

Responses of neurons in area 7 of the parietal cortex to objects of different significance

E. T. ROLLS, D. PERRETT, S. J. THORPE, A. PUERTO, A. ROPER-HALL and S. MADDISON
Oxford University, Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD (U.K.)

(Accepted February 15th, 1979)

Mountcastle and his colleagues have described neurons in area 7 of the primate parietal cortex which fire during eye and hand movements directed towards desired objects, such as food when the animal is hungry^{5,7}. As the responses of these neurons appear to be 'conditional on the nature of the object and the motivational set of the animal'⁷, they would seem to have similarities with a class of neurons found in the lateral hypothalamus (LH) and substantia innominata (SI). These neurons respond to the sight of food⁹ as long as the animal is hungry¹, and also in a visual discrimination task to stimuli which the animal has learned are associated with food^{6,9,11,12}.

In order to compare the properties of cells in the two areas, we have analyzed the responses of neurons in area 7 with the same tests used to investigate the LH/SI units with food-related activity. Such a study is of particular interest in view of the anatomical projection from the substantia innominata to cortical areas including area 7^{3,4}.

Using methods similar to those described elsewhere^{9,10,12}, the activity of 310 neurons in area 7 of 3 hemispheres in 2 rhesus monkeys (*Macaca mulatta*) was analyzed. The recording sites were in the same region used in the previous studies^{5,7}, and were verified histologically. Neurons belonging to the 'visual fixation' category of Mountcastle et al.^{5,7}, were tested in 4 situations.

First, the neuronal activity was measured over a period of several seconds in which the monkey was shown and fixated objects of differing significance. These included desirable objects such as foods (peanuts, oranges, bananas, etc.) and 2 ml syringes from which the monkey was fed fruit juice or glucose solution, aversive objects such as a 1 ml syringe from which the monkey was fed hypertonic saline and a squeeze bulb with which air was puffed gently onto the monkey, and relatively neutral objects such as black/white gratings and simple geometrical shapes^{9,10}. The objects were shown against a white background and advanced slowly from a distance of 1 m towards the monkey so that the food could be given or the liquid delivered. Whereas the LH/SI units described previously fired only to the food objects^{9,11,12}, 67 of the 73 'visual fixation' neurons responded to aversive and neutral as well as to desirable objects. An example is shown in Fig. 1a. For the remaining 6 neurons the evidence was inconclusive. Although some (15) 'visual fixation' cells did give differential responses

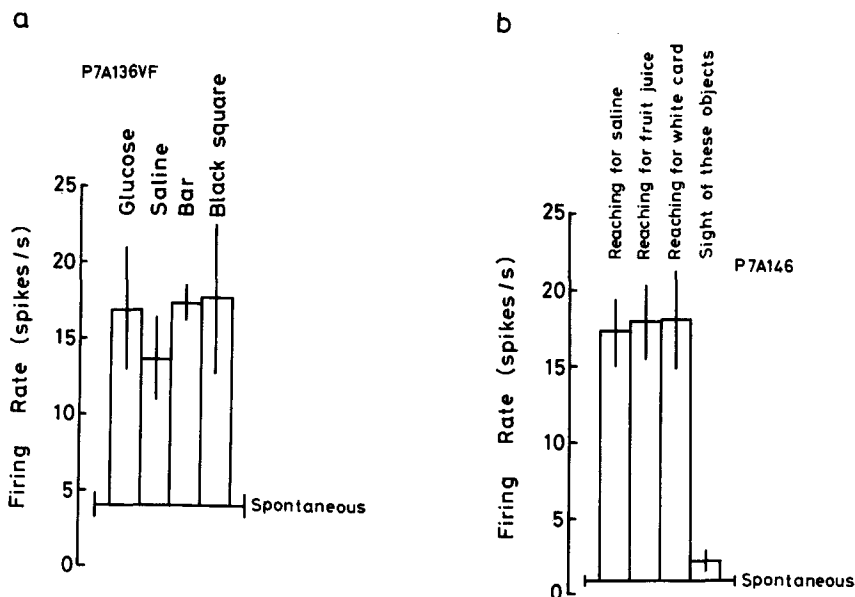


Fig. 1. a: firing rate (mean \pm S.E.M.) of a visual fixation neuron in a period of several seconds in which a monkey fixated a desired object (a 2 ml syringe from which he was fed glucose solution), aversive objects (a 1 ml syringe from which he was fed hypertonic saline, and a bar), and a relatively neutral square black card. b: firing rate (mean \pm S.E.M.) of an arm projection neuron during reaching made to displace a 1 ml syringe containing aversive hypertonic saline, during reaching made to obtain the desired 2 ml syringe containing fruit juice, and during reaching made to touch a relatively neutral white card. (There was no neuronal response when reaching movements were not made — see last bar of histogram.)

