli ($P < 0.002$ each comparison).

Cells were screened to check that the response differences to different stimuli were not due to differences in eye position or movements. No relation was observed between responses and eye movements for any of the 43 cells where eye movements were recorded. Figure 2 gives an example of eye position recordings during an effective (moving) stimulus and ineffective (static) stimulus. Recordings show the monkey fixating the position of the coloured LED before stimulus onset (0 ms) and maintaining fixation for at least a further 200 ms. With the stimuli moving to the left, the cell responded at a latency of 110–130 ms regardless of the latency and pattern of subsequent eye movement. The pattern of eye movements elicited to static stimuli was similar, yet the neural response was abolished. As with all cells reported in this study, there was little if any response to static stimuli. The cell was also tested with movements to the right and towards the subject (not shown in Fig. 2). These directions of motion produced different patterns of eye movement after the data collection period but similar neuronal responses. Importantly the monkey was fixating during the sample period on which the analysis was based (100–350 ms post-stimulus onset) for all except one trial. This pattern of maintaining fixation during the sample period was observed for almost every trial where eye movements were recorded. On the occasional individual trials when the monkey broke fixation before 350 ms, we could find no clear evidence of a change in the response, either before, during or after the saccade. As the performance of the subjects at the LED colour discrimination task was consistently high with multiple licks, we have no reason to suspect that fixation patterns differed for the other tested cells.

As mentioned above, all the cells were routinely tested for six different directions of movement along three orthogonal axes. If a cell was found responding preferentially in only one of these directions it was classified as a *unidirectional* cell. Based on the routine screening testing, Table 1 presents the distribution of the preferred directions of unidirectional cells recorded from all five subjects. Of 553 (39%) non-form-selective, motion-sensitive cells, 216 were classified as unidirectional. *Bidirectional* cells were classified as cells that showed roughly equal responses to two directions with responses in between which were substantially weaker. Twenty-three of the 553 (4%) non-form-selective, motion-sensitive cells were classified as bidirectional. Finally, the remaining cells showed approximately equal responses to motion in many or all directions and were classified as pandirectional (314/553 or 57%). This class of cell may have included cells displaying the radial type of motion sensitivity described by Bruce et al. (1981).

After initial directionality screening, the directionality of 43 cells was tested with eight directions of motion in a given plane. Three cells were tested twice in the same plane to assess reliability of testing, 8 cells were tested in two different planes and 1 cell was tested twice in one plane and a third time in a second plane, giving a total of 56 regression analyses. Of this total of 56, 50 (89%) were found to give a significant relation between response and the 2nd order cardioid function of direction of movement. Of these 50 cells 19, 18 and 9 cells were studied in the horizontal, fronto-parallel and sagittal planes, respectively. (The 3 cells retested in the same plane, 8 cells tested in two planes and 1 cell which was both retested in the same plane and tested in a second plane all gave significant fits.)

The responses of 32 of the direction-selective cells followed a *unimodal* pattern (unidirectional cells), with one direction evoking the optimal response. An example of a unimodal or unidirectional cell is given in Fig. 3. For this cell, movement with a downward directional component elicited a strong response, whereas movement to either side of the subject or upwards produced responses no different from SA.

Five direction-selective cells were classified as bidirectional because their responses to two directions were significantly ($P < 0.05$) higher than intervening directions. Figure 4 shows responses of a bidirectional cell selective

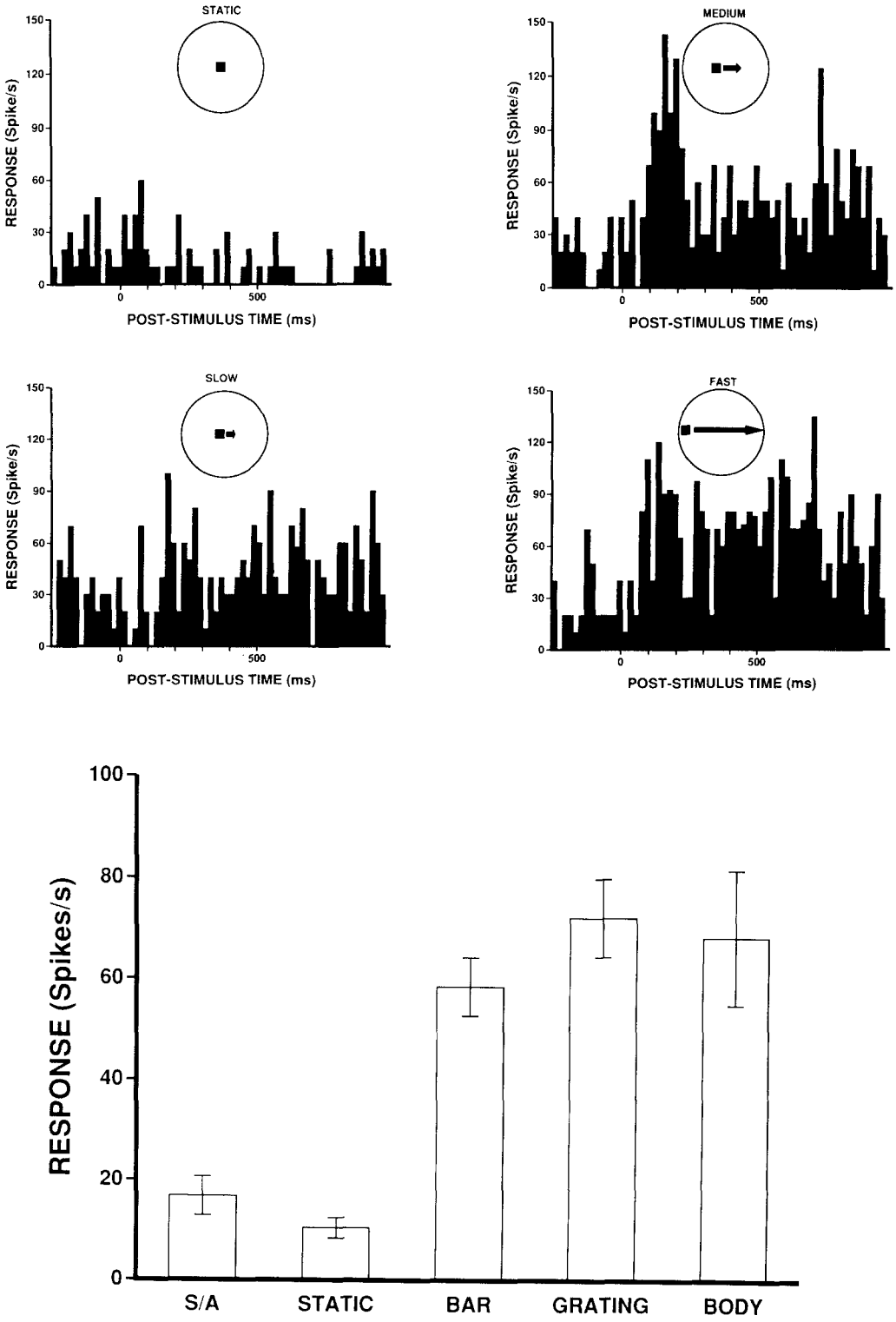

Fig. 1. *Top*: peri-stimulus time histograms (PSTHs) of responses of one cell (J119-2899) to static and moving stimuli (five trials per PSTH, bin width 20 ms) Stimulus: experimenter moving under strong, diffuse room lighting; movement speeds: static, slow, medium, fast, approximately 0, 7, 13, 40°/s or 0, 0.5, 1.0, 30 m/s at the viewing distance of 4.0 m. *Above each PSTH* is a schematic depiction of the motion. The *circle* depicts the visual field through the shutter (the fixation light-emitting diode, LED, is central); the *square* gives the approximate starting position of the (already moving) stimulus at zero time when the shutter opened; and the *arrow* indicates the direction of movement. The *tip of the arrow* indicates the approximate end position of the stimulus when the shutter closed. The response to any motion produced a response above static stimuli ($P < 0.01$ each comparison). There was also an effect of speed (fast and medium > slow, $P < 0.005$ each comparison). Overall effect of conditions: $F_{4,20} = 16.6$, $P < 0.0005$. *Bottom*: histogram of response magnitudes of the same cell to three different stimuli (*BAR*, subtending 2°; *GRATING*, subtending 5° and *BODY*, subtending 20°) moving at 20°/s, spontaneous activity (*S/A*) and static objects (static bar, grating and body). All three objects produced equivalent responses when moving ($P > 0.2$ each comparison) which were greater than spontaneous activity or the static presentation of the same objects ($P < 0.002$ each comparison). Overall effect of conditions: $F_{4,20} = 14.9$, $P < 0.0005$

for motion to the subject's left and right. For all bidirectional cells in this study the two preferred directions were approximately 180° apart, even though we could have found a cell with two preferred directions only 90° apart. The criteria for classification as bidirectional used here were fairly stringent and a further three cells, classified as unidirectional, showed a degree of bidirectional direction tuning, in that their response to a second or minor direction was greater than half the response to the optimal direction (with other intervening directions evoking less than half the maximal responses). These five bidirectional cell were unlikely to be the radial type reported by Bruce

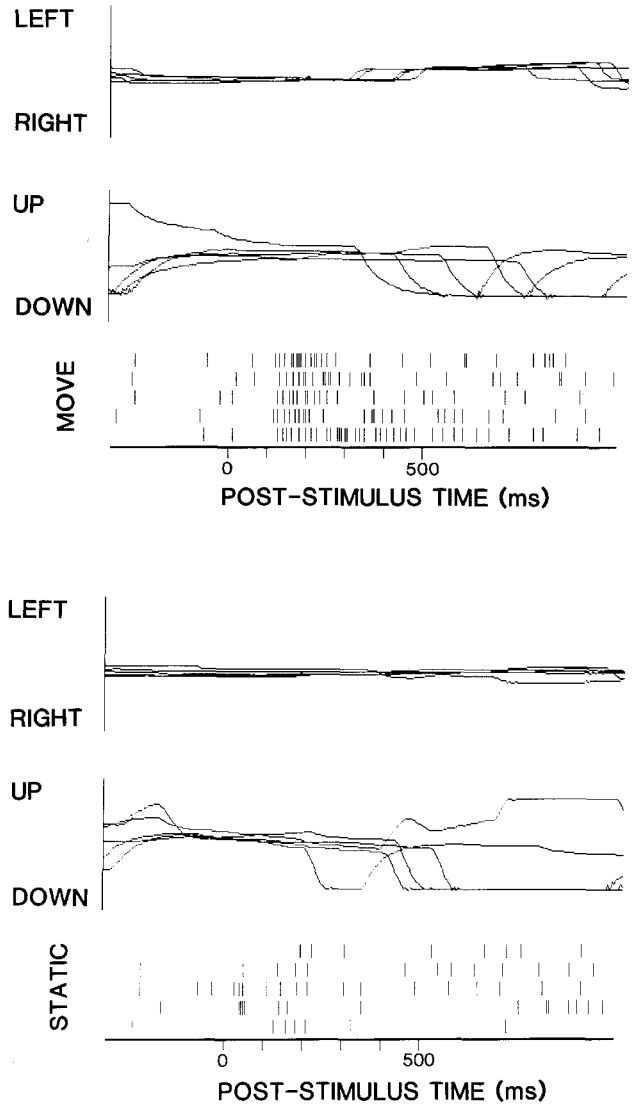

Fig. 2. Eye movements during effective and non-effective stimulus presentation. *Top*: eye position (*upper traces*) and responses (*rasters*) of one cell (J33-2585) to five presentations of an effective stimulus. For this cell, movement to the subject's left in the lower half of the visual field elicited a good response (stimulus: hand-moved red square under bright, diffuse room lighting subtending 3°, moving 10°/s). At the onset of trials the subject fixated a centrally positioned LED to determine its colour. Later in the trials the subject made saccades down to the stimulus. *Bottom*: eye position (*upper traces*) and cell responses (*rasters*) to five trials of the same object presented stationary in the lower half of the visual field. The eye movements are comparable for the two experiments, yet only when the stimulus was moving was there a cell response

et al. (1981), as the radial motion that occurred when the stimulus was moved in the directions intervening between optimal directions produced only weak responses. Bi-directional cells responding to movements left and right did not respond to movement up or down, when in all cases there was equivalent radial motion.

