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Object-centered encoding by face-selective neurons in the cortex in the superior temporal sulcus of the monkey

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Summary. Neurophysiological studies have shown that some neurons in the cortex in the superior temporal sulcus and in the inferior temporal cortex respond to faces. To determine if some face responsive neurons encode stimuli in an object-centered coordinate system rather than a viewer-centered coordinate system, a large number of neurons were tested for sensitivity to head movement in 3 macaque monkeys. Ten neurons responded only when a head undergoing rotatory movements was shown. All of these responded to a particular movement independently of the orientation of the moving head in relation to the viewer, maintaining specificity even when the moving head was inverted or shown from the back, thereby reversing viewer-centered movement vectors. This was taken as evidence that the movement was encoded in object-centered coordinates. In tests of whether there are neurons in this area which respond differently to the faces of different individuals relatively independently of viewing angle, it was found that a further 18 neurons responded more to one static face than another across different views. However, for 16 of these 18 cells there was still some modulation of the neuronal response with viewing angle. These 16 neurons thus did not respond perfectly in relation to the object shown independently of viewing angle, and may represent an intermediate stage between a viewer-centered and an object-centered representation. In the same area as these neurons, other cells were found which responded on the basis of viewer-centered coordinates. These neurophysiological findings provide evidence that some neurons in the inferior temporal visual cortex respond to faces (or heads) on the basis of object-centered coordinates, and that others have responses which are intermediate between object-centered and viewer-centered representations. The results are consistent with the hypothesis that object-centered representations are built in the inferior temporal visual cortex.

Key words: Inferior temporal visual cortex – Face – Visual encoding – Object-centered representation

Introduction

The visual image of an object varies with its distance and the angle at which it is observed by the viewer. The use of such a viewer-centered coordinate system for the representation of objects in the visual system requires the storage of a separate representation for each different angle of view. This is a highly inefficient method of storage (Marr and Nishihara 1978). In contrast, an object-based representation would be more efficient, for then only a single representation need be stored. This representation in object-centered coordinates provides independence from the angle of viewing. A further advantage of an object-centered representation is that when an association is made to an event in another modality, such as a taste, then it is an advantage to have only one, view-independent, representation. If there were multiple, view-dependent, representations, then not only would multiple associations have to be stored, but also there would be no guarantee that when an association was made to one view, there would be any association at all made to another view, so that inconsistent behavior would result.

Some cortical lesions in humans may impair the matching of particular viewer-centered images with

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an object-centered representation. In a recognition test of common prototypical views of objects and unusual views (Warrington and Taylor 1978), right posterior cerebral cortical lesions caused a deficit on the identification of unusual views of objects and the matching of unusual views with prototypical views. Right posterior lesions also cause deficits on matching parts of faces with whole faces (DeRenzi et al. 1968) and on the matching of faces of the same identity photographed with different orientations or lighting conditions (Benton and Van Allen 1968). This is dissociated from the syndrome of prosopagnosia, in which matching different views of unfamiliar faces is not necessarily impaired (Benton and Van Allen 1972; Malone et al. 1982).

These impairments may be due to damage to a system involving regions homologous with the inferior temporal visual cortex in monkeys. Lesions of the inferior temporal cortex may cause impairments in size constancy (Mishkin and Hall 1955; Humphrey and Weiskrantz 1969; Ungerleider et al. 1977). Inferior temporal cortex lesions impair the discrimination of objects transformed by size, orientation, or shadow configuration after learning in untransformed mode (Weiskrantz and Saunders 1984). From these results, Weiskrantz and Saunders (1984) hypothesized that anterior portions of the inferior temporal cortex were involved in storing the prototype of a visual object.

Some neurons in the inferior temporal cortex and in the cortex in the superior temporal sulcus respond with selectivity to faces (Perrett et al. 1982; Baylis et al. 1985; Rolls 1984, 1989a). The responses of face selective neurons could be in one of three possible coordinate systems: retinal, viewer-centered or object-centered. Many neurons in this region have responses which are relatively independent of viewing distance and size, so that the neurons do not respond to the basis of retinal coordinates (Rolls and Baylis 1986; Desimone et al. 1984; Bruce et al. 1981; Gross et al. 1985). This leaves as alternatives the possibilities that these neurons respond on the basis of viewer-centered or object-centered coordinates.

One way in which the coordinate system used by neurons in this region were investigated was by analyzing the responses of neurons in this region which respond only to face or body movements. Of 105 such neurons analyzed in the cortex in the superior temporal sulcus 45 responded specifically to movements towards or away from the viewing monkey (Perrett et al. 1985a; Jeeves et al. 1983), so that the responses of these neurons were in viewer-centered co-ordinates. However, a further, smaller group of 24 cells responded when the viewed monkey's head rotated about one of its axes. In the first experiment described here we investigated whether the responses of these latter neurons were in viewer-centered or object-centered coordinates by inverting the stimulus head, which reversed the viewer-centered movements but did not alter the movements described in object-centered coordinates. We found that the neurons' responses reflected the object-based and not the viewer-based description of the movements.

In a second experiment, we investigated whether there are neurons in this region which respond differently to the faces of different individuals irrespective of the viewing angle. Although many cells in this region do respond differently to different views of the same individual (Perrett et al. 1985b), so that their responses are in a viewer-centered coordinate system, some cells appear to respond consistently on the basis of the identity of the face and independently of the angle of view (Perrett et al. 1984). To test systematically for such object-centered encoding of identity across different angles of view, the second experiment described below was performed.

Methods

The activity of single neurons was recorded with glass-insulated tungsten microelectrodes (after Merrill and Ainsworth 1972, but without the platinum plating) in 3 alert macaque monkeys (1 Macaca mulatta, weight 6.5 kg, and 2 Macaca fascicularis, weights 3.5 and 4.5 kg) seated in a primate chair using techniques that have been described previously (Rolls et al. 1976). The action potentials of single cells were amplified using techniques described previously (Rolls et al. 1979), were converted into digital pulses using the trigger circuit of an oscilloscope, and were analyzed on-line using a Microvax 2 computer.

X-radiographs were used to locate the position of the microelectrode on each recording track relative to permanently implanted reference electrodes and bony landmarks (Aggleton and Passingham 1981). These measurements were made in the standard stereotaxic plane and expressed relative to the posterior wing of the sphenoid bone, which is 18–23 mm anterior (in different sizes of monkey) to the standard anterior-posterior reference. The positions of cells were reconstructed from the X-ray coordinates taken together with serial 50 μ histological sections which showed the reference electrodes and micro-lesions made at the end of some of the microelectrode tracks.