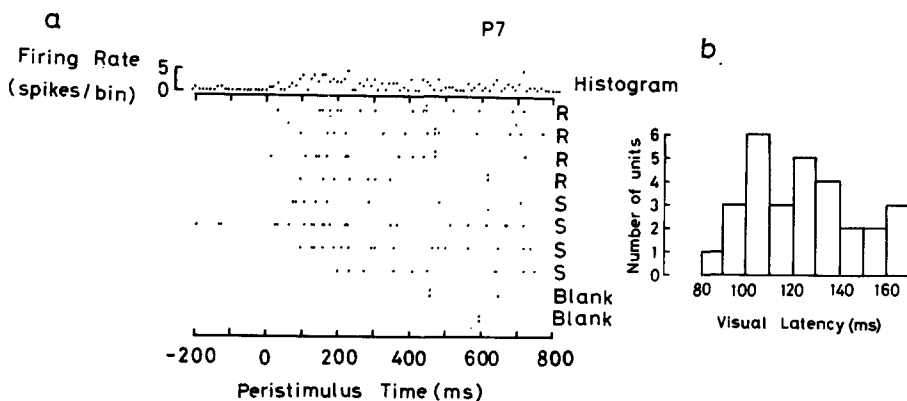


Fig. 2. a: response of a visual fixation neuron in the shutter-controlled visual discrimination. After a signal tone, the shutter opened at time 0, and the neuron responded as shown in the dot display approximately 100 msec after the shutter opened on trials on which a reward-associated visual stimulus was shown indicating that the monkey could lick (double dot) to obtain fruit juice (upper 4 R-trials), and also responded on trials on which an aversive saline-associated visual stimulus was shown indicating that if licks were made they would be punished by the delivery of aversive hypertonic saline from the tube (lower 4 S-trials). The trials were run in random order but are grouped together for convenience. It is also shown that this neuron did not respond if the shutter opened to reveal only a blank field (even though the monkey treated this as a rewarded stimulus) — see lowest 2 trials. b: response latencies of 29 different visual fixation neurons following opening of the shutter to reveal visual stimuli, either in the visual discrimination or in a passive condition when no response was required from the monkey.

to different stimuli, the responses were not grouped according to the significance of the stimuli shown, but rather could be shown in a number of cases to depend on sensory features such as size or colour.

This indication that these neurons were not responding on the basis of the desirability of the object was confirmed in a second test, in which the significance of an object was altered from rewarding to aversive or vice versa while the activity of the neurons was recorded. In such discrimination reversal learning tests, the monkey learns, for example, to reject the syringe from which he was previously fed glucose if it now contains aversive hypertonic saline, and the LH/SI neurons reverse their responses during this learning⁶. However, in none of the replications of this type of experiment performed on 9 different visual fixation neurons was there any evidence that their responses depended on the desirability of the object.

Third, the responses of visual fixation neurons were measured in a shutter-controlled visual discrimination. After a signal tone to ensure fixation, a large-aperture shutter opened to reveal in random order either a reward-associated visual stimulus which indicated that the monkey could lick a tube in front of his mouth to obtain fruit juice, or a different visual stimulus which indicated that if the monkey licked he would obtain aversive saline. In this situation, LH/SI units respond only to the reward-related stimulus with a latency of 150–200 msec¹². However, visual fixation cells fired to both the reward-related and the aversive stimuli (see Fig. 2a). It was also found that the visual fixation neurons would respond to rewarding, aversive, or neutral stimuli presented simply by the shutter opening, although differential responses independent of significance were sometimes found as noted above. Further, it was found that the latency of the responses of 'visual fixation' neurons could be measured relative to the opening of the shutter, and was in the range of 80–170 msec for the 29 different neurons tested (Fig. 2b).

In a fourth test, performed on 5 different visual fixation neurons, it was found that feeding the 18-h food-deprived monkey to satiety with glucose did not abolish the neuronal responses associated with the fixation of the feeding syringe. For comparison, the responses of LH/SI neurons to the sight of the feeding syringe become suppressed during satiety¹, as the syringe loses its desirability and becomes neutral and then aversive.

These experiments demonstrate that the responses of 'visual fixation' cells do not depend critically on whether the object fixated is desired or is aversive or neutral, or on the animal's internal state. We note that because the 'visual fixation' neurons responded to neutral and aversive as well as to desirable objects, controls for adequate fixation were not strictly necessary, but nevertheless, fixation was checked by the experimenter, and was confirmed in the same visual discrimination situation using recordings of the electro-oculogram. The effect of interest and novelty was also tested for 9 'visual fixation' cells using repeated presentation of neutral stimuli. As testing proceeded the duration of fixation elicited by the presentation decreased, but as long as fixation was occurring neuronal responses were apparent for often 20–40 trials with no indication of habituation.

