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The effects of lighting conditions on responses of cells selective for face views in the macaque temporal cortex

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Summary. Neural mechanisms underlying recognition of objects must overcome the changes in an object's appearance caused by inconsistent viewing conditions, particularly those that occur with changes in lighting. In humans, lesions to the posterior visual association cortex can impair the ability to recognize objects and faces across different lighting conditions. Inferotemporal lesions in monkey have been shown to produce a similar difficulty in object matching tasks. Here we report on the extent to which cell responses selective for the face and other views of the head in monkey temporal cortex tolerate changes in lighting. For each cell studied the (preferred) head view eliciting maximal response was first established under normal lighting. Cells were then tested with the preferred head view lit from different directions (i.e. front, above, below or from the side). Responses of some cells failed to show complete generalization across all lighting conditions but together as a "population" they responded equally strongly under all four lighting conditions. Further tests on sub-groups of cells revealed that stimulus selectivity was maintained despite unusual lighting. The cells discriminated between head and control stimuli and between different views of the head independent of the lighting direction. The results indicate that constancy of recognition across different lighting conditions is apparent in the responses of single cells in the temporal cortex. *Lighting constancy* appears to be established by matching the retinal image to view-specific descriptions of objects (i.e. neurons which compute object structure from a limited range of perspective views).

Key words: Lighting – Face – Single cell – Temporal cortex – Macaque monkey

Introduction

A fundamental problem facing the visual system is the extraction of an object's form under different viewing conditions. Factors such as perspective view, object orientation, distance, movement, or lighting may produce enormous variations in the retinal image, yet the visual system is able to interpret and recognize objects correctly.

One of the largest changes imposed on an object's appearance is that caused by a change in lighting which can vary in strength, direction and number of illumination sources. As objects are not generally illuminated uniformly from all directions, lighting under one set of conditions can produce shading and shadows which obscure features visible at other times. We are unaware of the sophistication of our perceptual ability in coping with different lighting conditions because recognition is usually carried out without effort. Thus in everyday life we may be aware of the end product of our recognition but we do not contemplate the effect shadows have in obscuring particular features visible in other circumstances.

In some conditions, shadows may aid recognition rather than hinder it. Shadows can provide three-dimensional information about surface structure of objects and the direction of illumination. Although a few formal models for determining structure from shading have been proposed (e.g. Horn 1975; Koenderink and van Doorn 1980; Cohen and Grossberg 1984), neurophysiological and psychological evidence for the applicability of the models to human object recognition is lacking. It is a common feature of such models (e.g. Horn 1975; Pentland 1982) that the retrieval of surface orientation and structure depends on advance knowledge of the position of the illumination source(s) and properties of the object surfaces (i.e. their reflectance etc.). Thus in general the utilization of shading information for deriving object properties would only be possible if this additional information is supplied from an analysis of other aspects of the image or from memory (Ikeuchi and Horn 1981; Pentland 1982; Shafer 1985; Gershon et al. 1986).

The effect of shadow information in provoking perception of three-dimensional shape is so strong that it can occur even when shadow areas have impossible (in natural conditions) colours and textures, or associated movements (Cavanagh and Leclerc 1989). The only re-

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quirements for the perception of depth due to shadows is that shadow areas are darker than the surrounding and that there is a consistent contrast polarity along the shadow border. Retrieving object shape from shading cues requires the light/dark borders caused by shadows to be differentiated from those arising from changes in surface pigmentation, reflectance or texture (Cavanagh and Leclerc 1989). Little is known about how the brain accomplishes this though it has been argued that receptive fields of cells in primary visual cortex may reflect this analysis (Lehky and Sejnowski 1988).

Brain damage and lighting constancy

After brain damage a patient may struggle with a perceptual task that is relatively straightforward for normal subjects. Some patients with brain lesions are reported to have difficulties in recognizing everyday objects in unusual lighting conditions (Warrington 1982). This deficit was found associated with posterior lesions in the right hemisphere.

These results together with similar problems in matching pictures of objects taken from unusual views, were taken by Warrington (1982) to suggest the existence of stored "prototype" representations of familiar objects. These "prototype representations" would be accessed under a variety of different lighting conditions and across different views and distances. The properties of such prototype representations would allow objects to be identified under novel viewing conditions (Warrington 1982; Weiskrantz and Saunders 1984). [Representations covering different viewing conditions have also been referred to by Marr and Nishihara (1978) as "object-centred".] Warrington and co-workers (Warrington 1982; Whiteley and Warrington 1977) have further suggested that prototypes for different stimulus categories, (e.g. objects, faces and letters) are processed by different brain mechanisms.

Lesions to the higher visual association cortex of monkeys also appear to produce problems in recognizing objects across viewing conditions. Weiskrantz and Saunders (1984) report a study in which monkeys were taught discrimination tasks involving the selection of particular 3–D objects to obtain food reward. After subjects had learned a discrimination, the viewing conditions for the test objects were occasionally transformed in various ways including the introduction of lighting from an unusual direction. Monkeys with bilateral lesions to the inferotemporal or prestriate cortex performed worse on these generalization trials compared to monkeys with lesions in other brain areas (posterior parts of the superior temporal sulcus or the posterior parietal cortex). These results were considered as evidence for the involvement of anterior regions of the temporal lobe in the storage of "prototype representations" of familiar objects.

Impairment in face recognition with unusual lighting

In human patients brain lesions involving the right hemisphere have repeatedly been shown to cause difficulties in face recognition (Bodamer 1947; Hecaen and Angelergues 1962; Benton and Van Allen 1968; De Renzi et al. 1968; Warrington and James 1967). Recognition problems vary in severity and selectivity; prosopagnosia represents one extreme where problems appear to be restricted to faces (Bodamer 1947; Meadows 1974; De Renzi 1986). One controversial issue which remains topical (Benton 1980, 1990; Meadows 1974; Malone et al. 1982) is the extent to which prosopagnosia reflects purely perceptual disorders or problems related to a defective memory.

Etcoff et al. (1991) recently reported a case of prosopagnosia where the Benton-Van Allen (1968) face matching task proved informative. The patient performed without error when the sample and match faces were identical but the performance decreased to 71% correct level when the target and match faces had different angles of view. When the faces were pictured in different lighting conditions his performance was clearly impaired (54% correct or chance performance). From the poor performance on this and other perceptual tasks several authors have argued for a deficit in high level perceptual integration or categorization as underlying the recognition impairment in many cases of prosopagnosia (e.g. Benton and Van Allen 1968; De Renzi et al. 1968; Newcombe 1969; Newcombe and Russell 1969; Whiteley and Warrington 1977).

It is possible, however, that in some cases face recognition problems arise from mnemonic disturbances and perceptual capacities appear relatively normal. Indeed, Malone et al. (1982) presented evidence for a double dissociation of impairments in perceptual matching of unfamiliar faces (Benton-Van Allen task) and the recognition of famous faces.

Cells selective for faces

Since in many cases of prosopagnosia patients suffer from high level perceptual deficits typified by their failure to cope with lighting change, we decided to investigate how different lighting conditions affect the responses of cells in the macaque temporal cortex. Sub-populations of cells in this area have been found to respond selectively to different views of the head: some respond most to the full face view, others to the profile view (Bruce et al. 1981; Desimone et al. 1984; Hasselmo et al. 1989; Kendrick and Baldwin 1987; Perrett et al. 1982, 1984, 1985, 1989, 1991a). The cells show considerable generalization for the preferred view across changes in retinal position (Desimone et al. 1984; Bruce et al. 1981), size and distance (Perrett et al. 1982, 1984; Rolls and Baylis 1986), isomorphic orientation (with the face upright, rotated to horizontal, or inverted; Desimone et al., 1984; Perrett et al. 1982, 1984, 1985, 1988) and luminance contrast (Rolls and Baylis 1986).

We report here that in addition to the capacity of cell responses to generalize across position, size, orientation and luminance contrast the cells also show lighting constancy. The cells considered as a "population" respond to one view of the head in a consistent way despite dramatically changing conditions of illumination where shadows arising from one part of the head obscure individual facial features (self-shadows).

Methods

Subjects

The activity of single cells was recorded from the temporal cortex of one female (J) and two male (D and H) rhesus monkeys (*Macaca mulatta* wt 4–8 kg).

Visual discrimination task

Before beginning recording the subjects were trained to sit in a primate chair and discriminate between the red or green colour of an LED. The LED was situated level with the monkey's line of sight on a blank white wall (projection screen) at a distance of 4 m. The monkeys were trained to lick a tube for fruit juice reward on trials with green LED but to withhold behavioural response at the sight of the red LED. Lick responses to the red LED were discouraged with a delivery of weak saline solution.