Experiment one – the coordinate system of head-movement selective neurons

Procedure

Neurons were tested on a set of head movements performed by one of the experimenters behind a 6 cm aperture (12 deg of viewing angle) in the screen which surrounded the monkey. The experimenter was at a distance of 1 m from the monkey, and the face expression was neutral. These movements included ventral flexion and dorsal flexion (of the neck), and counterclockwise and

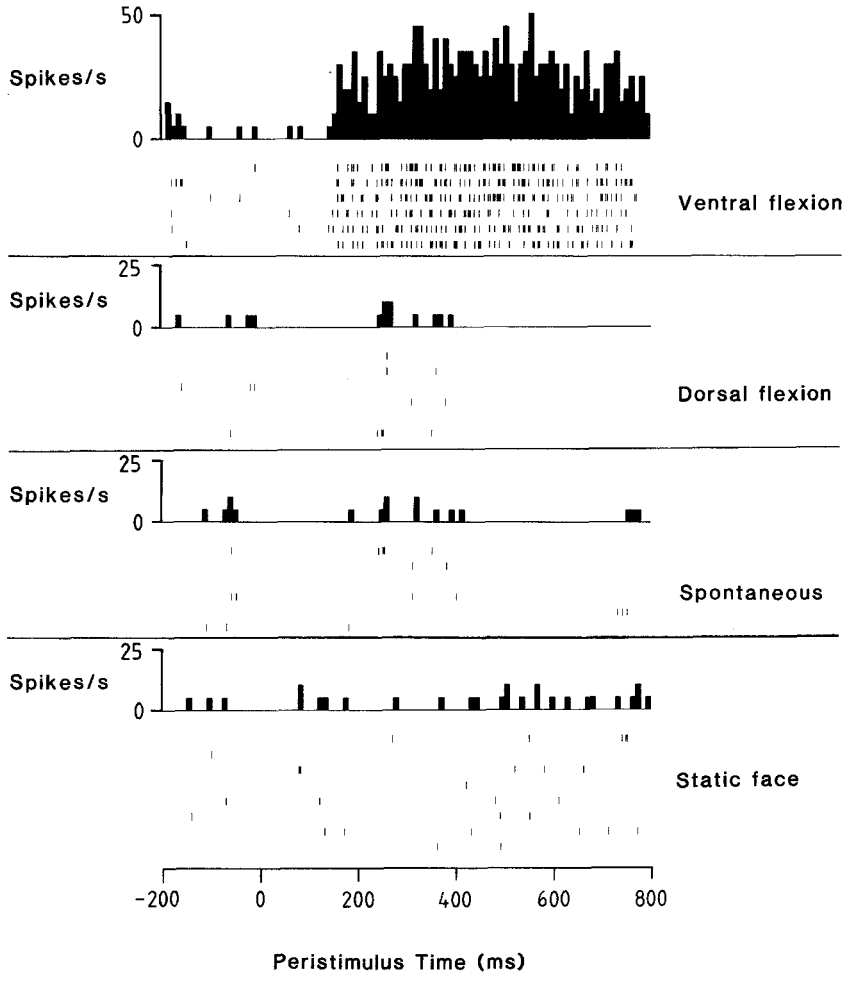

Fig. 1. Examples of the responses of one head-movement selective neuron (II1176) to some of the stimuli: ventral and dorsal flexion of a head presented through the shutter, and static faces presented on a video monitor. The spontaneous activity during presentations during which the shutter was opened with no stimulus visible is also shown. Six or 7 peristimulus time rastergrams and a peristimulus time histogram are shown for each stimulus. The onset of the visual stimulus was at time 0. The bin width was 10 ms. The means and the standard errors of the responses are shown in this and subsequent figures

clockwise anisomorphic rotation of the head. The angle of the movements was approximately 90 deg made in 1.5 s. If a neuron showed signs of responsiveness, the response was tested quantitatively using a running count, which computed the number of spikes per second during a period triggered manually, which started at the onset of the movement, and ended before the movement ended. The cells were tested extensively on a set of different head movements to determine the preferred orientation of movement and the consistency of response. Once the preferred orientation of movement was determined, the cell was tested for invariance. The preferred head movement, and the opposite direction of movement (which typically produced little response) were tested with a wide range of reference (mid) point orientations. The orientation conditions listed for the various tests indicate the orientation of the head at the mid point of the movement. The movements with the real head in different orientations were made by bending the body, and for images on the screen were made by rotating the video monitor. The opposite direction of movement provided a control which represented the same series of image states with a different transition sequence. If the cell had any specificity for a particular image configuration passed through in the movement, it would respond equally well during the opposite movement. The head movements consisted of rotations through approximately 90 deg in the azimuth or sagittal planes with the following midpoint orientations:

1. front view of upright face,
2. front view of face rotated 90° isomorphically (i.e. sideways),
3. front view of face rotated 180° isomorphically (i.e. upside down, sometimes described as inverted for clarity),
4. side view of face (left profile or right profile),
5. back view of head.

Isomorphic and anisomorphic orientation changes could be combined, so that additional conditions, such as inverted profile, could be tested. Cells responding to movement were tested on up to sixteen conditions, with the order of presentation either randomized or systematically balanced.

Where possible, further tests of invariance were performed, including the presentation of more than one identity of face for the movement, the presentation of 3-D models of heads, and presentation of movements at different distances. A video recording of head movements was used to test if the cells would respond to movements represented in two dimensions.

In addition to a standard set of control non-stimuli such as gratings and complex non-face images which were tested with all cells (Baylis et al. 1985), the cells were also tested with moving control stimuli of the type which elicited responses from some cells in previous studies (Perrett et al. 1985a). These included vertical and horizontal translation in both directions, looming, appearance and disappearance, and isomorphic rotation of a head. Also, a wide range of body and object movements were tested, to ensure

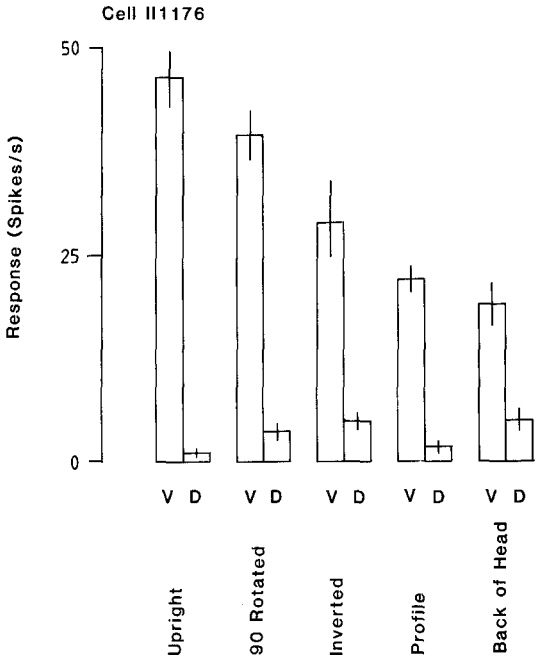

Fig. 2. The responses of neuron II1176 showing selectivity for ventral flexion of a head across a wide range of cases, tested in upright, inverted and other midpoint orientations. These responses were maintained across different individuals. V = ventral flexion; D = dorsal flexion

object specificity. Unless stated otherwise, these control movements and stimuli did not cause a significant change from the baseline firing-rate.