As already noted, the majority of non-form-selective, motion-sensitive cells recorded were responsive to movement of an object in any direction. Some of these cells (e.g.

Table 1. Distribution of anterior superior temporal polysensory region cells tuned to different directions. Classification of preferred directions of cells from qualitative assessments in five subjects

	Preferred direction						
Subject	U	D	R	L	T	A	Total
B	1	3	10	10	4	8	36
F	26	13	4	0	39	13	95
D	6	7	9	6	15	5	48
H	1	1	0	0	2	0	4
J	7	5	1	7	9	4	33
Total	41	29	24	23	69	30	216

U, up; D, down; L, left; R, right; T, towards; A, away

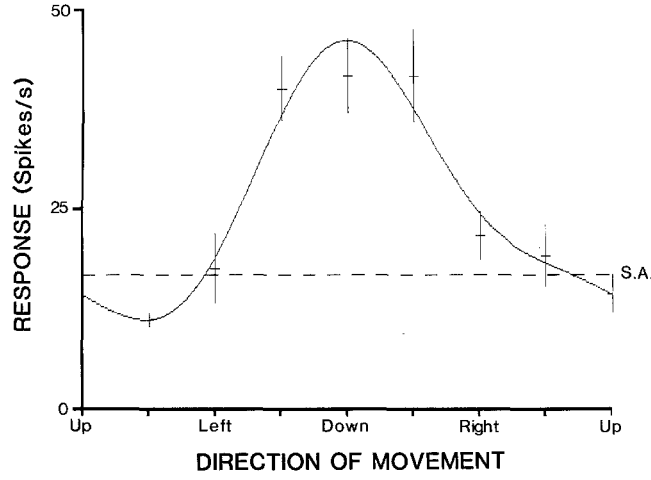

Fig. 3. Responses of a unidirectional motion-sensitive cell. The mean responses (±1SE) are illustrated for one cell (J68-2925) to eight directions in the fronto-parallel plane (stimulus: hand-held light bar in blackout conditions swept across visual field at approximately 50°/s). Direction is expressed as the angle of rotation from upwards (0°, *up*; 90°, *left*; 180°, *down*; 270°, *right*). The curve is the best fit cardioid function, relating response to direction ($R^2 = 0.675$; $F_{4,35} = 18.2$, $P < 0.0005$). The *dashed line* denotes spontaneous activity (*S.A.*). Responses to movements downwards (down and left, down and right, and straight down) were significantly greater than movements in other directions and spontaneous activity ($P < 0.005$ each comparison), but were themselves equivalent ($P > 0.75$). Overall effect of conditions: $F_{8,36} = 10.6$, $P < 0.0005$

Fig. 5) also exhibited weak directional selectivity. For the cell illustrated in Fig. 5, movement of an object in any direction in the fronto-parallel plane caused the cell to respond, whereas the same object held stationary elicited no response. The responses to all movements were not equivalent; movement to the subject's left and downwards was significantly greater than movement upwards.

Whilst the majority of the cells were tested only once, four cells were subjected to two identical testing paradigms to assess the reliability of the responses and directional tuning assessments. For each of these cells the optimal direction and tuning to non-optimal direction was highly similar across tests. Figure 6 gives an example

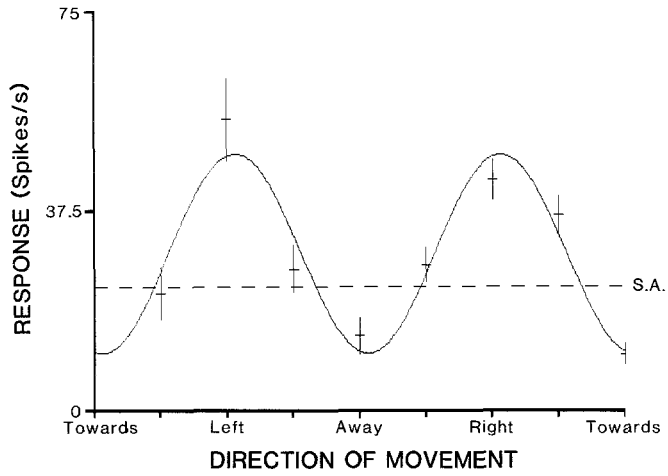

Fig. 4. The responses of a bidirectional, motion-sensitive cell. Responses (mean ± 1SE) of cell D58-3078 to eight directions in the horizontal plane (stimulus: experimenter walking 3 m/s under strong, diffuse room lighting, at a mean distance 2 m). Direction is expressed as degrees of rotation away from movement towards the subject (0°, *towards*; 90°, *left*; 180°, *away*; 270°, *right*). The curve is the best fit cardioid function, relating response to direction ($R^2 = 0.604$; $F_{4,43} = 16.5$, $P < 0.0005$). The *dashed line* represents spontaneous activity (*S.A.*). The cell responded to movements left or right more strongly than to movements towards or away from the subject ($P < 0.0005$ each comparison). The responses to movements left and right were statistically indistinguishable ($P = 0.09$). Overall effect of conditions: $F_{8,45} = 9.1$, $P < 0.0005$

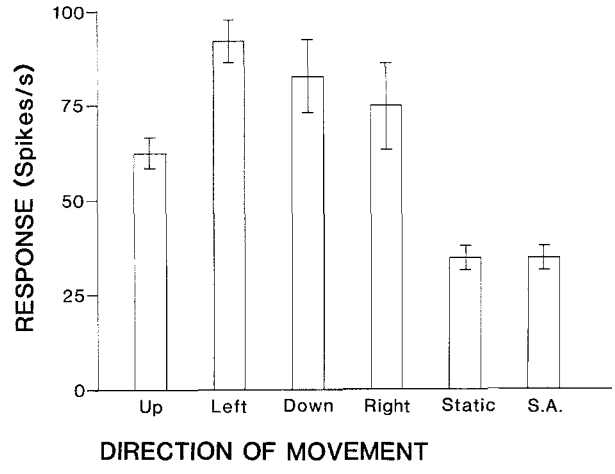

Fig. 5. The responses of a cell responsive to multiple directions of motion. Responses of cell J131-2611 to four directions in the fronto-parallel plane (stimulus: hand-held green box subtending 30 × 50°, moving at 40°/s). Movement in any of the tested directions gave a response that was greater than spontaneous activity (*S.A.*) and static views of the same object ($P < 0.01$ each comparison). The cell responses, however, showed slight selectivity for direction of movement, with a significantly greater response to movement to the left and down than movement up ($P < 0.05$). Overall effect of conditions: $F_{5,24} = 12.0$, $P < 0.0005$

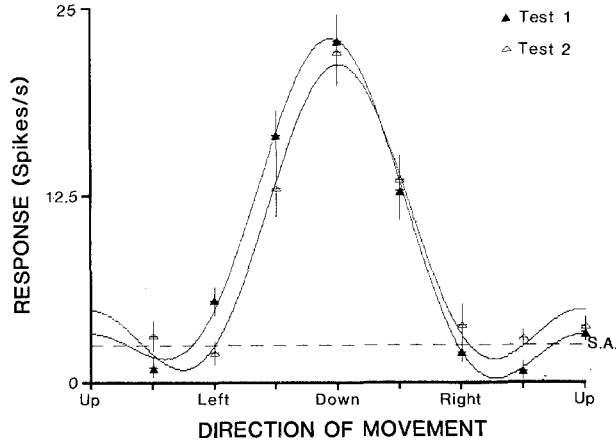

Fig. 6. Test-retest reliability from repeated direction analysis. Responses and regression curve of one cell (F34-2648) to two tests of eight directions in the fronto-parallel plane (see text for stimulus details). The cell showed strong responses to movement downwards in both tests. Estimated maximal responses are at 174° and 180°. Overall effects for test 1: ANOVA $F_{8,54} = 54.1$, $P < 0.0005$; regression, $R^2 = 0.882$, $F_{4,45} = 84.4$, $P < 0.0005$. Overall effects for test 2: ANOVA, $F_{8,57} = 25.7$, $P < 0.0005$; regression, $R^2 = 0.751$, $F_{4,48} = 36.2$, $P < 0.0005$

of the similarity of results for one cell tested twice for directionality (with a delay of 5 min filled with other testing). In both tests a variety of different objects were moved by the experimenter under strong, diffuse room lighting, including hands, gratings and other objects. If the directional selectivity were due to co-incidental variations in speed, position or form it would be expected that the cell responses would show markedly different tuning curves. As can be seen, the similarity was remarkably high. This shows that the directionality estimates obtained here were accurate using hand-held stimuli and quantitative analysis of cell response magnitudes. Indeed, other investigators have noted that even hand-held testing with subjective assessment of responses can yield good estimates of directionality compared with computer-controlled stimulus presentation, data collection and accurate fixation (Thier and Erickson 1992).

It is of course possible that speed sensitivity could have influenced directional tuning estimates. However, we made sure that directional testing was done at speeds within each cell's optimal speed range. Our testing revealed that most STPa cells were not selective for speed over the range tested. This was not due to the range of tested speeds being too small, since the method was sensitive enough to pick up speed sensitivity amongst some STPa cells (see Fig. 1). The consistency of stimulus speed during testing was thus sufficient to pick up speed sensitivity amongst STPa cells and more importantly cannot account for the directional tuning estimates (see Fig. 6).