During the task the red or green LED lights were presented in random order for 1.0 s, after a 500 ms tone. The monkey was trained to perform the task irrespective of the presence of additional "test" visual stimuli. Test 2–D stimuli were projected onto the wall on which the LED was located and the 3D stimuli were presented to either side of the LED. The monkeys performed the LED colour discrimination task at a high level of accuracy ($>90\%$) and independent of simultaneous presentation of test stimulus.

Recording procedures

Single unit recording was performed using standard techniques (see Perrett et al. 1985, 1991a). Briefly, when discrimination training was complete each monkey was sedated with a weight-dependent dose of intramuscular ketamine and anaesthetized with intravenous barbiturate (Sagatal). Full sterile precautions were then employed while 2 stainless steel recording wells (16 mm internal diameter, ID) were implanted 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.

Two weeks after implantation the subjects were retrained to perform the discrimination task for 1–4 h in the primate chair with additional head restraint. 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 trans-dural guide tube was inserted 3–5 mm through the dura and a tungsten in glass microelectrode (Merrill and Ainsworth 1972) advanced with a hydraulic micro-drive to the temporal cortex. The target area for recording was the anterior part of the upper bank of the STS (areas TPO, PGa, TAa of Seltzer and Pandya 1978). Single cell activity was isolated with a window discriminator (Digitimer D130). Neuronal firing rates were measured in a period of 250 or 500 ms beginning 100 ms after stimulus presentation. These data were analysed on-line by a AT compatible PC microcomputer.

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 and 20% glycerol (Rosene et al. 1986).

Location of recording

Frontal and lateral X-radiographs were taken of the position of the microelectrode at the end of each recording session. Reconstruction of electrode position was achieved by reference to the positions of micro-lesions (10 microamp DC for 30 s) made at the end of some electrode tracks which were subsequently identified using standard histological techniques. 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 3 recording tracks. For these markers the position of injection, recorded in X-radiographs, could be compared to the anatomical location of injection revealed through normal or fluorescence microscopy.

Eye movement recording

Horizontal and vertical eye movements were monitored and recorded during the electrophysiological recording by using an infra-red corneal reflection system allowing recording of both signals from one eye. The eye position signals were filtered and digitized every 5 ms and stored together with the single unit activity.

Testing procedure

All cells were first assessed for their response to the sight of different views of the head under normal lighting. Each cell was tested for 5 trials of at least 4 different views of the head and control stimuli under computer controlled random order. Control stimuli included objects matched for approximate size and having a range of colours and textures. Firing rates across conditions were analysed on-line using 1-way ANOVA. When there was a significant variance ratio, protected least significant differences (PLSD, Snedecor and Cochran 1980) post-hoc testing was carried out on differences between individual conditions. A cell was defined as head selective if at least one view of the head elicited a response that was significantly different from the response to control objects and the cell's spontaneous activity.

Further tests were performed with modified lighting conditions only on cells which were found with on-line statistical assessment to discriminate one or more head views from spontaneous activity and from control stimuli.

Stimulus lighting

The stimuli for the experiments were different views of heads illuminated from different directions. Eight views of the head were used to cover 360 degrees of rotation in the horizontal plane. These included the front or face view, left profile, back of the head and right profile, (referred to as 0, 90, 180 and 270 degree views respectively) and four views at intermediate angles (45, 135, 225 and 315 degrees). In all tests the stimulus head was upright with respect to gravity.

The direction of lighting was defined with respect to the observer (and gravity). For "front" lighting a light source pointed from the observer or camera to the stimulus (i.e. parallel to the observer's line of sight). Front lighting produced an image showing fully all the

internal features of the view without any strong shadows. The other forms of lighting employed were "unusual" in that they were designed to create heavy shadows across different parts of the stimuli (see Figs. 3, 5 and 7).

For "top" and "bottom" lighting a single uni-directional light source was aimed at the stimulus from directly above or below (i.e. as far as possible the source pointed along the gravitational axis and was approximately perpendicular to the observer's line of sight).

For "side" lighting the light source was aimed at the stimulus from the observer's right or left (i.e. perpendicular to the line of sight). For profile views with the stimulus head pointing to the observer's left (at 45, 90 and 135 degrees) the light source was also on the left. For right profile views (at 225, 270 and 315 degrees) the light source was on the observer's right.

To examine whether selectivity in cell responses generalized across lighting conditions, cell responses to a view evoking maximal responses were compared with responses (a) to a control object (the experimenter's hand and arm, see Fig. 3) and/or (b) to a second view of the same head also illuminated with a comparable range of lighting.

Silhouette or shadow stimuli

For these stimuli the head of one of the experimenters was positioned in front of the slide projector such that it cast a shadow on to the test projection screen containing the LED. The head causing the shadow was screened from the observing subject with curtains. In other tests, video film was made of different views of a human head against a white background. This film was processed using a luminance keying function of a video effects unit (Fairlight CVI) converting the picture to 2 grey levels (black shadow/silhouette head against white background). This allowed video images of head views under normal lighting to be compared with video images containing exactly the same views depicted as a shadow. A further means of creating silhouette stimuli was achieved by illuminating a real 3–D head with a strong unidirectional light source from behind. Internal features in this "back" lit condition were absent and only a dark head shape remained with bright silhouette outline.

Stimulus media

Three different media of stimulus presentation were used. The majority of experiments were performed with 2–D still frame video images but during the early stages of study real 3–D stimuli and 2–D photographic slides were used.

3–D stimuli. Different views of real heads and control objects were shown at the distance of 1–1.5 m from the monkey. The different lighting conditions were produced by shining a single bright source of light (60 Watt electric lamp) onto the stimulus head from different directions (specified above) in an otherwise darkened room. These 3–D stimuli were presented from behind a 20 cm square liquid crystal shutter (Screen Print Technology Ltd., rise time < 15 ms). On each trial the shutter became transparent for 1.0 s. after a 0.5 s signal tone. It otherwise remained opaque white.

2–D slides. Stimuli (different views of heads and controls) were photographed on 35 mm colour slide film. Slides were loaded into a random access projector (Kodak S–RA2000) and projected onto a screen situated 4 m from the monkey. Projection was controlled with a tachistoscope shutter (Forth Instruments, rise time < 10 ms) internal to the projector.

2–D video images. Finally, the stimuli were filmed with a video camera (JVC BY–110E), recorded on 3/4 inch U-Matic videotape, edited on a JVC editing suite (control unit RM–88U) and transferred on a laser video disc (RLV Mk II, Optical Disc Corp.). The video stimuli were then replayed with a video disc player (Philips VP406 LaserVision Disc Drive) and projected onto the display screen (using a Sony colour video projector VPH–1041QM). Testing involved computer controlled selection of desired still frames of stimuli and "unblanking" (switching on with 0 ms delay) the video signal to the projector for a 1 s stimulus presentation.

Computer randomized testing

Once selectivity for one or more views of the head was established, lists of relevant stimulus conditions (views and lighting conditions) to be tested were drawn up. Experimental testing with protocols involving 5 trials of each stimulus type, in random order, was then controlled on-line by computer program.

Data analysis

Cell responses to different head views, controls and spontaneous activity were first compared on line using 1-way ANOVA and post-hoc tests (PLSD). Further testing of the effects of different lighting conditions on the response to an optimal view was performed using 1-way ANOVA. Two-way ANOVA (stimulus type and lighting conditions) was used to measure the effects of lighting on the discrimination between different types of stimuli (head views and control stimuli).

Stimulus luminance

For real 3–D head stimuli, illuminated with a 60 Watt light source held close to the head, the maximum luminance (L_{max}) of bright stimulus regions, from the subject's viewing position ranged between 60 and 100 cd/m^2 (measured with a Tektronix J16 digital photometer). In the unusual lighting conditions (i.e. top, side, bottom lit) the contrast ($L_{max} - L_{min}/L_{max} + L_{min}$) between light and dark shadow areas was greater than 0.97.

The luminance levels of projected video stimuli were considerably lower than those of real 3–D stimuli. With normally lit video images of the head which were used for the initial screening of view sensitivity the mean luminance of bright areas was 9.8 cd/m^2 (range 4.0 to 11.9 cd/m^2 depending on the skin region measured). Under unusual (front, top, side or bottom) lighting conditions the luminance was even lower (mean luminance of bright areas was 1.2 cd/m^2, range 0.4 to 2.3 cd/m^2 depending on the lighting direction and skin region measured). The contrast between bright and dark areas for top, side and bottom lit stimuli was again extremely high, minimum = 0.98. For the front lit stimuli the contrast between bright and dark regions of the face was lower (0.25).