The results were analyzed with a two-way analysis of variance which compared the response to the preferred direction of movement with its opposite over a wide range of treatments.

Results

1865 neurons in the cortex in the superior temporal sulcus and in the inferior temporal cortex were tested on the preliminary set of head rotations. A total of 12 neurons in three monkeys was found to respond selectively to anisomorphic rotation of the head, of which 10 were tested on a wide range of different starting orientations. Four cells responded selectively to ventral flexion, 5 cells to dorsal flexion, 2 cells to counterclockwise anisomorphic rotation, and 1 cell to clockwise anisomorphic rotation. None of these neurons responded to any stationary stimuli. The testing procedure was biased toward finding rotation sensitive neurons, but 5 other cells with sensitivity to head movements were found. Two of these responded to movements which involved turning away from the monkey, 1 responded to movement of a face into view, 1 responded to upward translation, and 1 responded to leftward translation (relative to the stimulus head). The last neuron was tested on three isomorphic rotations.

Thirteen other neurons were found which responded only to moving visual stimuli, but these neurons were not selective for heads as the moving object. Of these, 3 responded to translation in all directions, 1 responded to leftward translation, and 2 responded to horizontal translation, 3 responded to the movement into view of heads and other objects, 3 responded to looming stimuli, and 1 responded to general visual movement. Neurons responsive to head movements were often located very close to neurons responding better to particular static views of the head, though the view in which the neighboring neuron responded did not necessarily correspond to the specificity of the movement selective neuron. For example, neuron II1176 was located close to cells responsive to a profile view. This proximity of head-movement selective neurons to static head view selective neurons has been noted previously (Perrett et al. 1985a).

The responses of a neuron (II1176) which responded selectively to a ventral flexion movement of a head are illustrated in Fig. 1. The peristimulus time histograms and rastergrams illustrate responses to head movements presented through a shutter, and to video images of static faces. The strong selectivity illustrated was characteristic of the neuronal responses of the neurons described here. The low spontaneous activity of the neuron was typical.

The mean responses of neuron II1176 to head movements performed in different orientations are illustrated in Fig. 2. The response was invariant across isomorphic and anisomorphic transforms. The neuron responded vigorously to ventral flexion whether the head was viewed full face, inverted, in profile, or seen from behind. It may be emphasised that inversion reverses the direction of movement on the retina, but leaves the object-centered description of the movement unchanged. Thus, this neuron responded similarly to head movements producing opposite directions of movement with respect to the viewer.

The results of two-way ANOVAs on the 10 rotation sensitive neurons and the one translation sensitive neuron tested on a wide range of starting orientations are summarized in Table 1. For each cell, the movement preference, the number of orientations tested, and the group F and p values are listed. The second experiment shown for cell QQ018 (QQ018v) was performed with video images. All 10 neurons had a highly significant group effect of direction of rotation (in object-centered coordinates) independently of starting position, indicating that the neuronal response was related to the direction of the

Table 1. Summary of the responses of the neurons described in Experiment 1. The data for each cell include the distance posterior to the sphenoid in mm, the preferred direction of movement (V = ventral flexion, D = dorsal flexion, CC = counterclockwise rotation, L = leftward translation), the number of different reference orientations tested, and the group F value and probability level from a two-way ANOVA of the preferred movement compared to the opposite movement. On the right, the mean firing rates in spikes/s for the preferred (Pr.) and for the opposite (Op.) movement are presented for a selection of orientations: head on view, left profile (L. Prof.), right profile (or 90 isomorphic rotation for the last 6 cells) (RP / 90 rot), back of head view (B.O.H.), and inverted. Cell QQ018 was tested with both real faces and with faces on a video screen (QQ018v)

Cell no.	Loc. A/P	Movement preference	N of orient.	Group F	*P*	Head on Pr.	Head on Or.	L. Prof. Pr.	L. Prof. Or.	RP /90 rot Pr.	RP /90 rot Or.	B.O.H. Pr.	B.O.H. Or.	Inverted Pr.	Inverted Or.
II1176	4.4	V	4	220.4	0.000018	40.0	1.4	21.7	2.2	–	–	17.1	6.2	21.8	5.9
II1246	7.6	D	5	93.3	0.0016	70.0	9.0	59.0	22.0	60.7	12.0	50.3	14.7	70.3	11.0
II1275	3.0	D & CC	4	5.6	0.007	23.3	13.7	15.0	7.7	19.7	11.7	57.0	11.3		
II1296	10.0	D	4	143.5	0.00014	26.5	6.3	33.0	15.3	40.8	6.5	40.8	8.3	–	–
II1361	4.0	V	3	100.9	0.00024	13.6	4.9	13.8	4.7	16.2	4.9	–	–	–	–
II1370	5.0	D	3	10.7	0.017	14.2	2.7	21.3	3.6	–	–	17.3	3.2	–	–
NN0521	4.0	V	8	215.1	0.0007	64.7	15.0	41.3	5.8	73.3	4.0	61.8	-2.0	54.3	2.5
NN0756	6.8	CC	16	2382.1	0.000001	51.5	4.3	58.0	0.3	53.0	3.5	42.0	-0.3	41.3	8.5
QQ0178	2.6	D	4	11.0	0.0012	13.4	2.3	6.8	3.4	10.0	1.0	–	–	9.0	2.0
QQ018	2.4	V	5	14.9	0.0050	35.8	15.9	49.8	25.3	25.6	18.1	36.6	17.5	43.4	28.3
QQ018v	2.4	V	3	19.5	0.00083	13.2	5.5	–	–	15.4	9.5	–	–	11.3	6.6
QQ0614	6.5	L	4	19.5	0.00018	23.5	4.8	–	–	17.5	4.0	15.8	4.0	–	–