Tuning across different planes

For nine cells, directionality was studied in two orthogonal planes. Each of these cells was found to show highly

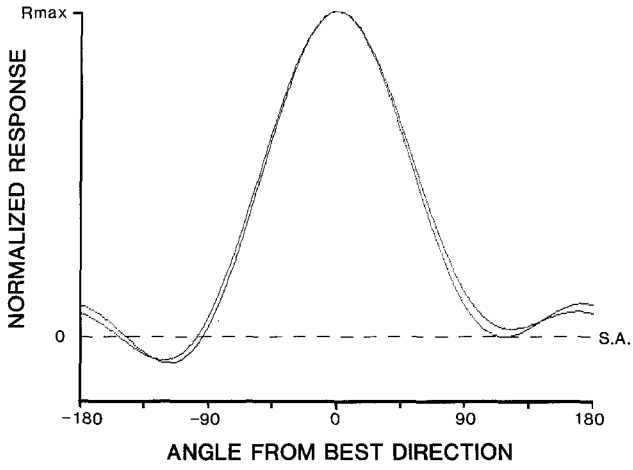

Fig. 7. Similarity of tuning across planes. Standardized regression curves of one cell (F98-2720) sensitive to movement downwards to testing in two planes (sagittal and fronto-parallel; stimulus: experimenter's hand subtending approximately 5°, moving at 30°/s). The curves have been aligned to the peak response. The similarity between the two curves shows that the tuning for direction is almost identical in both planes. Regression: sagittal plane, $R^2=0.648$, $F_{4,35}=16.1$, $P<0.0005$; fronto-parallel plane, $R^2=0.768$, $F_{4,35}=28.9$, $P<0.0005$

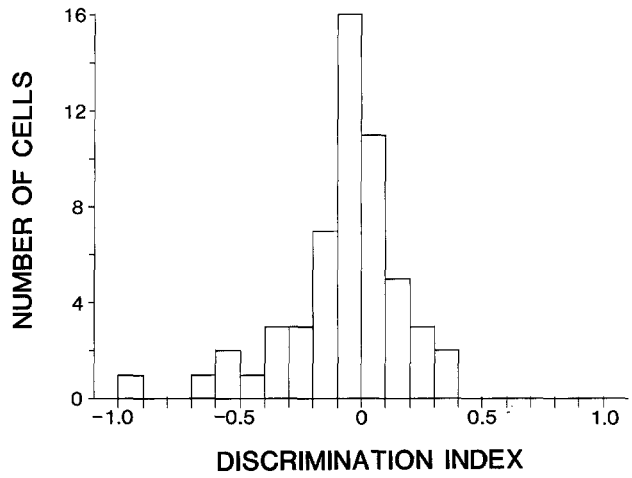

Fig. 8. Index of discrimination: comparing best and worst directions. The responses to the least effective direction (R_{min}) are expressed as a fraction $[(R_{min}-SA)/(R_{max}-SA)]$ of the responses to the most effective direction (R_{max}). SA, spontaneous activity

similar directional tuning functions in the two planes. Figure 7 shows the result from one representative cell. One curve was derived from testing in the sagittal plane, where the estimated optimal direction was down and slightly towards the subject (14° off vertical). The second curve represents tuning in the fronto-parallel plane where the optimal direction was down and slightly to the left (9° off vertical). To facilitate comparison across planes, the tuning curves in the figure have been shifted so that the peaks are co-incident and the response magnitudes normalized (R_{max} was 17.2 and 15.2 spikes/s in the two planes).

Discrimination between directions

In a study of the tuning of cell responses to different views of the static head and body, we used a discrimination index to quantify discrimination between different perspective views (Perrett et al. 1991). The index was defined as $(R_{min}-SA)/(R_{max}-SA)$ where R_{min} and R_{max} were the minimum and maximum responses, respectively, to different views.

To facilitate comparison between tuning for perspective view and direction in the same brain area, we computed the same discrimination index for the cells studied here. As ANOVA revealed no significant differences between planes for the index ($P=0.28$), the data for cell testing in different planes were combined. Figure 8 shows the frequency histogram of the discrimination index for 55 cells. Only the first estimate is given for cells which were tested more than once. For all cells the response to the worst direction of motion was less than one-half of the response to the optimal direction. Negative index values indicate responses to non-preferred directions that were less than the spontaneous activity.

For 55 direction-selective cells the mean value of the discrimination index was −0.07 (±0.032 SE). The discrimination of direction amongst this population of motion-sensitive cells was compared to discrimination of perspective view amongst cells selective for the static form of the head and body. The discrimination index measured for 110 view-sensitive cells was found to have a mean of 0.04 (±0.031; Perrett et al. 1991). The discrimination of direction was significantly greater than the discrimination of perspective view ($t_{144}=2.378$, $P<0.02$, using Satterthwaite's approximation for heterogeneity).

A number of other indices have been used to estimate the discrimination between directions. A commonly used direction index is $I_d=1-(R_{opp}-SA)/(R_{max}-SA)$, where R_{opp} is the response magnitude to motion in the opposite, or null, direction to that which gives the maximal response magnitude (R_{max}). For comparison with directional tuning in other studies, this index was also calculated (see Fig. 9). Not surprisingly, bidirectional cells showed less discrimination between preferred and opposite directions than cells displaying unidirectional responses. Consequently bidirectional (Fig. 9, top) and unidirectional (Fig. 9, bottom) cells have been plotted separately. The mean value for the 44 unidirectional cells tested with stimulus motion in the null direction was 1.01 (±0.037).

Width of tuning of direction-selective cells

Width of tuning was calculated as the mean angle required to reduce firing rate to half of the difference between response to the most and least effective directions $[(R_{max}-R_{min})/2$; or half-width at half-height measure]. As no significant differences were found for cells sensitive to motion in different planes ($P=0.26$), the estimates from all three planes were combined.

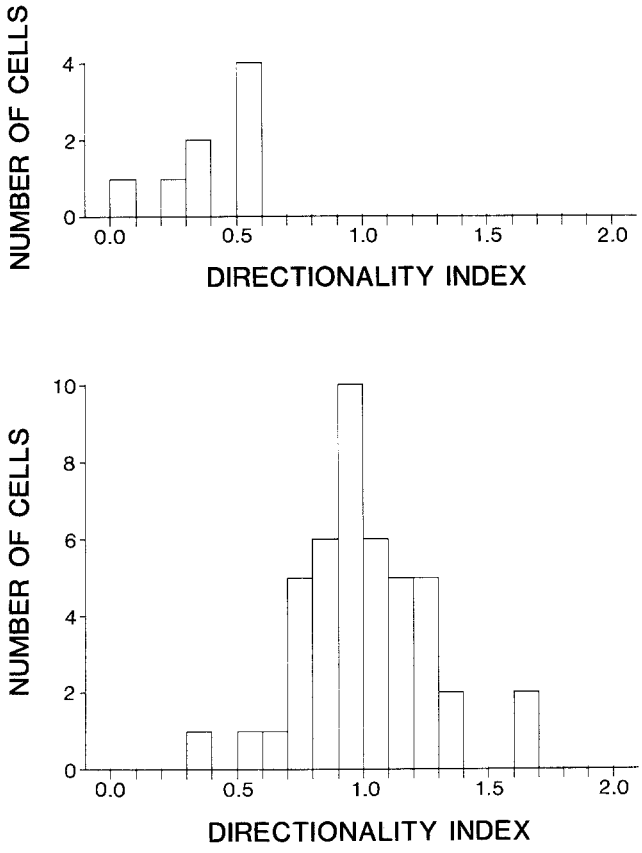

Fig. 9. Index of directionality: comparing best and opposite directions. Responses to direction 180° from the optimal direction (R_{opp}) are expressed as a fraction of responses to the optimal direction (R_{max})[$(R_{max}-R_{opp})/(R_{max}-SA)$ or $1-(R_{opp}-SA)/(R_{max}-SA)$], where SA is spontaneous activity. A directionality index of 0 indicates no difference in response magnitude to the two directions, a value of 1 indicates that there was no response above SA to the null or opposite direction, and values greater than 1 indicate suppression of activity below SA to motion in the opposite direction. *Top*, cells classified as bidirectional; *bottom*, cells classified as unidirectional

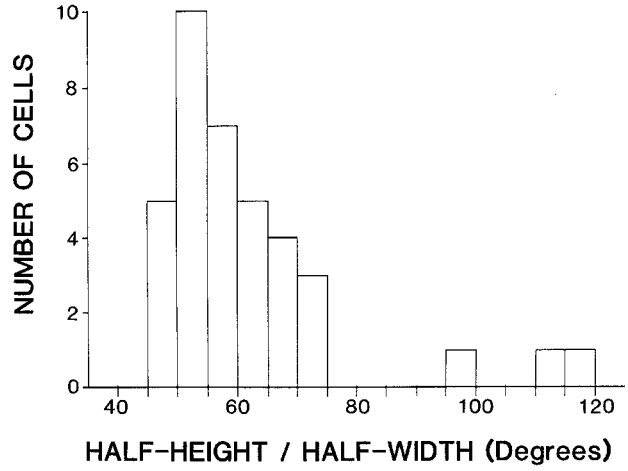

Fig. 10. Width of directional tuning. The mean angle of rotation required to reduce response by half of the difference between response to the most and least effective direction [$(R_{max}-R_{min})/2$] is plotted for 37 direction-selective cells

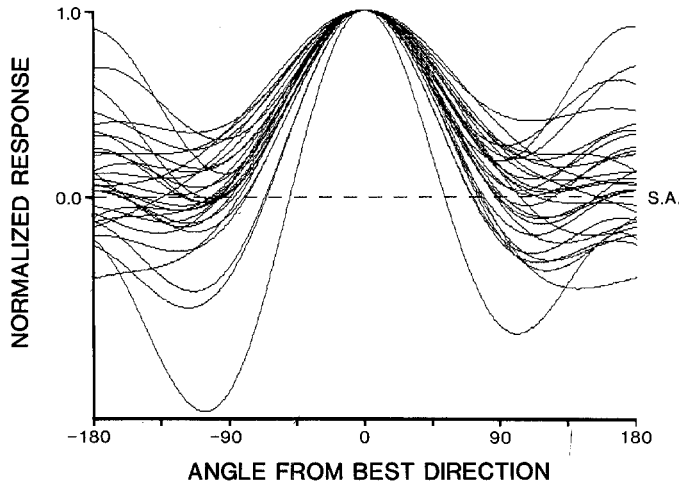

Fig. 11. Tuning curves of direction-selective cells displaying unidirectional narrow tuning. The tuning curves (estimated from best fit cardioid function relating response to angle of direction) for 29 unidirectional direction-selective cells. Each tuning curve is normalized so that maximum response = 1.0 and spontaneous activity (*S.A.*) = 0. Direction is expressed as an angle of rotation from optimal direction for each cell (q_{max})

Figure 10 illustrates the width of tuning estimate for all direction-selective cells tested with eight directions and with significant cardioid regressions (one value per cell). Half-width at half-height ranged from 45 to 120°. The distribution of directional tuning in Fig. 10 illustrates two important points: first, the majority of cells have tuning less than 75° (half-height, half-width); and second, the distribution does not appear continuous. Using 90° half-width tuning as a cut-off point, 34 cells were defined here as having relatively "narrow" tuning for direction and 3 cells as having "broad" tuning.

The distribution of width of tuning is skew positive, with no cells having half-height, half-width less than 45°. This is in part an artefact of regression analysis, since the cardioid equation used cannot follow changes in response from maximum to minimum in less than 90°. From visual examination of the tuning curves and cell responses, for only five cells the estimated width of tuning was artificially broad (by an estimated 5–15°). Since this error affected a minority of cells only, it does not affect estimates of the width of tuning of the cell population unduly. The distribution of values were compared with those obtained for cells sensitive to different views of head and body using the non-parametric Mann-Whitney *U*-test and found to be similar (direction median half-width = 55.5°, view median = 57.7°, $U_{54,34} = 1374.5$, $P = 0.24$).