Results

Cell classification

In all, 23 cells with selective responses to the face or other view of the head were tested in different lighting conditions. Investigations of the effects of harsh lighting on responses to the preferred view were made for 21 of these cells. The effects of lighting were also studied in special ways for two further cells (see below).

The cells studied were a subset of those found to be selective for head view (see definition in methods) that have been reported elsewhere (Perrett et al. 1991a; Harries and Perrett 1991). The frequency with which cells were found to be selective for the sight of the head varied

from subject to subject (from 4–11% of the total sampled 500–1400 cells per monkey).

Assessments of view tuning (Perrett et al. 1991a) indicated that the 23 cells studied here preferred views of the head in which the facial features were visible (i.e. between left and right profile). The optimal views lay between 0 and 128 degrees or between 270 and 359 degrees. No cell was selective for a rear view of the head (i.e. no cell exhibited an optimal angle of view within 50 degrees of the back of the head). (This observation indicates that none of the cells examined were simply responsive to the presence of the hair.)

Testing the effects of lighting on cell responses to faces and other head views took two major lines. The first line of testing assessed *"generalization"* i.e., the extent that cells selective for a given view of the head continued to respond to that view despite unusual conditions of lighting. The second line of experimentation assessed *"discrimination"* i.e., the extent that differences in cell responses between stimuli were maintained across changes in lighting conditions. Discrimination was assessed by comparing responses to head views with responses to control objects illuminated under a comparable range of conditions. Discrimination was also assessed by contrasting two views of the head which for a given cell were found under normal lighting to produce good and poor responses respectively.

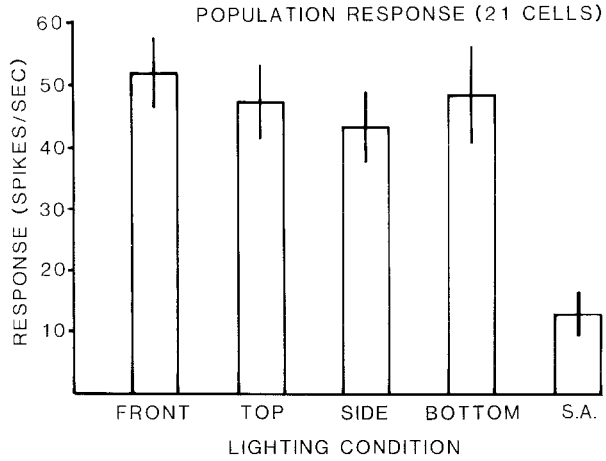


Fig. 1. Generalization of cell population response across different lighting conditions. The mean response (+/− 1 S.E.) of 21 cells is illustrated. For each cell, response was measured to cell's preferred view of the head under 4 different lighting conditions. The cells showed a clear response to the preferred head views in all lighting conditions which was greater than spontaneous activity ($p<0.001$, each comparison). For the population of cells 1-way ANOVA showed no differences between responses under different lighting conditions ($p>0.05$, each comparison). [Overall effect of conditions, $F_{4,80}=20.0$, $p<0.001$]

Response across different lighting conditions

Generalization at the cell population level. The effects of abnormal lighting conditions on the cell responses were tested after establishing the head view eliciting maximal responses under normal lighting. The preferred head view was then tested in a block of trials with some or all of the following lighting conditions; front, top, side and bottom lighting.

The average responses of each of the 21 cells to their preferred head views in the tested lighting conditions were calculated first and these data were used to calculate a "population" mean response for each four lighting conditions (see Fig. 1). [The term population here is used to refer to the sample of cells studied making the assumption that they would be a part of a much larger collection of cells responsive to the head.] Comparison of these mean responses and the cells' spontaneous activity (using 1-way ANOVA) revealed that the cell population did not differentiate between the four lighting conditions (PLSD test, $p>0.05$, each comparison; overall effect of conditions $F_{4,80}=20.0$, $p<0.001$). The responses of the cell population to the head under each lighting conditions were greater than the average spontaneous activity ($p<0.001$, each comparison). Thus there was no single lighting condition that proved more detrimental to responses than other lighting conditions.

Generalization at the single cell level. Although the analysis of the sample of cells as a whole showed equal responses to all lighting conditions, not all cells showed complete generalization across lighting conditions. 1-way ANOVAs and posthoc comparisons (PLSD test) indicated that on *an individual cell basis* different cells showed different degrees of generalization over the top, side, bottom and front lighting conditions. Six cells showed complete generalization, each responding at significantly higher rates to the preferred head view under all of the tested lighting conditions (from the 4 possible) than to controls and spontaneous activity. For the other cells the most common pattern of failure was an apparent absence of activity to one or more of the lighting conditions, with responses to other lighting conditions being equivalent. Nine cells failed to respond to the head under 1 of the tested lighting conditions above controls and spontaneous activity; 3 cells failed to respond under 2 of the lighting conditions and 3 cells failed to respond to any of the images of the preferred head view under experimental lighting conditions. [These 3 cells responded to 2–D images of heads during initial tests of view selectivity with high luminance video images. The failure of the cells to respond in the lighting tests was probably due to the low luminance of these video images (see methods).]

For the vast majority (18/21), no differences in responses were detected between lighting conditions which evoked a response significantly above spontaneous activity. This indicated that the cells' generalization across different types of lighting worked in an "all or none" fashion. Only 3 cells (3/21) showed a more graded degradation of responses to sub-optimal lighting. Figure 2 illustrates responses of one of these cells. This cell responded equivalently to the full face view under front and top lighting. Response to bottom lighting was, however, not significantly above spontaneous activity. More-

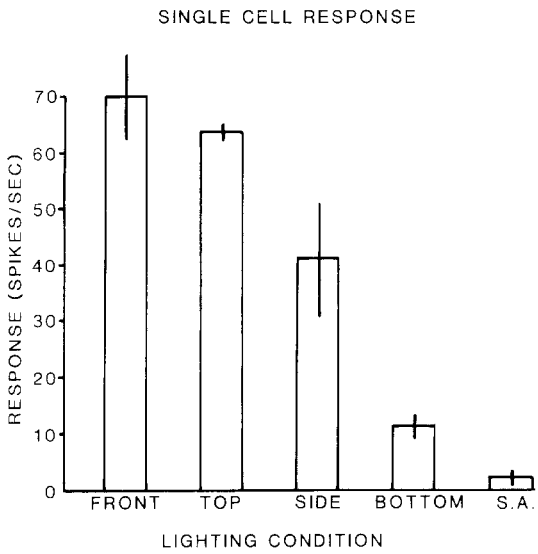


Fig. 2. Incomplete generalization of a single cell response under different lighting conditions. Histogram presentation of the mean responses (+/− 1 SE) of the responses of one cell (H40 31.44) to the face under different lighting conditions. The cell gave responses greater than spontaneous activity (S.A.) to the face lit from the front, top or side ($p<0.05$, each comparison). Responses to the bottom lit face, however, were not significantly different to spontaneous activity ($p>0.05$). Responses to the front and top lit face were significantly stronger than in the side lit face ($p<0.05$, each comparison). [Overall ANOVA effects of conditions, $F_{4,19}=25.7$, $p<0.001$]

Table 1. Number of cells responding to the preferred head view under a given lighting condition, expressed as a fraction of the number of cells tested in that lighting condition

Lighting condition	Front	Top	Side	Bottom
Number of cells responding	17/21	13/19	10/20	12/19

over, side lighting produced an intermediate level of response greater than spontaneous activity but significantly less than that produced by front and top lighting conditions.

Since some of the cells were not tested with all lighting conditions, Table 1 gives the number of cells responding at rates significantly higher than spontaneous activity (using 1-way ANOVAs and PLSD tests) in each particular lighting condition expressed as a fraction of those cells tested. There are 2 points to be noted from Table 1. First, 4 cells failed to respond to the front lighting condition. Three of these cells responded only weakly to all video images of the head in the lighting tests (see above). These 3 cells were included in the analysis because they responded well to 3–D or 2–D head views presented at a high luminance. Thus the overall illumination level appears to affect the responses of some cells and the extent of generalization to different lighting directions appears to be affected by the luminance of the test stimuli. The second point of interest from Table 1 is that, as noted earlier, there was no significant tendency for cells to fail more often in the bottom and side lit conditions (*Chi-squared* = 4.48, df = 3, $p=0.21$). These lighting conditions might be considered special as they are less likely to occur in the natural environment.