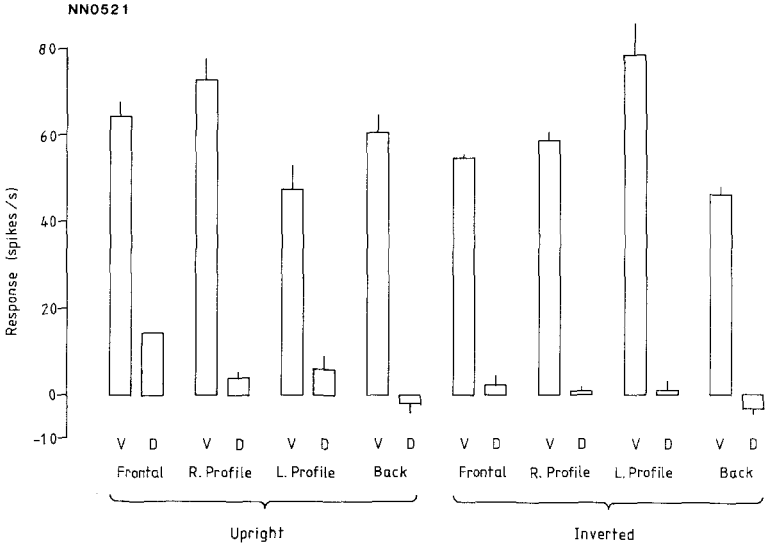

Fig. 3. A neuron (NN0521) responsive to ventral flexion (V) versus dorsal flexion (D) tested across a wide range of treatments. These include full-frontal view, right and left profile, and back of the head, in both upright and inverted conditions

movement about the object's axis, and not with respect to the view plane. The single neuron which responded to leftward translation showed this response consistently for object-centered encoding across the three isomorphic rotations, indicating that its responses reflected object-centered coordinates when information was available from only two dimensions of space. Six of the rotation sensitive neurons were tested for whether the movement specificity was maintained across inversion. All of these neurons responded to their specific movement whether the head was upright or inverted. Four out of 4 neurons tested generalized across different heads performing the same movements. The mean responses of the neurons to the preferred movement and the opposite movement are shown in Table 1 for some of the orientations tested.

The responses of neuron NN0521 are illustrated in Fig. 3. Data from this neuron were tested with a three-way ANOVA. Ventral and dorsal flexion were tested across four anisomorphic conditions of face forward, left profile, right profile, and back of head, in two overall conditions of upright and inverted. Ventral versus dorsal flexion was highly significant ($F(1,3) = 215.1$, $P < 0.001$), and no other effect or interaction approached this level of significance. This

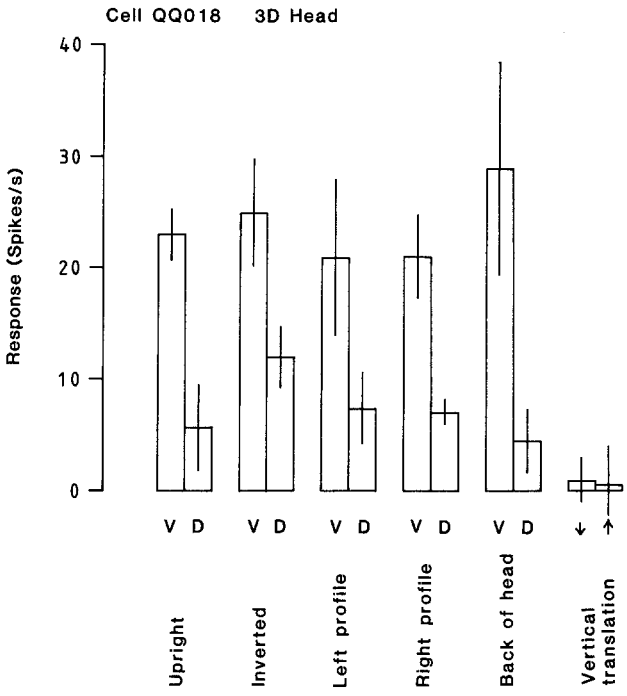

Fig. 4. Responses of a neuron to ventral flexion of the head viewed in 3 dimensions, showing invariance across isomorphic and anisomorphic transforms. The neuron shown here (Cell QQ018) responded vigorously to a head undergoing ventral flexion (V), whether the head was viewed upright, inverted, presented in either profile, or seen from behind. There was little response to dorsal flexion (D), and the response to vertical translation was minimal

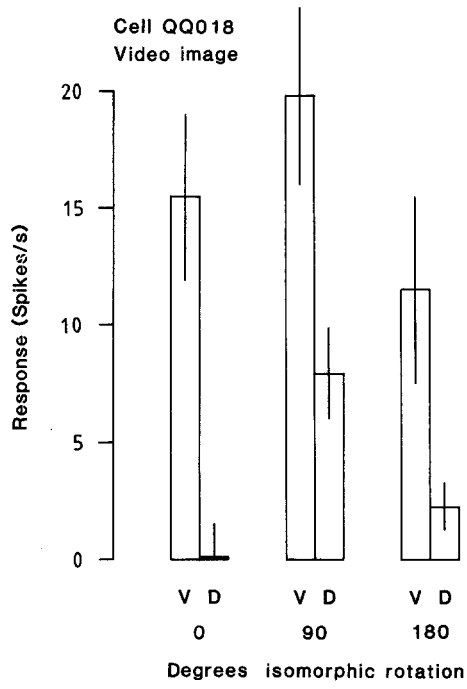

Fig. 5. Responses of the neuron in the previous figure (QQ018) to a video sequence showing ventral flexion of the head. Specificity for ventral flexion (V) versus dorsal flexion (D) was maintained across 90 deg and 180 deg isomorphic rotation

neuron showed no response at all to hand and brush rotations, or to hand and face translational movements.

The mean responses of a neuron (QQ018) with selectivity for ventral flexion of the head are illustrated in Fig. 4. The neuron responded vigorously to ventral flexion whether the head was viewed full face, inverted, presented in either profile, or seen from behind. The responses to downward and upward vertical translation of the head are also shown. Note that the response to these movements was not significantly different from baseline, as were the responses to other head and body movements. These control conditions were tested on all rotation sensitive neurons, and none showed responses significantly different from baseline.

The responses of this same neuron (QQ018) to video images of head movements are shown in Fig. 5. The individual in the stimulus video tape was different from the individual for which the 3-D head response is illustrated. A strong response to ventral flexion occurred for all cases of isomorphic rotation of the monitor displaying the stimulus video tape. This experiment confirmed that the neuron responded to the movement described in object-based coordinates in a test in which the identical moving image was shown in a range of different orientations with respect to the viewer.