Mean shape of directional tuning

To make a visual comparison across different tuning curves, the raw data for each cell were rescaled (so that

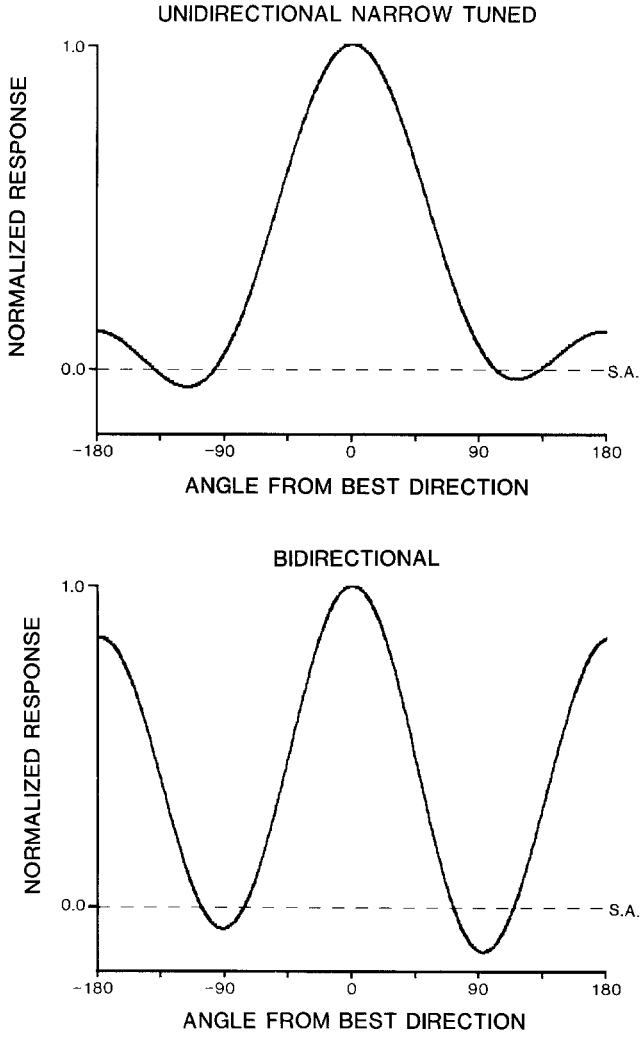

Fig. 12. Mean tuning curves for different classes of cell. *Top*, narrow band direction-selective cells ($n=29$); *bottom*, bidirectional direction-selective cells ($n=5$)

$R_{max}=1.0$ and SA $=0.0$) and directions expressed as angles of rotation from optimal (Soodak and Simpson 1988). Figure 11 illustrates the range of the individual tuning curves for a sample of 29 unidirectional cells with narrow tuning.

To obtain the mean tuning curve for different cells, the coefficients of the regression analysis (Eq. 1, above) of normalized data were averaged. Figure 12 displays the mean tuning curves for uni- and bidirectional cells. For both types of cell the mean tuning curve exhibits a dip in response to directions some 90° away from optimal view. This dip falls below spontaneous activity and may well arise from inhibition from cells tuned to these orthogonal directions.

Distribution of optimal directions

The optimal response directions were analysed for cells which (a) were tested with eight directions, (b) displayed a significant ($P<0.05$) relation between response and a cardioid function of angle of motion (Eq. 1), and (c) for which χ^2 comparisons between predicted and observed response indicated a good fit of the cardioid function. Thus, data were considered for only those cells for which regression analyses produced appropriate optimal response angles.

Figure 13 shows the distribution of the optimal directions from the 46 appropriate analyses. For each cell the optimal direction is represented by a single line. For cells tested twice in the same plane the first estimate of optimal direction is plotted. Where testing was performed in two planes, both estimates have been entered in the appropriate figure.

As shown in the upper part of Fig. 13, the optimal directions of cells appear clustered around cartesian axes, (up/down, left/right and towards/away). To evaluate this clustering the estimated optimal direction is expressed as the angular rotation from the nearest cartesian axis (Fig. 13, bottom). Statistical analysis confirms that significantly more cells have optimal directions that are "on axis" (within 22.5° to a cartesian axis) than would be expected by chance (binomial test $P<0.0005$).

Temporal characteristics of cell responses

We have recently investigated the temporal characteristics of the responses of cells within STPa to static form (Oram and Perrett 1992). Whilst there were insufficient data available to perform a complete analysis of the same characteristics of cells selective for the direction of motion in the same brain area, analysis allows a partial comparison of the two populations.

Latency estimates were obtained for 15 cells where the data had been collected to 5.0 or 5.2 ms accuracy. The mean was 90.9 ms (see Table 2). The static form cells, under similar presentation conditions, had a mean latency of 119 ms (Oram and Perrett 1992). These are statistically different ($t_{57}=3.34$, $P=0.001$), with direction-selective cells responding at earlier latencies than form-selective cells. As response magnitudes were almost identical (67.3 spikes/s and 66.9 spikes/s during the first 100 ms of the response), this difference in latency was not due to stronger responses in the cells of the present study.

As with cell responses to static-form information, the responses of the cells in the present study to moving objects showed a fast rising phase to a peak, then a more gradual decay down to an apparently steady firing rate. The steady firing rate (estimated from the final 100 ms of the data collection period) was found to be above the spontaneous activity level for all cells.

Table 2 summarizes the parameters used to define the time course of responses for 15 motion-sensitive cells lacking form selectivity. The mean values for STPa cells selective for static form (different views of the head) are given for comparison. The table indicates the overall similarity of the temporal profile of the responses of the two cell types.

Figure 14 shows the population mean of the responses of nine cells where spike activity was collected in 5.2-ms

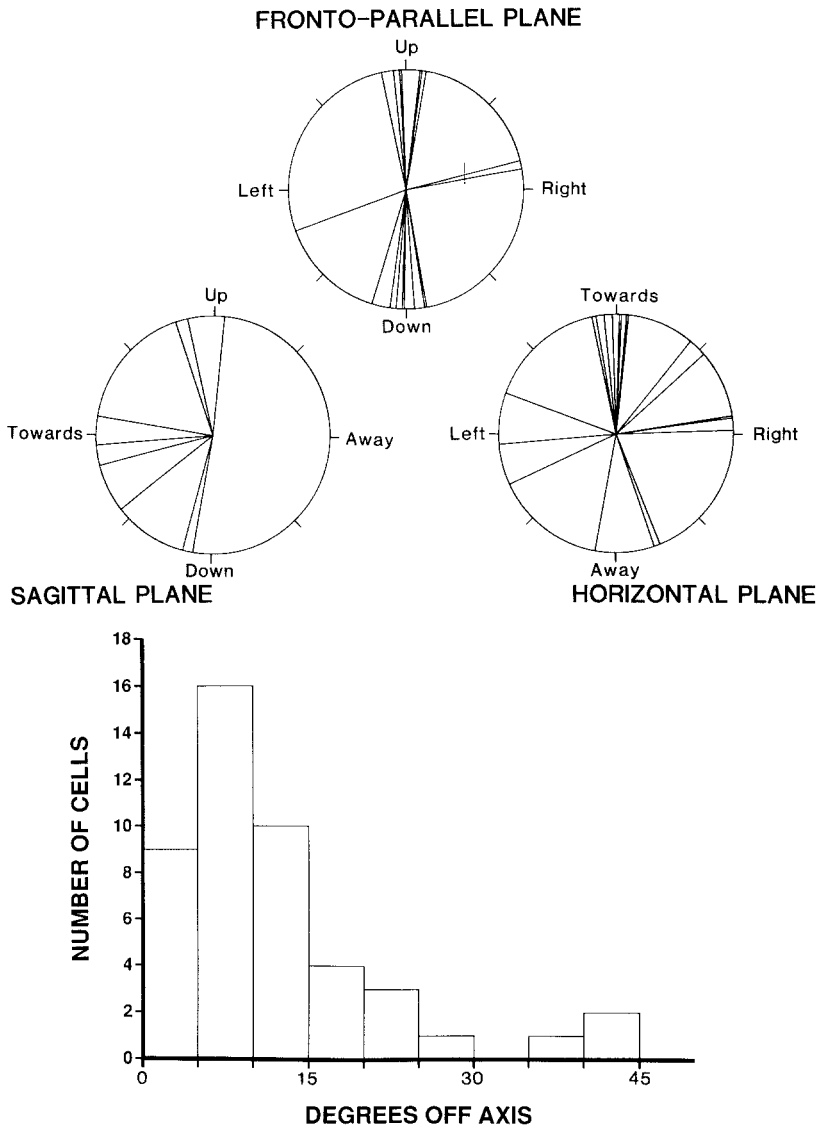

Fig. 13. The distribution of preferred directions across the population of motion-sensitive, anterosuperior temporal polysensory region (STPa) cells. *Top*, polar plots, with each *line* representing the direction estimated from regression analysis to evoke maximal response for one cell, plotted separately for each plane. *Bottom*, histogram of the number of cells for a given rotation away from a cartesian axis independent of the plane of testing. Significantly more cells exhibit a preference for directions within 22.5° of cardinal directions (up, down, left, right, towards and away) than for intermediate directions (44 of 46, $P < 0.0005$)

Table 2. Time course of responses of motion-sensitive STPa cells lacking form selectivity. Measurements from STPa cells involved in static-form processing and selective for the perspective view of the head for comparison (from Oram and Perrett 1992)

	Direction		Mean static form
	Mean	Range	
Timing (ms)			
Latency	90.9	35.0 – 126.4	119.1
Rise time	69.4	10.4 – 175.0	58.2
Half fall time	59.0	20.0 – 124.8	40.0
Decay time	134.4	20.8 – 754.0	93.4
Duration	168.6	15.6 – 764.4	112.5
Firing rates (spikes/s)			
SA	11.4	0.8 – 40.8	8.6
Peak	108.3	62.2 – 175.9	115.1
First 100 ms	67.3	34.7 – 89.2	66.9
Second 100 ms	53.1	20.7 – 84.0	48.1
Fifth 100 ms	31.9	3.0 – 56.3	28.5
End 100 ms	30.6	5.4 – 59.2	24.7

time bins. The population latency of this sub-sample was 58.8 ms. This is shorter than the population latency for cells sensitive to static form (95 ms; Oram and Perrett 1992), confirming the statistical assessment of the individual latency estimates. Other temporal measures of the population response of direction-sensitive cells were similar to those obtained for the view-selective population response (e.g. rise times of 69.4 ms and 62.4 ms for direction-selective and view-selective population responses, respectively).