Effects of lighting on discrimination between head and control stimuli

For 9 cells testing included measurement of responses to the preferred head view and to a control object displayed under all four lighting conditions. The response of each of the 9 cells was analysed individually using 2-way ANOVA with stimulus type (head vs control) and lighting condition (front, top, side, bottom) as main factors (e.g. Fig. 3). For each of the 9 cells, analysis showed a significant main effect of stimulus type (with head views producing significantly larger responses than control stimuli). For 8 of the 9 cells the effect of lighting condition was non-significant and there was no significant interaction between lighting and stimulus type in 7 cases. One exceptional cell (showing a significant main effect of lighting, see Fig. 2) failed to respond to the preferred head view in the bottom lit condition.

The comparison between responses to head views and control stimuli was also made at the population level. Figure 4 presents the average responses of the 9 cells tested. A 2-way ANOVA performed on these data showed no effect of lighting ($F_{3,24}=0.7$, $p=0.57$) but a significant effect of stimulus type ($F_{1,8}=34.7$, $p<0.001$) and no interaction between lighting and stimulus type ($F_{3,24}=0.6$, $p=0.60$).

Effects of lighting on discrimiation between views

The discrimination between two views of the head was examined under different lighting conditions for 9 cells. [Eight of these cells were different from those considered in the previous section investigating discrimination from controls.] For these 9 cells an initial analysis was made of the tuning for perspective view. Two head views (a preferred view producing maximal response and a non-preferred view producing a significantly weaker response) were then retested in different lighting conditions.

Figure 5 presents the results of one such experiment. Under normal lighting the cell responded to the full face view significantly stronger than to the half profile view ($p<0.001$). This difference between head views was maintained under different lighting conditions with strong directional lighting from the top, side and bottom. 1-way ANOVA and post-hoc comparisons showed that responses to full face view in all lighting conditions were significantly stronger ($p<0.001$, each comparison) than responses to the half profile view. [Overall effect of conditions $F_{8,54}=67.9$, $p<0.001$]. For this cell 2-way ANOVA revealed a significant effect of view ($F_{1,48}=394$ $p<0.001$) and lighting ($F_{3,48}=8.9$, $p<0.001$) and a significant interaction between view and lighting

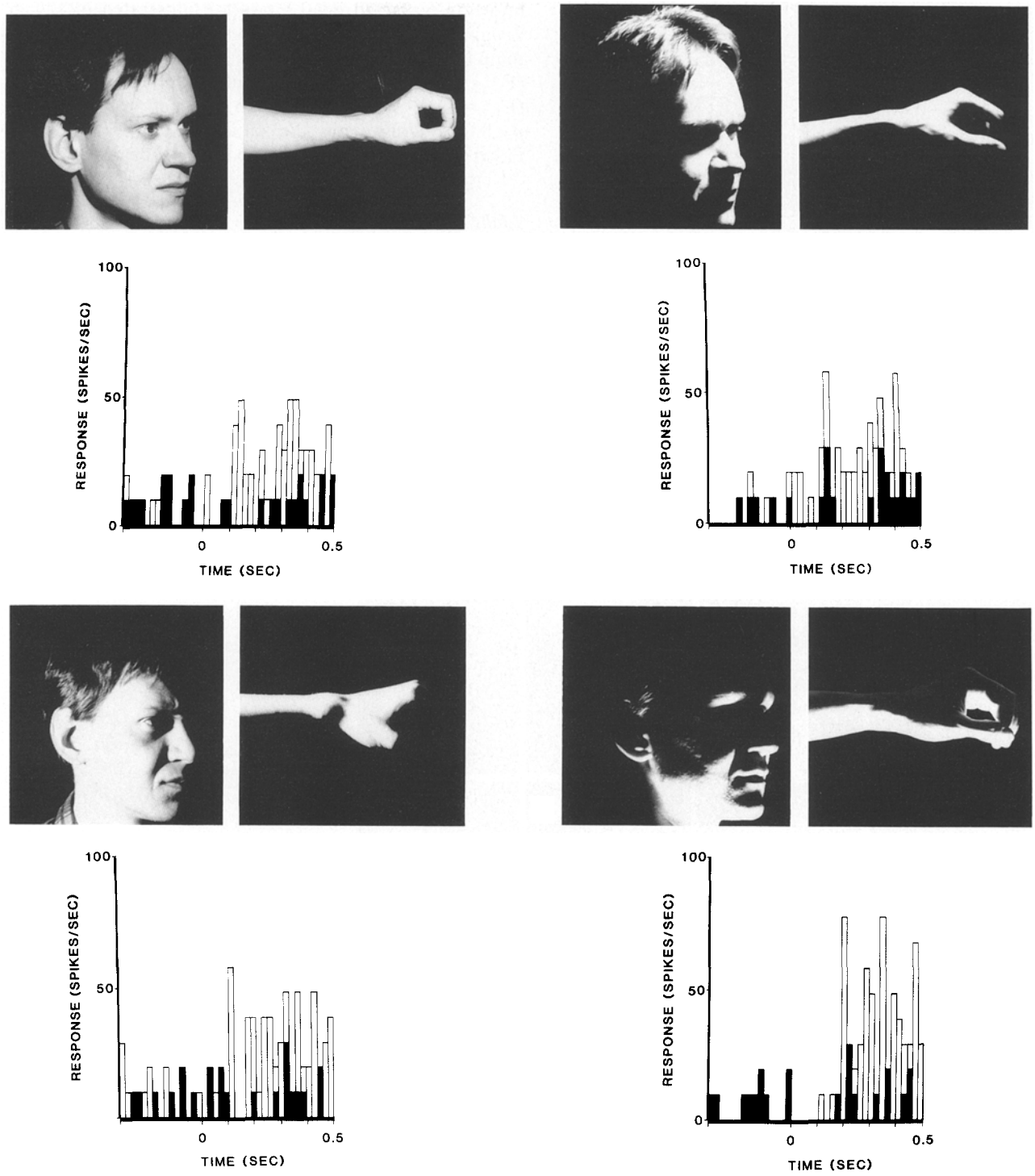


Fig. 3. Single cell discrimination between profile and control independent of lighting. *Upper:* examples of stimulus pairs used to examine effects of front, top, side and bottom lighting. *Lower:* peri-stimulus time histograms (mean of 5 trials per condition) of responses of one cell (J18 24.99) to a right half profile of a head (white bars) and to a control stimulus (black bars) under each lighting condition. 2-way ANOVA showed a significant main effect of stimulus type ($F_{1,32}=52.0$, $p<0.001$) but no effect of lighting condition ($F_{3,32}=0.1$, $p=0.95$) and no significant interaction between lighting and stimulus type ($F_{3,32}=0.1$, $p=0.95$)

($F_{3,48}=6.7$, $p=0.001$). The main effect of lighting is attributable to higher responses (for both views) for normal lighting compared to those with unusual lighting (bottom, top and side).

2-Way ANOVA for each of the 9 cells for which view discrimination was examined, revealed significant main effects of view for all 9 cells, significant main effects of lighting for 2 of the 9 cells and significant interactions for 4/9 cells.

The responses of the cells were also analysed as a "population". The average responses of 8 cells (each tested with 4 lighting conditions) to different preferred