The responses of a neuron (II1296) which responded preferentially to dorsal flexion are illustrated in Fig. 6. Again, the response preference was maintained across all conditions: full-face, left and right profile, and back of the head. The responses to a range of control movements are also illustrated. There was little response to clockwise or counterclockwise anisomorphic rotation of the head. In addition, the rotation response was selective for a face as the moving object, as shown by the lack of response to movements of other objects such as hands or brushes. (One neuron showed responses to rotatory movement which generalized for hands as well as faces.)

Neuron NN0756 responded to counterclockwise anisomorphic rotation as shown in Fig. 7. Upright and inverted conditions were tested for face forward, left profile, back of head, and 90 deg isomorphic rotation. Within each of these categories a leftward and a rightward phase were tested. With regard to each reference position, four different movements were tested:

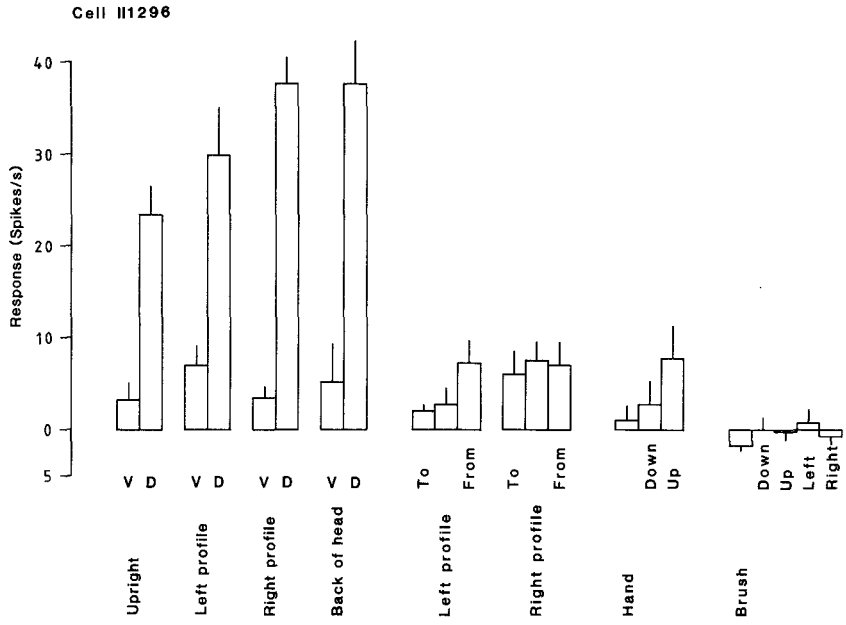

Fig. 6. Selective response of a neuron (II1296) for dorsal flexion (D) versus ventral flexion (V). Included are examples of some of the control movements used. These include movement to and from profile, and translational movements of hands and brushes

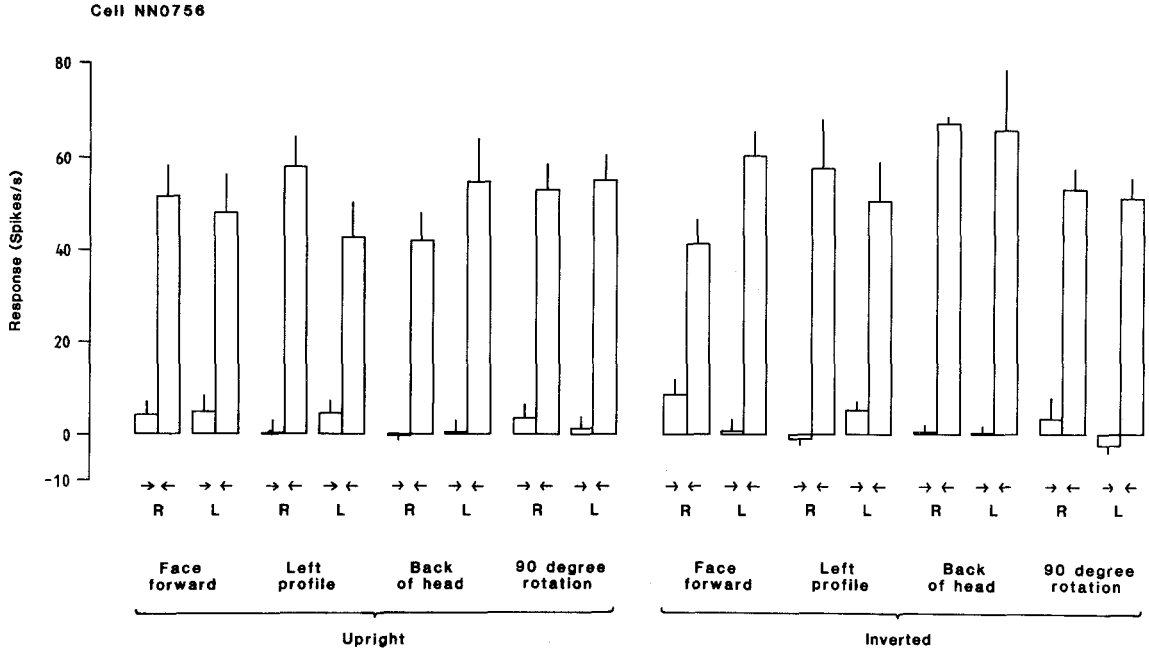

Fig. 7. The responses of a neuron responding to counterclockwise movement of the head (as viewed from above). This neuron (NN0756) was tested across a wide range of cases. Upright and inverted conditions were tested for face forward, left profile, back of the head, and 90 deg isomorphic rotation. Rightward arrows indicate clockwise rotation, and leftward arrows indicate counterclockwise. The sector from which the head rotated to center (full face) is indicated by R or L (see text)

Phase	*Direction*	*From*	*To*
Left	Clockwise	L profile	Full face
	Counter c/w	Full face	L profile
Right	Clockwise	Full face	R profile
	Counter c/w	R profile	Full face

In Fig. 7, rightward arrows indicate clockwise rotation, and leftward arrows indicate counterclockwise. The sector from which the head rotated to center (full face) is indicated by R or L. Again, the object centered rotation condition proved highly significant ($F(1,3) = 2382.1$, $P < 0.001$), while all other treatments showed no significance. This cell showed no response to translational head movements, or hand and object rotations.