Location of cells

Histological reconstruction of the positions of cells recorded in monkeys F, B, D (e.g. Fig. 15) indicated that the majority of non-form, motion-sensitive cells were located in the cortex of the upper bank of STS (areas TPO and PGa of Seltzer and Pandya 1978). The proportions of cells

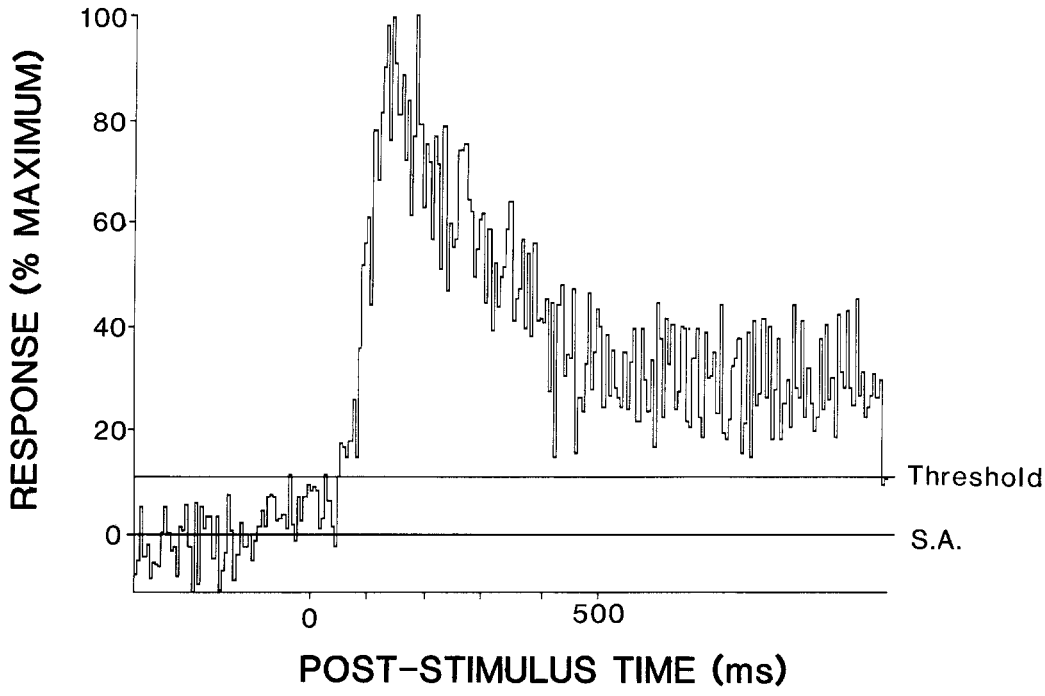

Fig. 14. Population response to objects moving in the most effective direction. The combined responses of nine cells are plotted as a percentage of the peak response. The population response latency was estimated at 58.8 ms. *S.A.*, spontaneous activity

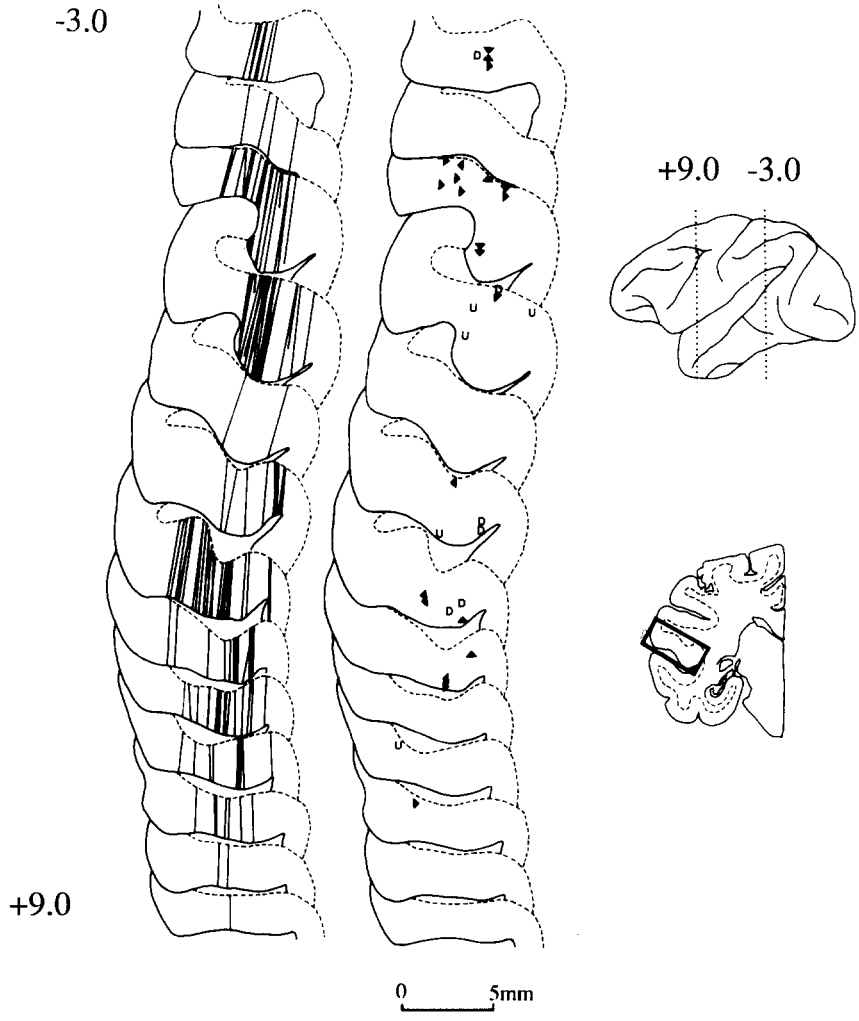

Fig. 15. Histological reconstruction of position of cells responsive to motion but lacking form sensitivity. *Upper right*, lateral view of the left hemisphere showing the antero-posterior extent of sampling. *Lower right*, coronal section at 3.0 mm posterior to the mid-geniculate level; the *box* shows the position of the superior temporal sulcus (STS). *Left*, serial sections (every 1.0 mm) of the upper bank of the STS from 3.0 mm posterior to 9.0 mm anterior to the mid-geniculate level from the right hemisphere of one monkey (D). *Vertical lines* indicate the position of all recording tracks in this hemisphere. *Centre*, position of movement-sensitive cells; the preferred direction of motion for each identified cell is indicated by the *symbols*: *upward and downward arrowheads*, motion towards and away; *leftward and rightward arrowheads*, motion left and right; *U* and *D*, motion up and down

responsive to movement but lacking form sensitivity out of the total number recorded within STPa varied from subject to subject – B, 10.6% (67/632); D, 11.1% (155/1397); F, 14.8% (225/1553). (N.B. these figures include cells responsive to motion that were not investigated in detail for direction selectivity.) The motion-sensitive cells constituted approximately 25% of all visual cells in the STPa. Measurements of the position of recording electrodes (from X-rays) indicated that cells sensitive to motion but not form in monkeys J and H were recorded in the same region.

Figure 15 illustrates reconstruction of the position of directionally selective cells that were recorded in the upper bank of the STS in the right hemisphere of one monkey (D). Neighbouring cells on the same track showed a tendency to display similar direction preferences, though within a given 1.0-mm patch of cortex multiple directions appear to be encoded. Thus, with the resolution of reconstruction present (± 1.0 mm), there was no obvious anatomical organization of direction coding within the cortex of this monkey at a macroscopic level.

Discussion

Motion coding in temporal cortex

Previous work with cells responsive to visual stimuli in the STPa focused mainly on coding of information about the form of the stimulus. Indeed, the cortex of the temporal lobe is often considered as containing high-level representations of form. The current study evaluated coding of direction information by cells with no apparent sensitivity to the form of the stimulus. Few studies have investigated motion processing within the temporal cortex, yet there is evidence that motion can be used as a source of information to define form within this area (Perrett et al. 1990a, b; Britten et al. 1992; Oram and Perrett, in preparation). The motion-sensitive cells studied here were found in the same locus (within the upper bank of the STP) as cells selective for the static form of the head and body (Perrett et al. 1991). This co-localization emphasises the anatomical convergence of streams of information processing for form and motion.

Eye movements and estimates of directional tuning

It has been reported that STP cells show differential responses depending on eye movements (Colby and Miller 1986; see Colby 1991 for an example of such a cell). As we did not test expressly for the effects of eye movements on cell responses and we did not monitor eye position for all the cells tested, we cannot exclude the possibility that some of the responses we observed were influenced by eye movements. However, the effects of eye movements are likely to be small, as only 20% (18/90) of cells in STP were found to be related to eye movements. Of these 18 cells, 9 were visual (responding to the onset of the target stimulus) and 4 were visuomotor (firing from target stimulus onset until the saccade was made), while only 5 cells were related exclusively to the saccade (C.L. Colby, personal communication). Thus, we would expect only 6% of cells in the present study (or 3 of the cells used to assess directionality) to be related solely to saccadic movements and not the stimulus. Further, it is not clear whether these cells were recorded from the STPp or STPa. Given the large proportion of eye movement-related responses in MST and that the input to STPa from MST is via STPp, we would expect there to be more eye movement-related responses in STPp than STPa. For several other reasons given below we believe that our estimates of the preferred directions for the cell responses do not reflect eye movements.

The experiments described in this study used a task in which the subject was not required to maintain steady fixation throughout the whole trial period. The monkey performed the LED colour discrimination task with a high level of accuracy, and more importantly obtained multiple rewards by repeatedly licking. The short period during which reward was available meant that the monkey had to be attending the LED from the trial onset in order to lick more than once. Examination of eye position records showed that this was indeed the case, and that fixation was only broken some 400 ms after stimulus onset. The analysis of the response magnitudes was based on spike counts between 100 and 350 ms (post-stimulus) and therefore during the period of maintained fixation. More than 90% of the cells responding to pursuit eye movements in MT and MST had the eye movement-related response starting *after* the onset of the pursuit eye movements (Newsome et al. 1988). This would suggest eye motion "contamination" of response is unlikely in our analysis period. As a consequence, directional preference of cell responses is taken as reflecting sensitivity to the direction of motion on the retina.

For the few trials where fixation was broken before 350 ms post-stimulus, we could observe no clear change in either the response latency or response magnitude (see Fig. 2). Furthermore, as can also be seen in Fig. 2, even when eye movements were comparable between two stimuli, only one (the preferred) stimulus would give a clear response.

Studies of MST neurons that responded with directional selectivity during pursuit eye movements (where there was no stimulus motion on the retina) also show clear directional responses to retinal motion when the animal was fixating throughout the trial period (stimulus motion but no eye motion). More important, the preferred directions obtained under pursuit and fixation tasks were coincident (Komatsu and Wurtz 1988a; Erickson and Thier 1991; Thier and Erickson 1992). Even if the directional selectivity we obtained in STPa reflected cell tuning for direction of pursuit eye movements, the findings in MST suggest that the directional selectivity would be the same under stimulus motion with maintained fixation.

It is also relevant to note that many cells recorded in MST do not respond to self-induced retinal motion produced by eye movements (Erickson and Thier 1991). Cells in STP receive a direct input from MST, so they may reflect other response characteristics of MST cells. Indeed

it has been argued that there is a trend for cell responses to become less sensitive to self-induced retinal motion higher in the motion-processing hierarchy (Erickson and Thier 1991). We have shown that STPa cells responsive to motion (and similar to those reported here) are not responsive to equivalent self-induced motion (Hietanen and Perrett 1993). If this is the case then the effects of eye movements on measurements of preferred directions in STP are likely to be small.