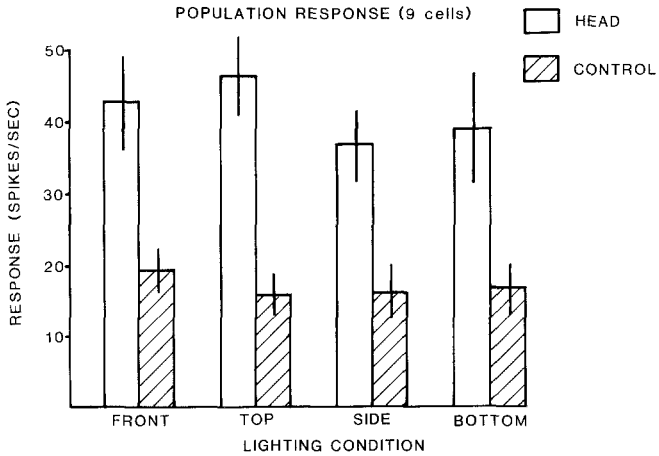


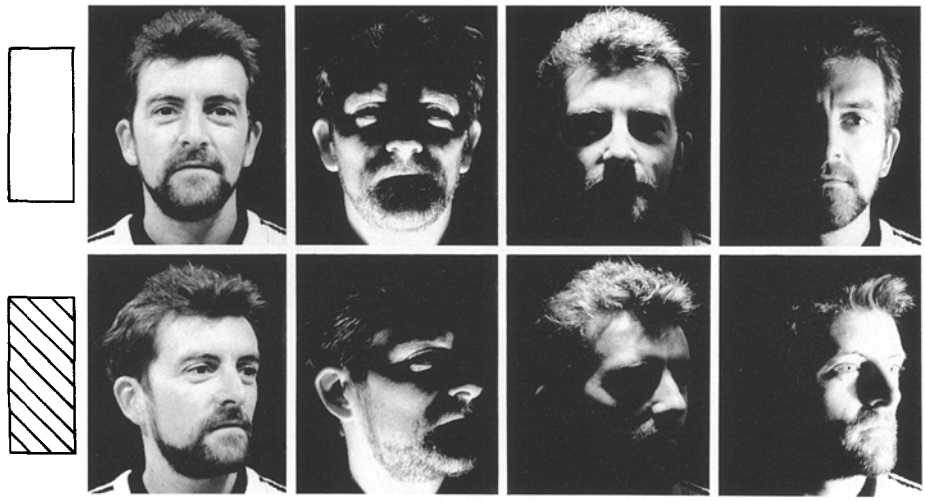
Fig. 4. Population discrimination of head views and controls. Histogram presentation of the mean responses (+/− 1 SE) of nine cells to the preferred head view for each cell and to a control object lit from four directions. 2-way ANOVA with stimulus type (heads vs control) and lighting condition as main factors showed a significant discrimination between head and control stimuli ($F_{1,8}=34.7$, $p<0.001$) but no effect of lighting ($F_{3,24}=0.7$, $p=0.57$) and no interaction between stimulus and lighting ($F_{3,24}=0.6$, $p=0.60$)

and non-preferred head views are illustrated in Fig. 6. 2-way ANOVA with head view and lighting condition as main factors revealed there was no main effect of lighting ($F_{3,21}=1.5$, $p=0.24$) but a significant effect of head view ($F_{1,7}=32.9$, $p=0.001$) and no interaction ($F_{3,21}=2.7$, $p=0.08$). Thus again the unusual lighting conditions failed to disrupt the selective coding of head views.

Lighting conditions and feature visibility

As noted above, in some cases abnormal lighting decreased responses to the preferred view. The decrease in response may be due to the strong shadows obscuring stimulus features necessary for the cell response. That lighting can alter cell responses by modifying the visibility of critical visual features is suggested from an experiment on one cell (see Fig. 7) modifying the appearance of a nonpreferred view with strong shadows.

This cell responded well to the left half profile of the head in front lighting but the full face failed to elicit a response above the cell's spontaneous activity. With



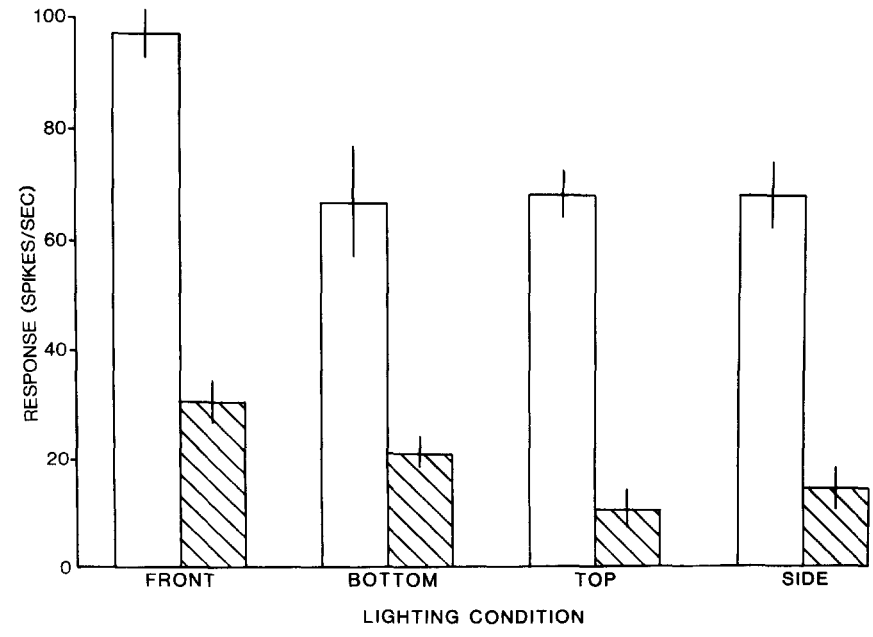


Fig. 5. Single cell discrimination between face and half profile views. *Upper:* examples of stimuli used. *Lower:* the mean response (+/− 1 SE) of one cell (D29 29.82) to the face (white bars) and half profile (hatched bars) views of the same face. Under normal lighting responses to the full face view were significantly higher than responses to the half profile view ($p<0.001$). While responses to the face were slightly reduced under strong directional lighting from the top, side and bottom, 1-way ANOVA showed that responses to full face view in all lighting conditions were significantly stronger than responses to the half profile view ($p<0.001$, each comparison). [Overall effect of conditions, $F_{8,54}=67.9$, $p<0.001$]

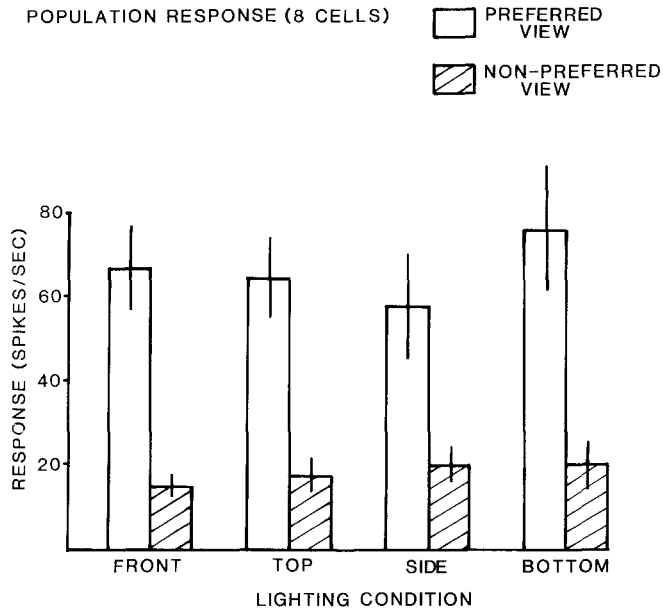


Fig. 6. Population discrimination between head views. Histogram presentation of the mean responses (+/− 1 SE) of eight cells to the preferred and nonpreferred head view in four different lighting conditions. A 2-way ANOVA with head view and lighting condition as main factors, showed no effect of lighting ($F_{3,21}=1.5$, $p=0.24$) but significantly stronger responses to the preferred than to the non-preferred head view ($F_{1,7}=32.9$, $p=0.001$) and no interactions ($F_{3,21}=2.7$, $p=0.07$)

strong illumination from the left side of the head, the cell was, however, found to respond to the face view at a rate greater than spontaneous activity and normally lit face view. (It is important to note that the cell still continued to discriminate the preferred profile view from the non-preferred face view even under the unusual lighting).

Under the side lighting condition the visual appearance of the face is in some respects more similar to the 1/2 profile (for example only one eye is clearly visible). Other experiments (not illustrated) confirmed that this cell was unresponsive to stimuli with two eyes symmetrically placed around the midline but responsive if only one eye or half face was visible.

For the other 9 cells tested for view discrimination under modified lighting (see above) no elevation of response to a non-preferred view was noted.

Responses to shadow silhouettes of the head

Shadow (silhouette) stimuli were used to examine whether STS neurons were capable of responding selectively to head views on the basis of outline information. For five cells the pattern of responses to different head views under normal lighting was compared to that obtained under silhouette lighting. Two cells failed to respond to silhouette versions of the preferred head view. The three