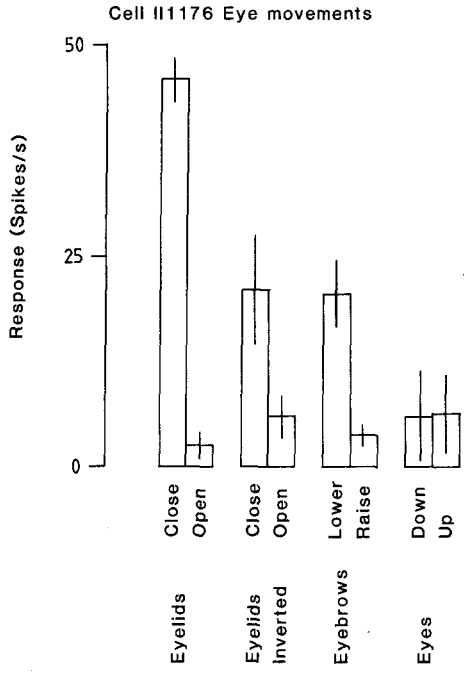

Fig. 8. The responses of neuron II1176 which showed selectivity for closing movements of the eyelids and movement of the brow toward the eye, maintained even when the face was presented in inverted orientation

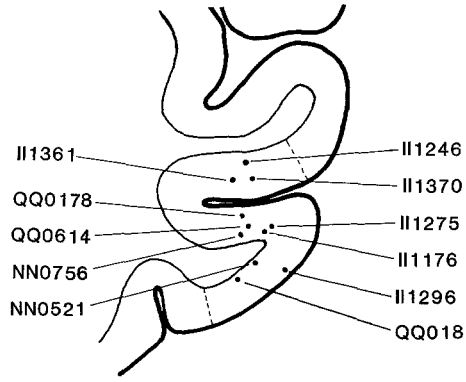

Fig. 9. A schematic representation of the location within the cortex in the superior temporal sulcus of the neurons described in experiment one. The antero-posterior position of each neuron relative to sphenoid is listed in Table 1. The population of neurons studied was located within the cortex lying between the dashed lines

In addition to responding to ventral flexion of the head, cell II1176 (Fig. 2) showed responses to particular movements of the face. These responses are illustrated in Fig. 8. In particular, the neuron responded to downward movement of the eyelids, closing the eyes. It responded (although to a lesser extent) to the closing of the eyes when the face was inverted, and to the lowering of the eyebrows. This response was not related to gaze direction or movement, since there was no difference in response to movements of the eye only. The specificity for both head and eye movements was maintained across several different individuals. The head movement response was not due to the configuration of the eyes only, since it was maintained in conditions where the eyes were not visible, such as profile, back of the head, and even when the head was covered with a sheet. This combination of responses is of interest since the downward eyelid movement and ventral flexion of the head often appear together in behavior. When tested, none of the other cells described above responded to face movements.

One neuron, II1275, showed strong responses to both dorsal flexion and counterclockwise anisomorphic rotation. This dual response preference was maintained across four different reference orientations. Another neuron (QQ0614) showed selectivity for leftward translation in the coronal (transverse) plane of the head. This neuron continued to show a greater response to leftward translation defined in object (head stimulus) coordinates, irrespective of the actual movement relative to the viewer. The orientations of the object in which rotations were tested included 90 and 270 deg isomorphic rotation, which resulted in movements perpendicular to the movement as viewed upright, and anisomorphic rotation to back of head view, which resulted in a movement in the opposite direction from the movement viewed full face.

The distance in mm posterior to the sphenoid is listed in Table 1 for each of the movement sensitive cells reported in the first experiment. Their laterality and depth is represented schematically in Fig. 9, which shows the position of each cell within the cortex in the superior temporal sulcus or in the inferior temporal cortex. The cells are not localized in one region, but appear in all architectonic regions in which face responsive neurons have previously been reported (Baylis et al. 1987). However, as noted previously, these neurons often appeared close to neurons responding to particular static head views.

Experiment two – Neuronal responses to anisomorphic views of different faces

A large number of neurons show face selective responses to static stimuli. To test if these responses reflect encoding in object centered or viewer centered coordinates, a number of cells (37) were tested on faces of different identity presented with different angles of view. The criteria for neurons to be classified as face-selective are described by Rolls (1984, 1989a) and by Baylis et al. (1985).

Procedure

For 9 cells, 3-D faces viewed from different angles were presented through a 6 cm shutter, which opened for 1 s to reveal the stimulus. The computer collected peristimulus rastergrams of neuronal activity for each trial and displayed, printed and stored each trial, as well as computing the peristimulus time histogram by summing trials of a given type. To facilitate latency measurements, the cumulative sum distribution was calculated from the sum peristimulus time histogram. For each trial the number of action potentials occurring in a 500 ms period starting 100 ms after the stimulus onset was printed. This period was chosen because the neurons studied responded to visual stimuli with latencies just greater than 100 ms, and the monkeys consistently fixated the stimuli for this period. Fixation of the stimuli was confirmed using permanently implanted silver/silver chloride electrodes for electrooculogram recording. The EOG recordings provided eye position with an accuracy of 1–2 deg, and were sampled by the computer every 10 ms and saved with the action potentials for each trial.

As one of the aims of the experiment was to investigate the variation of neuronal response as a function of viewing angle using completely systematic presentation of well defined stimuli, with the monkey's attention held constant across all the stimuli, for the other 28 neurons the face stimuli were digitized with a video framegrabber, stored on disc, and then loaded by the computer into the framestore for display on a video monitor with the order of the presentation of the members of the set of stimuli randomized (see Baylis et al. 1985). The resolution of the images was 256 pixels wide by 256 pixels high with 256 gray levels. The computer randomized the order of presentation of these stimuli, switched the stimuli on and off for each trial, and synchronized its data collection so that the stimulus was turned on at the start of the 21st bin of the 100-bin peristimulus time histogram. Data from trials during which the monkey was not already fixating the screen when the stimulus was switched on or during which eye movements of more that 3 deg occurred in the first 600 ms (while the firing rate was being measured) were rejected.