Coding of direction in STPa

In keeping with the relatively low rate of spontaneous activity, *optimal* directions appeared to be coded by excitation rather than inhibition. That is, no cells were found coding the presence of one direction by a selective reduction of response rate below spontaneous activity with no change in activity for other directions of motion. There was, however, some evidence for a role of inhibition in the coding of non-preferred directions.

It is interesting to note the "Mexican hat" shape of direction tuning amongst the majority of directionally selective cells. The dip in response, for directions approximately 90° to the cells' preferred direction, may represent inhibitory interactions between cells tuned to different directions. Indeed inhibition relative to spontaneous activity was observed for many cells to *non-optimal* directions and also static stimuli (e.g. Fig. 1). Inhibition has been reported to motion in the null direction for some 90% of MT cells. Direction selectivity in MT would seem to be established by both inhibition in the null direction (as suggested by Barlow and Levick, 1965) and facilitation of the response in the preferred direction (Mikami et al. 1986a). The degree of inhibition for non-optimal directions exhibited by STP cells was not as great as that reported for cells in other visual systems (e.g. the rabbit accessory optic system; Soodak and Simpson 1988).

The amount of inhibition found in the present study of STPa direction coding was substantially greater than that found in STPa coding of the perspective view of static objects. In the present study the mean tuning curve for direction drops below spontaneous activity for non-optimal directions (Fig. 2, top), whereas the mean view tuning curve for cells responsive to the head remains well above spontaneous activity throughout the full 360° of head rotation (see Fig. 9 of Perrett et al. 1991). In a detailed examination of the responses of cells selective to static head views, very little evidence was found of inhibition to non-optimal views (Oram and Perrett 1992). The increased suppression and/or inhibition seen in motion-selective STP cells compared with form-sensitive STP cells may therefore reflect a qualitatively different process for establishing tuning.

The range of the direction tuning defined by half-height, half-width measure in the present study was 45–120°. This range was similar to the range of tuning exhibited by cells selective for head view. The difference in the amount of inhibition seen between form- and motion-sensitive cell responses does not therefore lead to tighter tuning of motion-sensitive cell responses.

Directional tuning and cartesian axes

Previous work has emphasized the prevalence of viewpoint-sensitive coding for static-form information in the STP (Bruce et al. 1981; Perrett et al. 1982, 1985a, 1991, 1992; Desimone et al. 1984; Kendrick and Baldwin 1987; Hasselmo et al. 1989). The current study also indicates that motion processing in temporal cortex is heavily influenced by the observer's viewpoint. Of course, in most brain areas direction of movement is specified relative to the viewer. Some processing of motion in the temporal cortex, however, is conducted in an object-centred framework where the direction of object movement can be understood best when specified relative to parts of the object being viewed. For example, head moving to chest regardless of orientation of the body relative to the viewer (head-nodding; Hasselmo et al. 1989) or arm moving to chest (Perrett et al. 1990), a person walking forwards (following their nose) as opposed to backwards (Perrett et al. 1985b; Oram et al., in preparation). In the present study we found that half of the motion-sensitive cells in STPa were selective for particular directions of motion relative to the observer. This viewpoint sensitivity could allow the motion information to be combined more easily with the form information that is processed in the same brain area.

One of the clearest findings of the present study was the prevalence of direction-selective coding clustered around particular cartesian axes. These axes correspond to the gravitational axis (up/down), an axis running towards/away along the line of sight and an axis running left/right. The width of the tuning of the cells suggests that coding of these six directions is sufficient to allow representation of all possible directions of movement within the STP. Movement at 45° to the cartesian axes would excite (half maximally) at least two cell populations tuned to directions along the cartesian axes. The preferential coding of orthogonal directions means that all directions in 3D space can be represented by the minimum number of directionally selective cell populations. Therefore, direction of motion is represented in STPa in the most efficient manner. Although an initial investigation of V5 (MT) suggested a bias in cell response preferences for movement towards the contralateral periphery (Dubner and Zeki 1971), subsequent studies have not drawn attention to any pronounced bias in the distribution of directional tuning (Zeki 1974; Albright 1984; and see Introduction). Cells in MST also exhibit no marked bias in directional preference, except in the horizontal plane where cells show a slight preference for motion towards the ipsilateral side (Komatsu and Wurtz 1988a), a property also seen in the visual tracking neurons in the lateral part of MST, MSTl (Thier and Erickson 1992). The biases reported for MT and MST were towards a particular hemispace (i.e. contralateral and ipsilateral) and not the strong preference along particular axes reported here.

Preferential coding of direction has been noted in sub-cortical structures. The neurons of the accessory optic system (AOS) of the rabbit, cat and monkey show preferential coding of directions of movement that coincide with the direction of retinal movement that would occur during

self-motion about the vestibular axes (Grasse and Cynader 1982, 1984; Grasse et al. 1984; Simpson et al. 1988; Soodak and Simpson 1988; Hoffman and Distler 1989). Coupling the sensory inputs from the semicircular canals with the optical changes resultant from self-motion could also be used to define the three axes of motion selectivity observed in STPa. Indeed real motion and retinal movement consequent of self-motion have markedly different effects on STPa cells selective for motion (Hietanen and Perrett 1993).

Given the importance of the cartesian axis system for the coding of motion and view it is also interesting to speculate on the development of preferential coding. The direction of motion of an animate object will be highly correlated with the perspective view of the moving body. For example, the left profile, head view would be correlated with motion of an animal to the observer's left. This relationship could underlie the correlation between the views preferentially encoded in STPa (front, left and right profile, and back) and the directions preferentially coded in the same area (towards, left, right and away). Furthermore, the cells coding head and body information associated with another individual's attention up and down could also be related to the body movements up and down (Perrett et al. 1992).

It is of interest to consider why these particular three axes are represented. If directional tuning is affected by experience then the axes utilized in STPa are not too surprising. The up/down axis is, of course, coincident with gravity; this axis could be defined through experience of objects falling. Movement towards any organism has strong survival implications and, for social animals such as macaques and humans, it is a powerful cue to social interactions. From optical considerations objects moving along this z-axis will change in retinal size. The presence of retinal expansion/contraction could therefore be used to define the selectivity of cells tuned for movement towards and away. With two axes defined, the third axis (left/right) can also be found by a system of coding which attempts to decompose movement into uncorrelated or orthogonal directions. Learning rules which maximise the difference between activity amongst cell populations (e.g. "decorrelation" of Foldiak 1991) will automatically extract orthogonal dimensions (or principal components amongst sensory inputs).

Relationship of motion processing in STPa to posterior areas

The obvious route for motion information to arrive in area STPa is from the motion pathway involving the magnocellular portions of the lateral geniculate nucleus (LGN) and areas V1, V2, MT and MST. Motion-sensitive visual inputs to STP may not be entirely dependent on the magnocellular-geniculostriate system. The visual responses in MT are largely dependent on the magnocellular pathway (Maunsell et al. 1990), but, after lesion of magnocellular LGN, there is evidence for additional parvocellular input to MT (Merigan et al. 1991). Motion sensitivity in STPa could also depend on inputs from the superior colliculus, which provides inputs to extrastriate visual areas via the lateral pulvinar (Bruce et al. 1986; Girard and Bullier 1989; Rodman et al. 1989, 1990; Girard et al. 1991; Gross 1991). The colliculus also projects to S and interlaminar layers of the LGN. These layers are the source of direct projections from the LGN to extrastriate areas V2, V3, V3a, V4 and MT (Wong-Riley 1976; Benevento and Yoshida 1981; Fries 1981; Bullier and Kennedy 1983), though there do not appear to be direct LGN connections to anterior temporal cortex (including area STP) or parietal cortex (area PG; Iwai et al. 1980; Fries 1981; Yukie and Iwai 1981).

It has been proposed that the residual vision seen after lesions to striate cortex is mainly due to neuronal activity in the dorsal pathway (Girard et al. 1991). Following unilateral lesions to striate cortex many STP cells remain visually responsive but selectivity for form and motion direction is largely abolished (Bruce et al. 1986; Gross 1991). Bruce et al. (1986) found only 2 out of 40 STP cells exhibiting residual directional selectivity. Thus, although the superior colliculus may provide some visual input to the STP, it does not seem to be the main source of directional selectivity in this area.

Interestingly, directional selectivity is maintained in many MT cells following V1 lesion, although response magnitudes are reduced (Rodman et al. 1989). This residual directionality is presumably due to input to MT from the superior colliculus, since lesions of both striate cortex and superior colliculus abolished all visual responses in MT and STP (Rodman et al. 1990; Bruce et al. 1986). It is not clear why the residual sensitivity to motion in MT which survives striate lesion is insufficient to drive directional selectivity in more than a minority (5%, 2/41) of STP cells (Bruce et al. 1986).

Temporal characteristics of the responses

Responses of MST cells show a phasic increase from response onset which lasts for some 100–300 ms. The tonic response which occurs after this transient burst lasts for the duration of the stimulus presentation (Duffy and Wurtz 1991a). This pattern of a transient burst followed by a period of tonic discharge throughout stimulus presentation was also seen in both STPa cells sensitive to motion (Fig. 14) and cells responsive to static stimuli (Oram and Perrett 1992). The latency of MT neurons is typically 40–60 ms (Mikami et al. 1986a), whereas the latency of the population curve of direction-selective STP neurons is 59 ms (Fig. 14). This is consistent with motion information arriving in STPa via MT. We have argued elsewhere that static information in STPa neurons arrives as quickly as possible via the ventral route (Oram and Perrett 1992), yet the latency of the cells in the present study was shorter than the latency of cells responding to static form. Most likely, therefore, the motion input derives from the dorsal route (involving MT and MST), as there is a pathway from V1 to STPa passing through fewer brain areas than in the ventral route. Conversely the static pattern input would derive from the ventral route involving V4 and inferior temporal cortex (Felleman and Van Essen 1991; Young 1992).

Proportions of motion-sensitive cells

In areas MT, MST and STPp, virtually all visual cells are non-selective for stimulus form but responsive to motion (98% of MT, 96% of MST, Tanaka et al. 1986; MST 99%, STPp 97%, Hikosaka et al. 1988; MSTd and MSTl 96%, Saito et al. 1986; MSTd 85%, Duffy and Wurtz 1991a). This is far above the proportion (25%) of visual cells in STPa displaying motion sensitivity but lacking form sensitivity.

A further difference between non-form, motion-selective cells in STPa and those of MT/MST lies in the increased number of pandirectional cells. Studies of MT revealed only 2% of motion-selective cells were pandirectional (Tanaka et al. 1986). A similarly low proportion (1%) of pandirectional cells was found in MSTd and MSTl; (Tanaka et al. 1986; Saito et al. 1986). In a third study of MSTd, some 30% of the cells were responsive to rotation, movement in the fronto-parallel plane and expansion/contraction but, of those tested in the fronto-parallel plane, only 7% responded to all 8 directions tested (Duffy and Wurtz 1991a). All these estimates are far lower than the 56% of STPa motion-sensitive cells found in the present study to be pandirectional. Hikosaka et al. (1988) also report that 30% of motion-sensitive cells are pandirectional in STPp. Thus the change in the ratio of unidirectional to pandirectional cell selectivities seen from MT/MST to STPa is due to a drop in the number of unidirectional, motion-selective cells, 86% in MT and 80–88% in MST (Tanaka et al. 1986; Saito et al. 1986). The proportion of bidirectional cells remains consistent across areas MT (6%; Tanaka et al. 1986), MST (1%; Saito et al. 1986) and STPp (4%; Hikosaka et al. 1988) and is far more comparable with the 4% found in STPa in the present study.