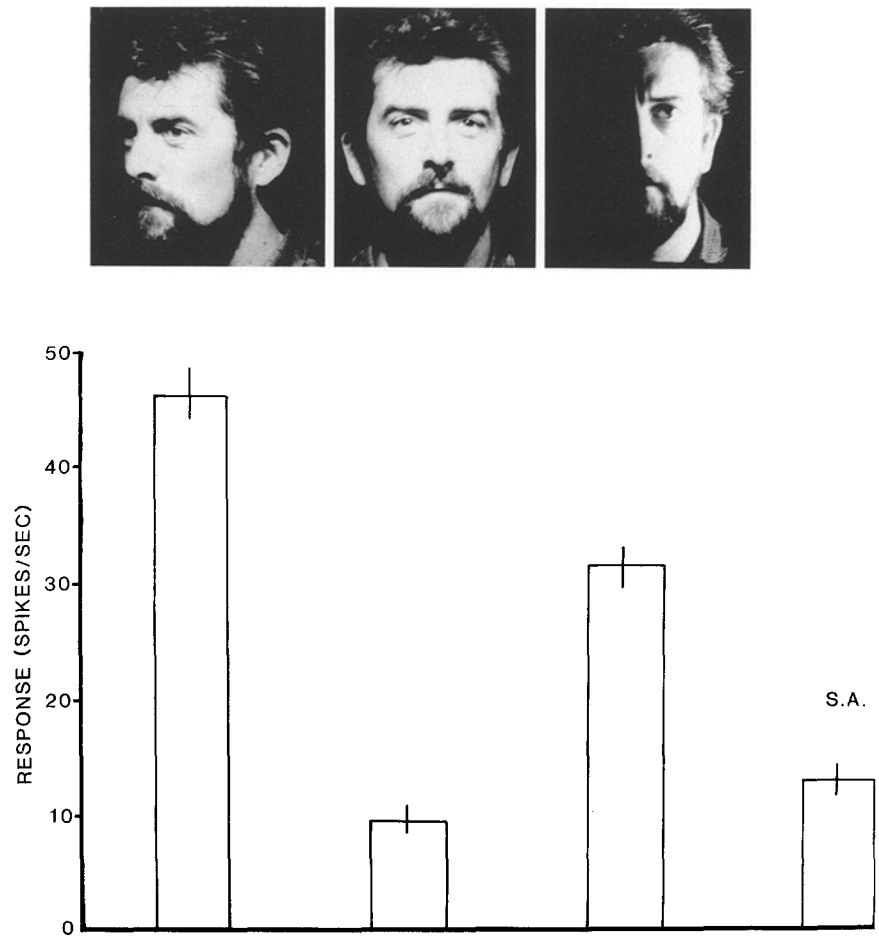


Fig. 7. Lighting altering response to a non-preferred view. *Upper:* examples of stimuli used. *Lower:* mean responses (+/− 1 SE) of one cell (D32 28.95) to the face and half profile views. The responses to the left half profile were significantly stronger than to the full face lit from the front or side and spontaneous activity ($p<0.003$, each comparison). For the non-preferred face view, lighting from the left side elevated response above spontaneous activity and the response to front lighting ($p<0.001$, each comparison). Response to the side lit face may have been due to certain visual similarities to the preferred half profile view. [Overall effect of conditions, 1-way ANOVA $F_{3.35}=25.5$, $p<0.001$]

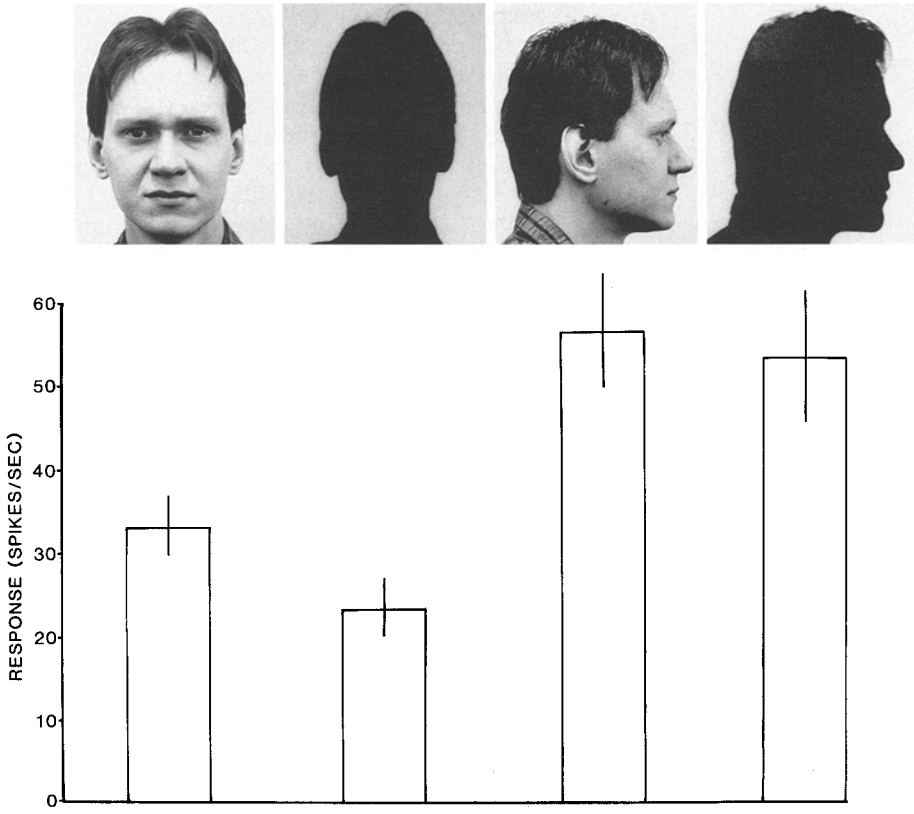


Fig. 8. Similar view discrimination for normal and shadow stimuli. *Upper:* examples of stimuli used. *Lower:* Mean response (+/− 1 SE) of one cell to two views of the head tested under normal lighting and with stimuli viewed as shadows (silhouettes). 2-way ANOVA showed significantly stronger responses to the profile than to the face view ($F_{1,20}=12.7$, $p=0.002$) but no effect of lighting mode (normal vs shadows, $F_{1,20}=0.3$, $p=0.58$) and no interaction between view and lighting ($F_{1,20}=0.5$, $p=0.48$)

other cells tested showed the same pattern of view preference for silhouettes and heads shown in normal lighting.

Figure 8 presents responses of one cell. For this cell testing under normal lighting showed a clear preference for the right profile view of the head. In Fig. 8 the responses to the preferred (right profile) and non-preferred (front) face views of the head are compared for normal and silhouette lighting. 2-way ANOVA with lighting condition (normal/silhouette) and head view (preferred/non-preferred) as main factors showed no main effect of lighting ($F_{1,20}=0.3$, $p>0.5$) but a significant effect of head view ($F_{1,20}=12.7$, $p=0.002$) with no significant interaction between view and lighting ($F_{1,20}=0.5$, $p>0.4$).

Eye movements

Eye position was recorded to exclude the possibility that observed differences in cell responses could have been caused by differences in fixation patterns during stimulus presentation. Eye movement recording indicated that the monkey fixated (and probably therefore attended to) the vast majority of presented stimuli. The small variations in fixation pattern across trials was not observed to correlate with cell activity for any of the recorded cells. Figure 9 shows eye movements and activity of one cell tested with left and right profile views under unusual (top) lighting. The cell responded clearly to the right profile of a head whereas the left profile of the head did not activate the cell. There was some variation in the eye position across trials but this variation was similar for both stimuli and cannot therefore account for differences in response to the two views.

Location of cells

Histological reconstruction of the positions of cells recorded in monkey D indicated that the majority of cells responsive to faces and other views of the head were located in the cortex of the upper bank of the superior temporal sulcus (areas TPO and PGa of Seltzer and Pandya 1978). The proportion of cells found selectively responsive to the head was 54/1,397. In subject D histological reconstruction confirmed that the subset of neurons responsive to head views that were additionally tested under different lighting conditions were all located in the anterior, upper bank of the STS cortex between 11.5 and 18 mm anterior to the interaural plane. Figure 10 shows the recording area and illustrates the position of four cells found to generalize response across unusual lighting.

X-ray measurements of recording positions in two other monkeys (H and J) confirmed that cells examined in the lighting experiments from these subjects were also located within this same area. Thus the cells described here were in the same location as those responsive to the face and other views of head that have been described in earlier studies (Perrett et al. 1982, 1984, 1991a).