The monkeys performed a visual discrimination task during the testing to ensure that they looked at the stimuli. If a small (0.5 deg) white circle, the positive discriminative stimulus (S+), appeared the monkeys could lick to obtain a fruit juice reward, and if a small black circle of the same area, the negative discriminative stimulus (S–), appeared the monkey had to withhold licking in order to avoid aversive hypertonic saline. The overall luminance of all the stimuli was kept approximately constant. A 0.5 s signal tone (400 Hz) preceded the presentation of the stimulus, and if the monkey was fixating correctly before the stimulus appeared, he had sufficient time to perform the discrimination and obtain multiple licks of the fruit juice tube in the short (1.0 s) period in which the stimulus was on. The monkey had to be looking at the centre of the screen at the start of each trial if he was to perform correctly with these S+ and S– stimuli. This procedure was designed to ensure fixation of the stimuli. If any stimulus other than the S– appeared (such a grating, or a face), then if the monkey licked he obtained fruit juice. This procedure did result in consistent fixation of the stimuli, in that EOG recording showed that eye movements were unusual in the first 600 ms, and in that the discrimination was performed correctly with the small S+ and S– stimuli. Each stimulus set consisted of 5–21 stimuli, and the stimulus sets were repeated 4–10 times (each time with a new random sequence) so that an ANOVA could be performed on the neuronal responses to the different stimuli.

For 13 of the 28 cells tested with digitized images presented with a video monitor, the stimulus set consisted of 8 different orientations of two different faces. The different angles of view were left profile, 45 deg left, full face, 45 deg right, right profile, upward, downward, and back of head. For the other 15 cells, a very comprehensive set of 21 orientations of each of three different faces was presented on the video monitor. The different angles of view were full face, left profile, back of head, and right profile, and all angles between at intervals of 22.5 deg (i.e. 0, 22.5, 45, 67.5, 90, 112.5, 135 etc.), and upward and downward, at intervals of 22.5 deg.

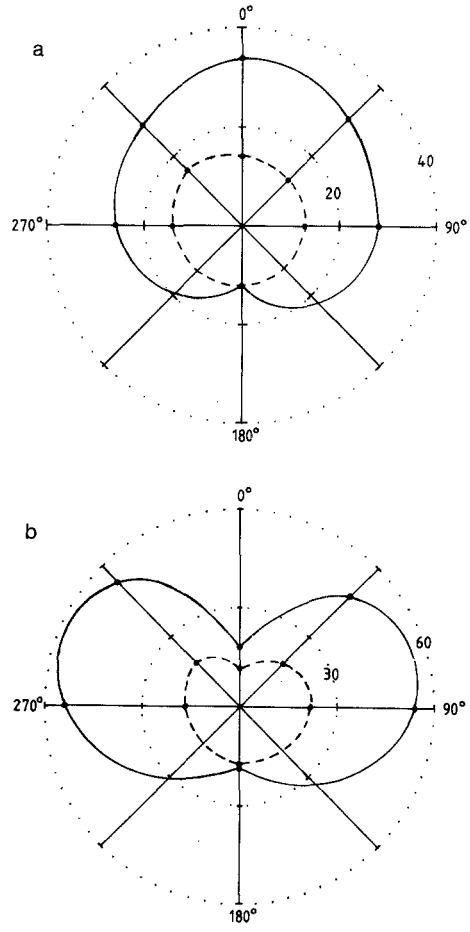

Fig. 10a, b. The responses of two neurons which responded differently to the faces of two individuals irrespective of viewing angle. Responses to two different faces are marked as solid and dashed lines on polar plots which show the viewing angle. Zero degrees is the front of the face, and 90 deg is the left profile of the stimulus face. The firing rate response is shown by the distance from the center of the polar plot, and the calibration circles show spikes/s. **a** This neuron responded consistently differently to two faces across most orientations except for the back of the head. **b** An example of a cell showing consistent differences between individuals with some modulation by viewing angle as well, in that the cell responded better to profile views than to other views

Results

The responses of a neuron showing differences between individuals irrespective of viewing angle are illustrated in Fig. 10a. This figure shows the response of the cell to two different faces (represented as

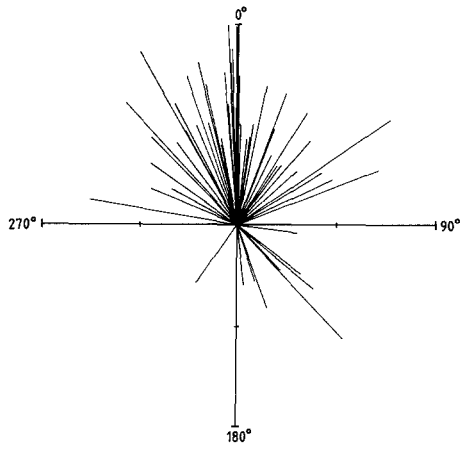

Fig. 11. This polar response plot shows the viewing angle at which the different neurons responded optimally. Each line represents the optimal viewing angle shown by one of the neurons to one face. The length of the vector indicates the sensitivity of the neuron to viewing angle, as described in the text

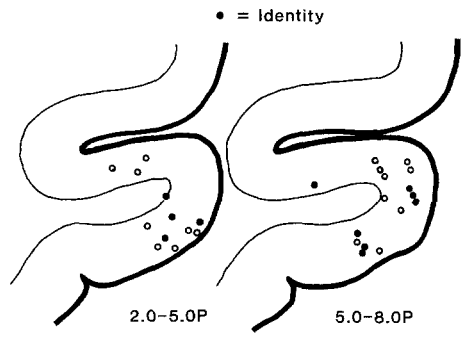

Fig. 12. A schematic representation of the location within the cortex in the superior temporal sulcus of the neurons described in experiment two. The responses of neurons which responded differently to different individuals across anisomorphic transforms are shown for two monkeys by the closed symbols. The open symbols show the recording sites of the other neurons analysed

dashed or solid lines) shown in a variety of stimulus orientations: 45 deg or full profile to right and left, and full face. Note that there is a consistent difference in the response of the neuron to the two faces at all viewing angles. In many cases (16/18 neurons) although identity of the face was reflected in the neuronal response, viewing angle also influenced the response. An example of this is illustrated in Fig. 10b. This neuron (QQ0740) responded more to individual GCB than to MEH, but the difference was more pronounced in profile, three-quarter and upward-looking orientations.

The results were analysed statistically by performing a two-way ANOVA for each cell, with the group factor being the effect of the identity of the face, and the treatment factor being the angle of view. Of the 37 face-selective neurons tested with a full range of orientations, 18 showed selectivity between faces across anisomorphic transforms of the stimulus (i.e. the group factor was significant). Although these neurons did thus distinguish between different faces, there was also for 15/18 of these neurons some modulation of the response of the neurons as a function of the viewing angle (i.e. the treatment factor was significant). Of the 19 neurons which did not show consistent differences of response between different faces, 16 did show significantly different responses to different angles of view (i.e. the treatment but not the group factor was significant).