Of the unidirectional cells in posterior regions relatively few respond to expansion or contraction: MT 3%; MST 5–23%; STPp 13% (Tanaka et al. 1986; Saito et al. 1986; Hikosaka et al. 1988). In the present study 46% of unidirectional cells responded to movement towards or away from the monkey. A similarly high number of cells responding to movement along the z-axis were found in STPa polymodal cells (Mistlin and Perrett 1990). This apparent discrepancy between posterior areas and STPa cell populations could be due to the observation that expansion/contraction cells respond preferentially to real 3D stimuli over projected stimuli (Tanaka and Saito 1989; cf. Hikosaka et al. 1988). The ratio of unidirectional cells in MSTd responsive to expansion compared with contraction ranges from about 2:1 (Saito et al. 1986) to 7:1 (Tanaka and Saito 1989). The ratio of the present study was 67:28. Thus in all areas there are more cells responsive to motion towards than away from the monkey but the proportion of cells sensitive to motion along the z-axis is much higher in STPa than in MT, MST or STPp.

Thus the changes that seem to occur between posterior motion areas (MT, MSTd/MSTl, STPp) and STPa can be summarized as follows: (1) the proportion of motion-sensitive cells decreases; (2) there is trend for fewer unidirectional cells and more pandirectional cells; (3) the proportion of bidirectional cells stays roughly equivalent, indicating that they form a separate population; and (4) the proportion of motion-sensitive cells preferring motion along the z-axis (towards and away) increases.

Directional tuning in different brain areas

It is also of interest to compare the I_d measures (Fig. 9) with other extrastriate brain areas. A number of measures of I_d have been made for MT (e.g. median 0.99, Saito et al. 1989; median 1.01, Snowden et al. 1992). Furthermore, the estimate of I_d is similar when isoluminant, colour-contrast stimuli are used (median 0.95, Saito et al. 1989). The median I_d of the unidirectional STPa cells in the present study was 0.97 (Fig. 9, bottom). In another study, more than 80% of the unidirectional cells in MT had I_d values greater than 0.8 (Mikami et al. 1986a). As the criteria for including a cell in their analysis was very stringent, the estimate is very unlikely to include any bidirectional cells. For the unidirectional cells in the present study, we also found more than 80% of cells had I_d values exceeding 0.8.

Estimates of directionality in MST (Duffy & Wurtz 1991a) are similar to those obtained here, though a greater proportion of STPa cells appear to have higher direction discrimination. Such a regional discrepancy may be due to our use of the minimum estimated response, whereas Duffy and Wurtz used the observed response magnitude to the null direction. Thus, the directionality in area STPa appears similar to that in MT and MST but greater than that estimated for V1 directional cells (e.g. $I_d=0.44$; Snowden et al. 1992). This suggests that STPa, MT and MST code movement with similar discrimination between directions.

It is worth noting that the discrimination between directions shown by cells in STPa (Fig. 8) is comparable with the equivalent measure for discrimination between views for cells selective for different views of the head in the same brain region (Perrett et al. 1991). Thus the discrimination, the breadth of tuning and distribution of preferred directions shown by STPa neurons processing motion appear comparable with that shown by neurons in the same area that process the static form of the head and body.

Establishment of direction tuning

We have argued that the tuning seen in static-form cells of STPa is derived in a feed-forward way with little lateral inhibition contributing to the initial view selectivity. This was based on the observation that view discrimination was present from response onset and that response latencies were so early that, even following the shortest route (involving only eight synapses) along the ventral ("form" or "what") pathway to the STPa, the responses had to be relayed between stages on the basis of the first one or possibly two spikes of the response (Oram and Perrett 1992).

The latency of the cells in the present study is on average statistically less than the latencies of cells selective for views of the head and body. As firing rates during the initial 100 ms of response were comparable. (67.3 in contrast to 66.9 spikes/s) and similar stimulus presentation

methods were used, this difference is unlikely to be due to differences in the adequacy of the stimulus. The difference in latency suggests that the input to motion-selective cells in STPa is established by a different route not involving the ventral pathway. The shortest route to STP from the striate cortex is via the dorsal pathway (V1–MT–MST/FST–STPa; Felleman and Van Essen 1991). Allowing for interneurons between input and output layers in MT and MST/FST (Zeki and Shipp 1988; Felleman and Van Essen 1991), a minimum of five synaptic relays are needed to pass information from V1 to the STPa cells recorded here. Latencies of V1 cell responses to strong contrast stimuli can be as early as 30 ms (J.H.R. Maunsell, personal communication). As the population latency of the STPa cells responsive to motion studied here was found to be 58.8 ms, this leaves 30 ms for activity to flow between V1 and STPa. Allowing for 4–5 ms for each synaptic relay, the difference in latencies fits well with a route through MST to the recording sites in STPa. The time constraints along this pathway seem therefore as tight as those for static-form processing, suggesting again that information must be passed between stages on the basis of the initial spike of the response.

Several studies have suggested that directionality can be established in a feed-forward manner (e.g. Soodak and Simpson 1988; Worgotter and Holt 1991), which is a requirement to obtain the fastest flow of information. Indeed, the changes in the creation of new directional-selective properties in MST can be explained by direct feed-forward input from MT (Saito et al. 1986; Tanaka and Saito 1989; Tanaka et al. 1989).

Unlike the cell population studied here, the optimal direction for MT and MST neurons is more evenly distributed around the fronto-parallel plane (Albright et al. 1984; Komatsu and Wurtz 1988a). From Fig. 13 it can be seen that more than 75% of the cells have optimal directions within 15° from the cartesian axes. If the directional tuning depended on input from MT/MST then the preferential coding of directions in STPa could be established from outputs of just a small fraction (5–10%) of MT/MST neurons.

Relationship to psychophysical studies

Motion processing at the cellular level in V1, MT and MST has been correlated frequently with motion sensitivity at the psychophysical level (Movshon et al. 1985; Mikami et al. 1986a; Newsome et al. 1986; Snowden et al. 1991). Using moving random dot displays, Levinson and Sekuler (1980) measured the elevation in luminance detection threshold for various directions following adaptation to motion of the display in one direction. The elevation in threshold varied with the direction of drift of the test stimuli from the adaptation direction. It was found that maximal elevation occurred when the test stimuli moved in the same direction as the adaptation stimulus and fell to a minimum for opposite directions of motion. From this the estimated band width of underlying directionally selective channels (half-width at half-height) would be between 40 and 60°, which is equivalent to the tuning (half-width at half-height) of STPa unidirectional cells reported here.

Adelson and Movshon (1982; see also Movshon et al. 1985) suggested a two-stage model of motion detection, with the first phase extracting local orientation-based velocities and the second phase combining these to get a measure of whole field movement. Psychophysical studies with plaid patterns support this two-stage model (Welch 1989), although the apparent direction acuity of plaid displays is greater along the horizontal and vertical directions than in oblique directions (Heeley and Buchanan-Smith 1992). Thus, if there was a neuronal correlate to the psychophysical observations, the cell responses would be expected to show preferential tuning to horizontal and vertical directions, have large receptive fields and have a band width of tuning of 40–60°. These properties, in particular the meridional anisotropy, correlate more closely with STPa cells than cells in MT/MST. Further work with plaid patterns would be needed to establish whether the properties of STPa cells account for the psychophysical results.

Conclusion

Measurements of response latency indicate that movement information arrives in the STPa via a different route from that supplying sensitivity to the form of biologically meaningful objects. The directional selectivity of cells within STPa is consistent with an input of motion information from posterior motion processing areas (MT and or MST). Unlike the posterior areas, however, the distribution of preferred directions amongst STPa motion-sensitive cells is highly clustered around the cartesian axes (towards/away, left/right, up/down). Cells in STPa that are selective for static information about heads and bodies also exhibit a preference for views clustered around cartesian axes (front and back, left and right sides). The employment of the same system of axes for visual processing by these two distinct cell populations may underlie the production of a further population of STPa cells which are conjointly sensitive to form and motion. The specialization of STPa cells for particular directions and object views may facilitate the integration of two streams of visual analysis and thus support the unified experience of moving forms.

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References

Adelson EH, Movshon JA (1982) Phenomenal coherence of moving visual plaids. Nature 300: 523–525

Albright TD (1984) Direction and orientation selectivity of neurons in the visual area MT of the macaque. J Neurophysiol 52: 1106–1130

Albright TD, Desimone R, Gross CG (1984) Columnar organization of directionally selective cells in visual area MT of the macaque. J Neurophysiol 51: 16–31

Barlow HB, Levick WR (1965) The mechanism of directionally selective units in rabbit's retina. J Physiol (Lond) 178: 477–504

Baylis GC, Rolls ET, Leonard CM (1985) Selectivity between faces in the responses of a population of neurons in the cortex of the superior temporal sulcus of the macaque monkey. Brain Res 342: 91–102

Benevento LA, Yoshida K (1981) The afferent and efferent organization of the lateral geniculo-prestriate pathways in the macaque monkey. J Comp Neurol 203: 455–474

Britten KH, Newsome WT, Saunders RC (1992) Effects of inferotemporal cortex lesions on form-from-motion discrimination in monkeys. Exp Brain Res 88: 292–302

Bruce CJ, Desimone R, Gross CG (1981) Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. J Neurophysiol 46: 369–384

Bruce CJ, Desimone R, Gross CG (1986) Both striate cortex and superior colliculus contribute to visual properties of neurons in superior temporal polysensory area of macaque monkey. J Neurophysiol 55: 1057–1075

Bullier J, Kennedy H (1983) Projection of the lateral geniculate nucleus onto cortical area V2 in the macaque monkey. Exp Brain Res 53: 168–172

Colby CL (1991) The neuroanatomy and neurophysiology of attention. J Child Neurol 6: S90–S118

Colby CL, Miller EK (1986) Eye movement related responses of neurons in superior temporal polysensory area of macaque. Soc Neurosci Abstr 12: 1

Desimone R, Albright TD, Gross CG, Bruce C (1984) Stimulus-selective properties of inferior temporal neurons in the macaque. J Neurosci 8: 2051–2062

DeValois RL, Yund EW, Helper N (1982) The orientation and direction selectivity of cells in macaque visual cortex. Vision Res 22: 531–544

De Yoe FA, Van Essen DC (1988) Concurrent processing streams in monkey visual cortex. Trends Neurosci 11: 219–226

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

Duffy CJ, Wurtz RH (1991a) Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. J. Neurophysiol 65: 1329–1345

Duffy CJ, Wurtz RH (1991b) Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. J Neurophysiol 65: 1346–1359

Erickson RG, Thier P (1991) A neuronal correlate of spatial stability during periods of self-induced visual motion. Exp Brain Res 86: 608–616

Felleman DJ, Van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex 1: 1–47

Foldiak P (1991) Learning invariance from transformation sequences. Neural Comp 3: 194–200