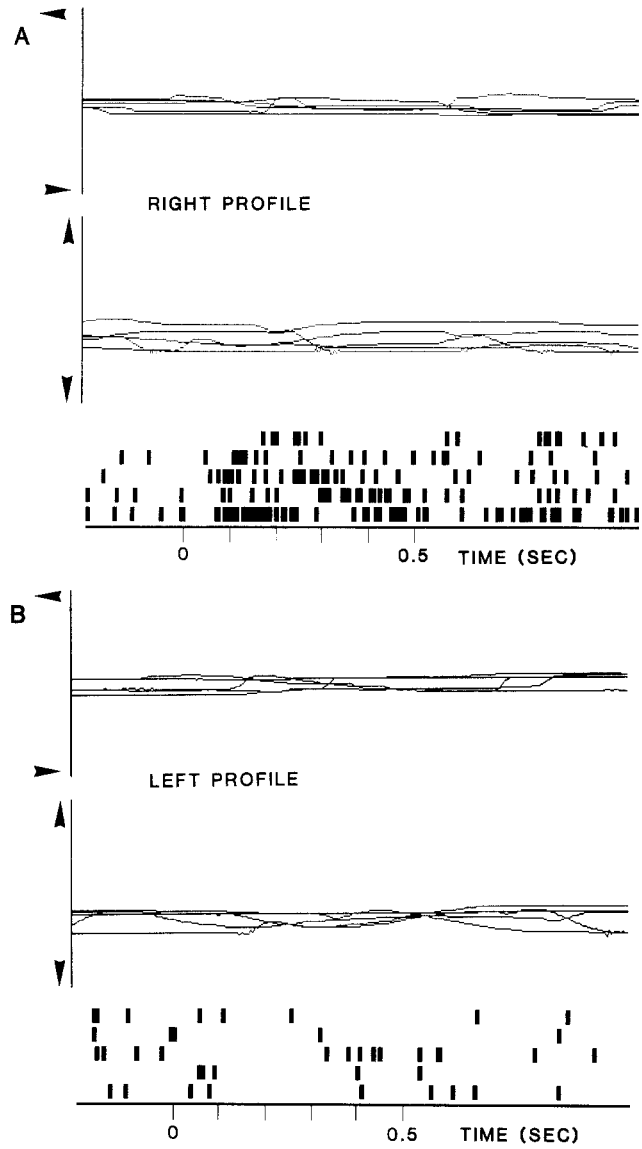


Fig. 9. Discrimination between profile views under unusual lighting. The activity of one cell (J52 25.45) is illustrated to left and right profile head views illuminated from above *(top lighting)* with simultaneous records of eye position. Eye movement traces display horizontal and vertical eye position simultaneously recorded on 5 trials while the right profile *(upper)* and left profile *(lower)* views were presented. Time relative to the presentation of video images of the stimuli is indicated at the base. The cell was consistently more responsive to the right profile than to the left profile view. Eye position recording indicates that the monkey fixated both stimuli though with some variation in eye position across trials. Since the variation in eye position was similar for the two views the discrimination in neuronal responses cannot be attributed to differences in eye movements

Discussion

Response generalization and discrimination

It has been shown here that cells in the STS selective for head views generalize response across different lighting conditions where harsh shadows are cast across the features of the face. The cells continued to discriminate the visual appearance of the head from control objects and even discriminated between different views of the same head, across a range of lighting conditions.

Generalization was evident in the responses of individual cells though, for some, generalization was incomplete with individual cells failing to respond to the preferred stimulus under particular lighting conditions. Our results showed that for most cells there were no differences in the responses to lighting conditions which elicited responses above spontaneous activity. Of course more extensive testing with a greater number of trials might well have revealed subtle but significant differences in response rates of individual cells to different lighting conditions.

Generalization across lighting conditions was complete, however, when the sample of 21 cells were considered together as population. Indeed it should be noted that more or less perfect generalization was exhibited by even a small sample of 8 or 9 cells (see Figs. 4 and 6).

The constancy of response across different lighting conditions parallels the constancy of STS cell response across transformation of stimulus position, size, orientation and contrast (Bruce et al. 1981; Desimone et al. 1984; Perrett et al. 1982, 1984, 1985, 1988). The findings here of the lack of effect of lighting direction are complementary to those of Rolls and Baylis (1986) who report that contrast has little effect on cell responses to faces in the temporal cortex. Considered as a population, the magnitude of cell responses to faces dropped by only 50% when the contrast was decreased by 80% from that typical of a normal lit face (Fig. 4b, Rolls and Baylis 1986). Tolerance of a wide range of stimulus contrast appears to be established at and maintained from early stages of visual processing, with the responses of cells in the temporal cortex and in the primary visual cortex both increasing approximately linearly as a function of the log of stimulus contrast (Tolhurst et al. 1981; Rolls and Baylis 1986).

It should be noted that of course humans can normally recognize objects under a wide variety of lighting conditions. They are not led astray by variation in luminance or manipulations of shade (Todd and Mingolla 1983; Cavanagh and Leclerc 1989). Similarly the behavioural responses of macaque monkeys have also been found to generalize across different lighting conditions (Dittrich 1990). In that study the animals discriminated different facial expressions correctly independent of the luminance.

Lighting and face detection in the natural environment

The generalization across lighting provides evidence on the question of whether the "alleged face cells *are* truly selective for faces?" (Desimone 1991). The shadows across the face (and other views of the head) undergo an enormous change in shape and appearance with the different lighting conditions used here. Yet because of the very high contrast used virtually all of the information about the underlying structure of the face/head was defined by the shape of the shadows.

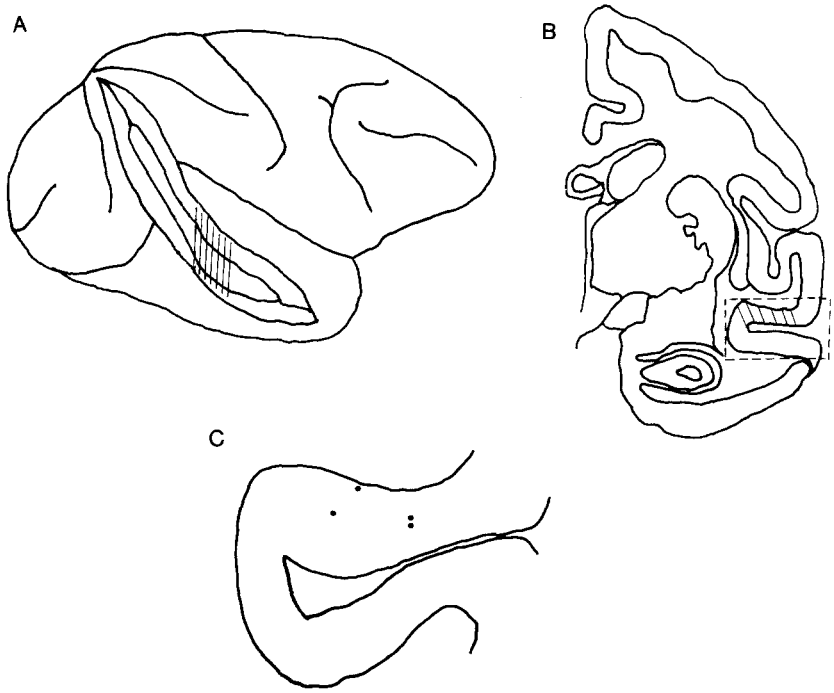


Fig. 10. Location of cells exhibiting lighting constancy. **A** Schematic drawing of a sagittal view of a rhesus macaque brain showing the position of recordings (cross-hatching) within the superior temporal sulcus (STS). **B** A coronal section of the right hemisphere with a box around the STS (9 mm anterior to the interaural plane). **C** An enlarged coronal view section (12 mm anterior to the interaural plane) of the STS in the right hemisphere of one monkey. The circles mark the position of four cells selectively responsive to the sight of the head and showing tolerance of different lighting conditions

It is difficult, if not impossible, to think of any simple visual feature (e.g. dark elongated blob) that would be found in each of the lighting conditions evoking large responses from one cell and absent from stimuli failing to activate responses in the same cell. Instead it is more parsimonious to assume that the cell responses reflect activation by several different patterns which have (through experience) come to be associated with a particular perspective view of the face or head.

Two possibilities could account for the selectivity exhibited by the cells across the lighting conditions. First the cells may have been responding to the characteristics of special facial features (such as the concentric pattern of iris and pupils) present at very low contrast levels and totally ignoring the shadow information present at high contrast levels. Alternatively the cells may have utilized the shadow patterns themselves to define the shape of facial features and the 3–D surface of the head. In this sense shadow information may contribute to the recognition process in the STS.

The question of whether shadow information is used by neural mechanisms in the STS as a source of information for face recognition or whether it simply interferes with pattern analysis has to be investigated in further studies. Either way it is clear that the STS cells would continue to function in detecting faces and other views of the head under a wide range of lighting conditions that would be encountered in the natural environment.

Abnormal lighting and facial feature visibility

Abnormal lighting conditions can change the visibility of features on the face. In the extreme conditions of a shadow or silhouette internal facial features are completely absent, though features such as the eye and nose and mouth become part of the external outline in the shadow profile. The incomplete generalization exhibited by some cells across different lighting conditions is interesting because it may reveal the visual information utilized by the cells.

It is known that for some cells presentation of the whole face is not necessary for the response to occur. Such cells may code the presence of a single facial component, e.g. the eyes or mouth (Perrett et al. 1982, 1985). It is quite plausible that for those cells failing to respond to particular lighting conditions the visibility of an essential facial feature was obscured by shadow. In general it might be assumed that cells with poor responses under unusual lighting are selective for internal features and those with good generalization are selective for the outline. Though this is plausible it does not seem to be the case. The two cells which failed to respond to the silhouette (and therefore presumed to respond to internal features) showed good generalization across top, side and bottom lit conditions.