The orientation (view) of each face to which each neuron responded maximally, and its selectivity for this view, is represented in Fig. 11. This figure shows the orientation specificity as a vector of particular orientation and length. Vector summation of the responses to all different angles of view was used to determine the angle of the orientation specificity vector. The following computation was used:

$$\tan \Phi = \Sigma (\sin \Theta \cdot X) / \Sigma (\cos \Theta \cdot X)$$

Where

Φ = angle of overall orientation specificity
Θ = viewing angle of stimulus n from face forward
X = response to stimulus n at angle Θ in spikes per second

The length of the vector represents how much the neuronal response varied with viewing angle. This was computed in a manner analogous to contrast as follows:

$$\text{vector length} = (X\,\text{max} - X\,\text{min}) / (X\,\text{max} + X\,\text{min})$$

The maximum possible length is thus 1.0, and the minimum is 0. It is shown in Fig. 11 that the different neurons responded best to a wide range of different views. The viewing angles eliciting the best response were not clustered around the forward (full face) and 90 deg (profile orientations) or any other particular viewing angle. However, there were more neurons which responded better if any part of the front of the head rather than the back could be seen, in line with the much greater information present in the front view. Further, it can be seen (from the contrast measure) that although some of the neurons were quite selective for certain views of the effective face stimulus, the majority of the neurons were not sharply tuned to one view, and responded with considerable invariance or generalization with respect to the view from which the face was seen. The cells studied in the second experiment were distrib-

uted throughout the same general regions where the cells reported in the first experiment were found, and their locations are shown in Fig. 12.

Discussion

The results described here provide evidence that there are some neurons in the inferior temporal cortex and the cortex in the superior temporal sulcus which represent information in object-centered coordinates. Strong evidence for this comes from the 6 neurons (including neurons QQ018, NN0521, NN0756, and II1176 illustrated in Figs. 3, 4 and 7) which responded to a particular movement such as ventral flexion of the head even when the head was inverted. The movements relative to retinal or viewer-centered coordinates are reversed by inversion, but the neurons continued to respond to the same movement described in object-centered coordinates. Further evidence described here which is consistent with object-centered encoding rather than viewer-centered encoding is that 18 neurons (of 37 analyzed) responded consistently differently to different individuals irrespective of the viewing angle, as shown in Experiment 2. Even though there was some modulation of the neuronal responses by viewing angle, these findings show that the responses of some neurons in this region are able to represent information about an object (in this case a person's head) which can generalize across different views of the object and produce a response which reflects primarily which object (face) is being viewed, even though the angles from which the object is viewed vary over a very wide range. These results are consistent with the possibility that view invariant representations are built in the visual system by forming associations between neurons the responses of which are closer to the stimulus in that they reflect both the view and the individual seen (Perrett et al. 1987; Rolls 1987, 1989a, b). There is no evidence from the results shown in Fig. 11 that only a few characteristic views of faces are stored in this system.

These neurons respond to object-centered movement even when the stimulus has only two-dimensional cues. As shown in Fig. 5 neuron QQ018 responded to the same head movement displayed on a video monitor independently of the isomorphic rotation of the video screen. In this case a 3D object-centered representation had to be computed from the 2D video image in order to account for the neuronal response. This controls for the possibility that particular depth cues, or changes in lighting could have accounted for the invariance of response with respect to viewing angle shown to three-dimensional images.

There is of course already considerable evidence that the responses of many neurons in these cortical regions show a number of types of invariance. Thus, many neurons have responses which are relatively independent of the size and contrast of a face (Rolls and Baylis 1986), of the spatial frequencies with which the face is represented (Rolls et al. 1985; Rolls et al. 1987), of its color (Perrett et al. 1982), and of its expression (Hasselmo et al. 1989). One additional point being made here is that the representation for some of the neurons about the identity of the individual is relatively invariant over changes of viewing angle, so that there is a view-independent or object-based description of the stimulus present in the responses of some neurons. Some preliminary evidence for this has been described before (Desimone et al. 1984; Bruce et al. 1981; Gross et al. 1985). A second point being made here is that there is not only an object-based description, but also that the coordinate system used to interpret objects must for some of the neurons described be object-centered coordinates, in that the response remains invariant for the moving object when the movement described in viewer-centered and retinal coordinate systems varies.

Although some of the neurons described here gave view-independent responses which were related to the individual face which was seen, the neurons did not respond to only one of the faces in the stimulus set, but instead had responses which differed in magnitude across different individuals in the stimulus set. This is in agreement with earlier investigations of these neurons (Baylis et al. 1985; Rolls 1984, 1989a), and shows that ensemble encoding of identity, and not "grandmother cell" encoding, could be performed by these neurons. The advantages of quite finely tuned but nevertheless ensemble encoded representations of information in neuronal networks have been described by Rolls (1987).

In the study described here, and elsewhere (Perrett et al. 1985a), neurons were found which responded to movements which can only be described in viewer-centered coordinates, such as neurons which respond to turning of the head away from the direction of the observer. The concept of turning away can only be accurately reflected in viewer-centered coordinates, since it can involve movements in opposite directions relative to the head. Further, there are neurons in the same region which respond to particular views of faces such as a profile view (Perrett et al. 1985a, b). The coexistence of viewer-centered and object-centered neuronal encoding of images in this region may mean that this area represents the processing stage at which 3D objects are computed from different views of objects.

This mixing of response characteristics in the same region supports the graded overlap of function postulated from the effects of lesions (Weiskrantz and Saunders 1984) or cooling (Horel 1984). Further it may be that damage to a region homologous to this gives rise to the difficulty with unusual views in patients with right posterior lesions (Warrington 1982; Ratcliff and Newcombe 1982).

The encoding of head position and movements has behavioral significance for monkeys. Head movements provide important cues in social interactions. For example, aggressive, threatening expressions are often accompanied by vertical movements of the head (Redican 1975), while fear expressions are accompanied by a horizontal turning away of the head. Responses to expression might depend upon the ability to detect dynamic changes, since static expressions are often unrecognizable (Salzen 1981). It is important that an object-centered representation of such movements be available to monkeys. For example, in social contexts these movements are very likely to be viewed in profile, from the back of the head, or even upside down. Of particular interest was the neuron (NN1176) which responded to either ventral flexion of the neck or to lowering (closing) of the eyelids (Figs. 2 and 8). These different movements often occur together, and are part of the same behavioral response of breaking social contact with another monkey during dominance interactions. The fact that the neuron responded to both movements (and both in object-centered coordinates) is consistent with the possibility that the responses of the neuron had been set up by a correlation learning mechanism as a result of which the neuron came to respond to correlations in its input information space (Rolls 1987, 1989b).

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