Fries W (1981) The projection from the lateral geniculate nucleus to the prestriate cortex of the macaque monkey. Proc R Soc Lond [Biol] 213: 73–80

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

Gattas R, Gross CG (1981) Visual topography of striate projection zone in posterior superior temporal sulcus of the macaque. J Neurophysiol 46: 621–638

Girard P, Bullier J (1989) Visual activity in area V2 during reversible inactivation of area 17 in the macaque monkey. J Neurophysiol 62: 1287–1302

Girard P, Saline PA, Bullier J (1991) Visual activity in areas V3a and V3 during reversible inactivation of area V1 in the macaque monkey. J Neurophysiol 66: 1493–1503

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15: 20–25

Grasse KL, Cynader MS (1982) Electrophysiology of medial terminal nucleus of accessory optic system in the cat. J Neurophysiol 48: 490–504

Grasse KL, Cynader MS (1984) Electrophysiology of lateral and dorsal terminal nuclei of the cat accessory optic system. J Neurophysiol 51: 276–293

Grasse KL, Cynader MS, Douglas RM (1984) Alterations in response properties in the lateral and dorsal terminal nuclei of the cat accessory optic system following visual cortex lesions. Exp Brain Res 55: 69–80

Gross CG (1991) 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: 497–515

Gross CG, Rocha-Miranda CE, Bender DB (1972) Visual properties of neurons in inferotemporal cortex of the monkey. J Neurophysiol 35: 96–111

Harries MH, Perrett DI (1991) Modular organization of face processing in temporal cortex: physiological evidence and possible anatomical correlates. Cogn Neurosci 3: 9–24

Hasselmo ME, Rolls ET, Baylis GC, Nalwa V (1989) Object-centered encoding by face-selective neurons in the cortex in the superior temporal sulcus of the monkey. Exp Brain Res 75: 417–429

Heeley DW, Buchanan-Smith HM (1992) Directionality acuity for drifting plaids. Vision Res 32: 97–104

Hietanen JK, Perrett DI (1993) Motion sensitive cells in the macaque superior temporal polysensory area. I. Lack of response to the sight of the monkey's own hand. Exp Brain Res 93: 117–128

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

Hoffman KP, Distler C (1989) Quantitative analysis of visual receptive fields of neurons in nucleus of the optic tract and dorsal terminal nucleus of the accessory optic tract in macaque monkey. J Neurophysiol 62: 416–428

Iwai E, Yukie M, Umistu Y, Kido S, Niihara T (1980) Geniculo-prestriate projection in the macaque monkey. Exp Brain Res [Suppl] 41: A19

Kendrick KM, Baldwin BA (1987) Cells in temporal cortex of conscious sheep can respond preferentially to the sight of faces. Science 236: 448–450

Koenderink JJ, Doorn AJ van (1979) The internal representation of solid shape with respect to vision. Biol Cybern 32: 211–216

Komatsu H, Wurtz RH (1988a) Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual response properties of neurons. J Neurophysiol 60: 580–603

Komatsu H, Wurtz RH (1988b) Relation of cortical areas MT and MST to pursuit eye movements. III. Interaction with full-field visual stimulation. J Neurophysiol 60: 621–644

Levinson E, Sekuler R (1980) A two-dimensional analysis of direction-specific adaptation. Vision Res 20: 103–107

Mansfield RJW, Ronner SF (1978) Orientation anisotropy in monkey visual cortex. Brain Res 149: 229–234

Maunsell JHR, Van Essen DC (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

Maunsell JHR, Nealey TA, DePriest DD (1990) Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. J. Neurosci 10: 3323–3334

Merigan WH, Byrne CE, Maunsell JHR (1991) Does primate motion perception depend on the magnocellular pathway? J Neurosci 11: 3422–3429

Merrill EG, Ainsworth A (1972) Glass-coated platinum-plated tungsten microelectrodes. Med Biol Eng 10: 662–672

Mikami A, Newsome WT, Wurtz RH (1986a) Motion sensitivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. J Neurophysiol 55: 1308–1327

Mikami A, Newsome WT, Wurtz RH (1986b) Motion selectivity in macaque visual cortex. II. Spatiotemporal range of directional interactions in MT and V1. J Neurophysiol 55: 1328–1339

Mistlin AJ, Perrett DI (1990) Visual and somatosensory processing in the macaque temporal cortex: the role of "expectation". Exp Brain Res 82: 437–450

Movshon JA, Adelson EH, Gizzi MS, Newsome WT (1985) The analysis of moving visual patterns. In: Chagas C, Gattass R, Gross C (eds) Pattern recognition mechanisms. Springer, Berlin Heidelberg New York, pp 117–151

Newsome WT, Mikami A, Wurtz RH (1986) Motion selectivity in macaque visual cortex. III. Psychophysics and physiology of apparent motion. J Neurophysiol 55: 1340–1351

Newsome WT, Wurtz RH, Komatsu H (1988) Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal to extraretinal inputs. J Neurophysiol 60: 604–620

Oram MW, Perrett DI (1992) The time course of neural responses of cells selective for faces in the temporal cortex. J Neurophysiol 68: 70–84

Perrett DI, Rolls ET, Caan W (1982) Visual neurons responsive to faces in the monkey temporal cortex. Exp Brain Res 47: 329–342

Perrett DI, Smith PAJ, Potter DD, Mistlin AJ, Head AS, Milner AD, Jeeves MA (1984) Neurons responsive to faces in the temporal cortex: studies of functional organization sensitivity to identity and relation to perception. Hum Neurobiol 3: 197–208

Perrett DI, Smith PAJ, Potter DD, Mistlin AJ, Head AS, Milner AD, Jeeves MA (1985a) Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc R Soc Lond [Biol] 223: 293–317

Perrett DI, Smith PAJ, Mistlin AJ, Chitty AJ, Head AS, Potter DD, Broennimann R, Milner AD, Jeeves MA (1985b) Visual analysis of body movements by neurons in the temporal cortex of the macaque monkey: a preliminary report. Behav Brain Res 16: 153–170

Perrett DI, Harries MH, Bevan R, Thomas S, Benson PJ, Mistlin AJ, Chitty AJ, Hietanen J, Ortega JE (1989) Frameworks of analysis for the neural representation of animate objects and actions. J Exp Biol 146: 87–114

Perrett DI, Harries MH, Benson PJ, Chitty AJ, Mistlin AJ (1990a) Retrieval of structure from rigid and biological motion: an analysis of the visual response of neurons in the macaque temporal cortex. In: Blake A, Troscianko T (eds) AI and the eye. Wiley, Chichester, UK, pp 181–201

Perrett DI, Harries MH, Chitty AJ, Mistlin AJ (1990b) Three stages in the classification of body movements by visual neurons. In: Barlow HB, Blakemore C, Weston-Smith M (eds) Images and understanding. Cambridge University Press, Cambridge, UK, pp 94–107

Perrett DI, Oram MW, Harries MH, Bevan R, Hietanen JK, Benson PJ, Thomas S (1991) Viewer-centred and object-centred coding of heads in the macaque temporal cortex. Exp Brain Res 86: 159–173

Perrett DI, Hietanen JK, Oram MW, Benson PJ (1992) Organization and functions of cells responsive to faces in the temporal cortex. Philos Trans R Soc Lond [Biol] 335: 23–30

Rodman HR, Albright TD (1989) Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). Exp Brain Res 75: 53–64

Rodman HR, Gross CG, Albright TD (1989) Afferent basis of visual response properties in area MT of the macaque. I. Effects of striate cortex removal. J Neurosci 9: 2033–2050

Rodman HR, Gross CG, Albright TD (1990) Afferent basis of visual response properties in area MT of the macaque. II. Effects of superior colliculus removal. J Neurosci 10: 1154–1164

Rosene DL, Roy NJ, Davis BJ (1986) A cryoprotection method that facilitates cutting frozen sections of whole monkey brains for histological and histochemical processing without freezing artifact. J Histochem Cytochem 34: 1301–1315

Roy J-P, Wurtz RH (1990) The role of disparity-sensitive cortical neurons in signalling the direction of self-motion. Nature 348: 160–162

Roy J-P, Komatsu H, Wurtz RH (1992) Disparity sensitivity of neurons in monkey extrastriate area MST. J Neurosci 12: 2476–2492

Saito H, Yukie M, Tanaka K, Hikosaka K, Fukada Y, Iwai E (1986) Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. J Neurosci 6: 145–157

Saito H, Tanaka J, Isono H, Yasuda M, Mikami A (1989) Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. Exp Brain Res 75: 1–14

Seltzer B, Pandya DN (1978) Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the Rhesus monkey. Brain Res 149: 1–24

Simpson JI, Leonard CS, Soodak RE (1988) The accessory optic system of rabbit. II. Spatial organization of direction selectivity. J Neurophysiol 60: 2055–2072

Snedecor GW, Cochran GW (1980) Statistical methods. Iowa State University Press, Ames, Iowa

Snowden RJ, Treue S, Erickson RG, Andersen RA (1991) The response of area MT and V1 neurons to transparent motion. J Neurosci 11: 2768–2785

Snowden RJ, Treue S, Andersen RA (1992) The response of neurons in areas V1 and MT of the alert rhesus monkey to moving random dot patterns. Exp Brain Res 88: 389–400

Soodak RE, Simpson JI (1988) The accessory optic system of rabbit. I. Basic visual response properties. J Neurophysiol 60: 2037–2054

Tanaka K, Saito H-A (1989) Analysis of motion of the visual field by direction, expansion/contraction and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. J Neurophysiol 62: 626–641

Tanaka K, Hikosaka K, Saito H-A, Yukie M, Fukada Y, Iwai E (1986) Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. J Neurosci 6: 134–144

Tanaka K, Fukada Y, Saito H (1989) Underlying mechanics of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal areas of the macaque monkey. J Neurophysiol 62: 642–656

Thier P, Erickson RG (1992) Responses of visual-tracking neurons from cortical area MST-1 to visual, eye and head motion. Eur J Neurosci 4: 539–553

Ungerleider LG, Mishkin M (1982) Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW (eds) Analysis of visual behaviour. MIT, Cambridge, Mass., pp 549–586

Welch L (1989) The perception of moving plaids reveals two motion-processing stages. Nature 337: 734–736

Wong-Riley MTT (1976) Projections from the dorsal lateral geniculate nucleus to prestriate cortex in the squirrel monkey as demonstrated by retrograde transport of horseradish peroxidase. Brain Res 109: 595–600

Worgotter F, Holt G (1991) Spatiotemporal mechanisms in receptive fields of visual cortical simple cells: a model. J Neurophysiol 65: 494–510

Young MP (1992) Objective analysis of the topological organization of the primate cortical visual system. Nature 358: 152–155

Young MP, Yamane S (1992) Sparse population coding of faces in the inferotemporal cortex. Science 256: 1327–1331

Yukie M, Iwai E (1981) Direct projection from the dorsal lateral geniculate nucleus to the prestriate cortex in macaque monkeys. J Comp Neurol 201: 81–97

Zeki SM (1974) Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. J Physiol (Lond) 236: 549–573

Zeki S, Shipp S (1988) The functional logic of cortical connections. Nature 335: 311–317