The effects of the significance of the objects in the monkey's extrapersonal space

on some of the other types of neuronal response described by Mountcastle et al.^{5,7}, were also analyzed. For example, the responses of 'arm projection' neurons were measured during a particular reaching movement, made either to obtain a desired object or to displace an aversive one. Of the 47 projection neurons tested quantitatively in this test, 44 responded similarly during equivalent reaching movements to the two classes of object (see e.g., Fig. 1b). The evidence was unclear in the remaining 3. It was also possible to obtain quantitative information on 'visual tracking' neurons, neurons with transient visual responses, and 'hand manipulation' neurons, in experiments of the type described above. In the great majority of instances it was found that the significance of the object did not alter the neuronal response obtained. As before, in a minority of instances the evidence was inconclusive.

Thus, on the basis of these quantitative studies, we conclude that the great majority of 'visual fixation' and 'arm projection' neurons in area 7 of the parietal cortex respond to aversive and even neutral as well as desired objects, and that in this respect their responses are independent of the significance of objects. Because the 'visual fixation' neurons respond to objects with different types of significance, respond independently of hunger, and respond with latencies less than those of the hypothalamic food-related neurons (which are 150–200 msec vs 80–170 msec for the 'visual fixation' neurons^{11,12}), it is unlikely that the firings of the visual fixation neurons could be directly dependent on an input from the hypothalamic neurons or vice versa. Also, our evidence does not provide support for the view that these 'visual fixation' cells contribute to 'a matching function between the neural signals of the nature of objects and the internal drive state of the organism'⁵.

If parietal neurons have a command function as suggested by Mountcastle and his colleagues^{5,7}, on the basis of our findings we would wish to include commands for eye and arm movements made towards aversive and relatively neutral as well as to desired objects. This is consistent with the evidence that humans and monkeys with parietal damage do not have deficits only in orientation to, and eye movements towards desired objects, but rather have a more general neglect of space contralateral to the lesion². However, the way in which parietal neurons contribute to this ability to detect objects, and make movements in space is, we believe, still a major topic for investigation, as we and others⁸ have noted that, for example, 'visual fixation' neurons fire providing that fixation of an effective visual stimulus is occurring (and is not conditional on the object fixated or on motivational set), and also respond with a relatively fixed stimulus-related latency even when no fixation movement is necessary (see e.g., Fig. 2), so that on this type of evidence these neurons could equally have a sensory function⁸ (perhaps afferent to a command system) as a 'command' function⁷.

This work was supported by the Medical Research Council.

1 Burton, M. J., Rolls, E. T. and Mora, F., Effects of hunger on the responses of neurons in the lateral hypothalamus to the sight and taste of food, *Exp. Neurol.*, 51 (1976) 668–677.

2 Denny-Brown, D. and Chambers, R. A., The parietal lobes and behavior. *The Human Brain and Behavior, Res. Publ. Ass. nerv. ment. Dis.*, 36 (1958) 35–117.

- 3 Divac, I., Magnocellular nuclei of the basal forebrain project to the neocortex, brain stem and olfactory bulb. Review of some functional correlates, *Brain Research*, 93 (1975) 385–388.
- 4 Kievit, J. and Kuypers, H. G. J. M., Basal forebrain and hypothalamic connections to frontal and parietal cortex in the rhesus monkey, *Science*, 187 (1975) 660–662.
- 5 Lynch, J. C., Mountcastle, V. B., Talbot, W. H. and Yin, T. C. T., Parietal lobe mechanisms for directed visual attention, *J. Neurophysiol.*, 40 (1977) 362–389.
- 6 Mora, F., Rolls, E. T. and Burton, M. J., Modulation during learning of the responses of neurons in the lateral hypothalamus to the sight of food, *Exp. Neurol.*, 53 (1976) 508–519.
- 7 Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H. and Acuna, C., Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space, *J. Neurophysiol.*, 38 (1975) 871–908.
- 8 Robinson, D. L., Goldberg, M. E. and Stanton, G. B., Parietal association cortex in the primate: sensory mechanisms and behavioral modulations, *J. Neurophysiol.*, 41 (1978) 910–932.
- 9 Rolls, E. T., Burton, M. J. and Mora, F., Hypothalamic neuronal responses associated with the sight of food, *Brain Research*, 111 (1976) 53–66.
- 10 Rolls, E. T., Judge, S. J. and Sanghera, M. K., Activity of neurones in the inferotemporal cortex of the alert monkey, *Brain Research*, 130 (1977) 229–238.
- 11 Rolls, E. T., The neurophysiology of feeding, *Trends Neurosci.*, 1 (1978) 1–3.
- 12 Rolls, E. T., Sanghera, M. K. and Roper-Hall, A., The latency of activation of neurones in the lateral hypothalamus and substantia innominata during feeding in the monkey, *Brain Research*, 164 (1979) 121–135.