The relationship between the capacity for generalization across different lighting and the sensitivity to individual facial features was not studied systematically but some observations are relevant to this issue. For example the cell illustrated in Fig. 7 was selective for the profile views of the head. Presentation of a full face in normal lighting proved to be ineffective, whereas the same full face view under side lighting succeeded in triggering the response. The cell may have been inhibited by the presence of two eyes or by the vertically symmetrical structure of the face. (Further experiments with chimaeric images composed of two mirror symmetric half profile faces inwardly pointing and joined together at a line passing vertically through the forehead and mouth of each face supported this explanation.) In exceptional circumstances, it appears then that shadows may elevate

response to a non-preferred view perhaps because the shadows obscure features which otherwise inhibit responses.

Shadow and silhouette stimuli

The maintained responses to silhouettes could suggest that the cells were selective only for the general outline of the stimuli and had no selectivity for the internal features. This is unlikely for two reasons. First, the unusual lighting conditions studied here (including side, top and bottom) produced radical modifications to the visible outline of the head (e.g. Figs. 3 and 5). The majority of cells generalized across these unusual lighting conditions despite the change in outline. The cells, therefore, could not be selective for some simple outline. If outline information was being utilized then the processing would require sensitivity to a variety of outlines consistent with a cell's preferred head view (as well as discrimination against a variety of outlines consistent with other head views). Second, while outline stimuli were not extensively tested, 40% of the cells examined failed to generalize to outlines of the preferred views.

Thus, whilst some cells are able to utilize the visual information about head view that is specified in the outline, it would seem that the use of outline is quite complex given its changing appearance across different lighting conditions. At least 40% of cells are insensitive to outline and presumably utilize information exclusively from the structure of internal features. The division between external and internal features is perhaps rather arbitrary; in the case of the profile view the outline from a silhouette defines several structures normally thought of as internal features in the frontal or face view.

It is quite probable that many cells utilize both external and internal features of static head views. The use of head silhouettes in studies of cells sensitive to head rotation indicates that the neuronal processing of head motion uses both internal features and outline. Many of the cells selective for head rotation respond to the rotation of both real and shadow head stimuli, though the directional selectivity changes between real and shadow rotation (Perrett et al. 1991b). Such a pattern of responses confirms sensitivity to dynamic changes in both outline and internal features.

Perceptual impairments following brain damage in humans

Since cells responsive to the face and other head views in the STS exhibit generalization across different lighting conditions, one would expect lesions in this brain area (or to equivalent neural mechanisms elsewhere) to result in impairments in recognition across changes in lighting. As noted in the Introduction such a failure in lighting constancy has been reported after damage to posterior visual areas in man (Warrington 1982).

The impairment in coping with lighting change in the Benton-Van Allen face matching task that may be exhibited after brain damage can be seen as a "mirror reflection" of the normal capacity of cell populations responsive to faces to generalize across lighting changes. Admittedly the Benton-Van Allen test requires the categorization and matching the identity of faces, whereas the cells we have studied here were not obviously sensitive to identity. Sensitivity to differences between individual faces is, however, exhibited by some 10% of STS cells responsive to the sight of one or more views of the head (Perrett et al. 1984, 1989, 1991a). In general, disruption or disconnection of higher perceptual processes equivalent to those studied in the STS could underlie the failure on face matching tasks that is found in many cases of prosopagnosia and in other clinical conditions.

Even when the performance of prosopagnosic patients on the Benton-Van Allen face matching task is relatively accurate, this does not guarantee that perceptual capacities are normal. Many of the test items can be matched using a strategy of comparing individual features (F. Lhermitte personal communication, 1991). Thus for a given sample item one might spot that the left eye brow or black smudge 1/2 way down the face was the same thickness as that in one of the target items. Such a feature by feature matching strategy is likely to be time consuming and less effective where test items are changed in lighting (e.g., Etcoff et al. 1991; though scores are not usually given for separate types of matching). The strategy could in principle be used even when the images are seen as patterns rather than meaningful faces. One would predict that "feature matching" would not be adversely affected by inversion of match and test items (cf. Ockleford et al. 1977). By contrast, this transform should impair matching for subjects using a normal "face matching" strategy since inversion impairs the ease of perception of faces and their features (e.g. Campbell et al. 1990).

The responses exhibited by STS that are described here indicate a high level of perceptual constancy. This would link the brain mechanisms to the perceptual side of processing. Yet in the same brain area and even amongst the same type of cell, it is often possible to detect effects of experience and memory for faces (Baylis et al. 1985; Yamane et al. 1988; Perrett et al. 1984, 1989, 1991a). Given this involvement of the neural populations in both perceptual and mnemonic aspects of face processing, it may be wrong to attempt to characterize the deficits underlying prosopagnosia as being exclusively perceptual or exclusively mnemonic.

Lesions in association cortex of the macaque

Weiskrantz and Saunders (1984) showed that monkeys with lesions in the inferotemporal cortex and the foveal prestriate region were impaired in object identification tasks when the objects were subjected to changes in lighting and shadows. The inferotemporal cortex has repeatedly been shown to be essential for normal object recognition in monkeys (Gross 1973; Dean 1976; Mishkin et al. 1983). As Weiskrantz and Saunders (1984) suggest, the inferotemporal cortex may be a processing

stage where high level "prototype" descriptions of objects are formed and stored. The destruction of prototypes by lesion to the inferior temporal cortex would deny generalization of object recognition across viewing conditions including changes in lighting.

Surprisingly, Weiskrantz and Saunders (1984) found no deficits with transformed objects after lesions to the posterior parts of the superior temporal sulcus. The lack of impairment may have been due to several reasons two of which are considered here.

(1) The STS lesions were posterior to the regions containing cells exhibiting constancy across viewing conditions. The lesions extended rostrally 9 to 12 mm to the junction of the Sylvian fissure and STS (corresponding to a level 2–5 mm anterior from the interaural plane). The STS cells responsive to faces described here were located at least 6.5 mm more anterior along the STS.

(2) The STS may contain descriptions of prototypes for faces and other biologically important stimuli but may not hold prototypes for arbitrary objects. These may instead be held in the inferotemporal cortex or in more anterior regions of the temporal lobe (Miyashita 1990). A lesion to the anterior STS may impair face matching across lighting change but not necessarily object matching.

This last prediction may be compromised by the findings of cells responsive to faces in areas projecting to the STS; most notably in the inferotemporal cortex (Rolls and Baylis 1986; Yamane et al. 1989; Tanaka 1990 personal communication). Therefore lesions restricted to the STS may not prevent matching of faces across unusual lighting because matching could rely on earlier face processing stages left intact after STS lesion. It remains to be seen whether these cells show the same degree of lighting constancy as the cells considered here.

Computational models of recognition

Most computational models of visual processing present general purpose solutions. Thus Marr and Nishihara (1978) suggested that any object is recognized by linking the object's visible surfaces (in a "2.5–D sketch") to a stored structural description (3–D model) of the object covering all possible vantage points from which the object might be seen. In a similar vein, algorithms for retrieving an object's structure from rigid motion (Ullman 1979) or even non-rigid biological motion (Johansson 1973) present general purpose solutions covering all possible object shapes undergoing all possible types of motion. General purpose solutions have also been proposed for defining surface structure from shading (Horn 1975).

One theme that is recurrent in the properties of neural mechanisms underlying the recognition of biologically important objects is the extent to which the brain's analysis is view-specific. It is true that some cells behave as might be predicted from the properties of Marr's 3–D (object-centred) descriptions of objects (Perrett et al. 1985, 1991a; Hasselmo et al. 1989). However, the vast majority of cells that are responsive to static visual information about the head and other parts of the body, are selective for perspective view (Perrett et al. 1984, 1985, 1991a). Similarly in the motion domain, neural sensitivity to the structural form of the body defined by rigid translation or by biological motion appears to be computed in a view-specific manner (Perrett et al. 1990a, b).

We have found here that tolerance to different lighting conditions appears again to be established in a view-specific manner. That is, cells may tolerate dramatic modifications to the direction and strength of illumination but can be rendered inoperative by modest changes in perspective view (e.g rotation of the head by 45 degrees as in Fig. 6).

As noted above, the cells studied here may well have used the shadow information to compute the underlying surface structure of the head. If this was so then the computation of surface structure must be regarded as view-specific. The general principle that is emerging from the properties of cells in the STS cortex is that the operations underlying recognition of objects are generally conducted in a view-specific framework. *Lighting constancy* appears to be established by matching the image of an object to neural mechanisms that compute object structure from a limited range of perspective views but tolerate or utilize a wide variety of shadows.

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