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Postcentral neurons of alert monkeys activated by the contact of the hand with objects other than the monkey's own body

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Yoshiaki Iwamura*, Michio Tanaka, Okihide Hikosaka[1], Masahiro Sakamoto[2]

Department of Physiology, Toho University School of Medicine, 21-16 Omori-Nishi 5 Chome, Otaku, Tokyo 143, Japan

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Abstract

In the caudal postcentral finger region near or in the anterior bank of the intraparietal sulcus of alert monkeys, we found neurons that were activated selectively by the contact of the hand to certain common objects such as bottle brushes, acrylic plates, parts of the stabilized monkey's chair, etc. All of these neurons were not activated when the monkey's hand was contacted with the monkey's own body. We concluded that these neurons are concerned with the haptic discrimination of common objects with the selectivity to one of various material variables of objects, and that the process involves differentiation of the object from the animal's own body.

Keywords: Monkey; Postcentral neurons; Haptic discrimination; Material; Softness; Hardness; Stability

The integration of sensory information from the hand proceeds within the postcentral gyrus in a hierarchical manner [4–10]. In the caudal part of the postcentral gyrus, many neurons failed to respond to simple skin or joint stimulation [10]. Specific types of stimulation such as rubbing of the skin in certain directions [8,15], static application of an edge in certain orientations, the contact of flat surfaces [5,9], etc. were effective for activating some of these neurons. We also found neurons that were activated when the monkey grasped objects actively [3,5]; in some of them responses were selective for the shape (e.g. cube/ball) of the objects [5]. In the present paper, we describe a group of neurons that were activated differentially by the contact of the hand to common objects, but not to the monkey's own body. Some of them responded with selectivity to one of various material variables such as softness, hardness, mobility or stability.

The results reported here are based on chronic experiments done in two adult Japanese monkeys (*Macaca fuscata*), trained to accept natural stimulation of their hand and fingers without struggling in fully awake condition. Details of the experimental procedure have been described elsewhere [6,10]. The receptive fields and submodality preferences of the neurons were examined by the experimenter's hand. We employed a variety of tactile stimuli such as simple touch or tapping, rubbing, scraping, twisting, or pulling of the skin or manipulation of the joints. We also applied common objects to the skin surface or brought the monkey's hand to the object: bottle brushes, rabbit fur, soft toilet paper, polypropylene fabric, sandpaper (no. 40 and no. 100), wooden balls or cubes, a plastic plate and a metal angle. We brought the monkey's hand in contact with various parts of the monkey's chair and the monkey's own body. The contact was made either in sight or out of sight. In addition, the neuronal response was recorded during the monkey's active hand movements to reach, grasp and hold bait or other common objects. The entire stimulation and recording procedure was video-taped through two cameras and the images were combined on one TV screen to examine the correlation between the unit activity and the stimulation procedures by frame-by-frame analysis.

Three hemispheres of two monkeys were explored. A total of 568 or 208 neurons were recorded in area 2 or a further caudal part of the postcentral gyrus, the anterior bank of the intraparietal sulcus (we designated this part as 'dIPS' [10]), respectively. Receptive field location and submodality were identified in 379/568 or 68/208 neurons

* Corresponding author.
[1] Department of Physiology, Juntendo University School of Medicine, Bunkyoku, Tokyo 113, Japan.
[2] Faculty of Foreign Languages, Hokuriku University, Kanazawa, Ishikawa 920-11, Japan.

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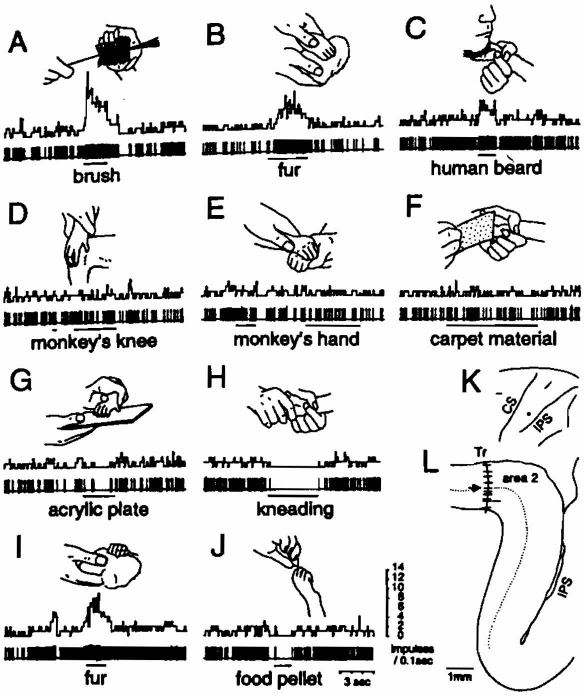

Fig. 1. An area 2 neuron selective to soft and shaggy objects. The palmar skin was contacted with various objects. In each of A–J, the upper trace indicates the peristimulus time histogram and the lower trace indicates the record of single neuronal activity. (A) A bottle brush; (B) a piece of rabbit fur; (C) the beard of one of the experimenters; (D) the monkey's own hair at the knee; (E) the dorsal surfaces of the monkey's opposite hand; (F) rubbing with a piece of tightly woven coarse carpet material; (G) pressing the palm skin with an acrylic plate; (H) an inhibitory response evoked by kneading of the palm; (I) and (J) responses evoked when the monkey grasped actively the rabbit fur (I) and a small piece of hard-baked food pellet (J). Bars indicate the period of contact judged from video records. (K) The site of electrode penetration on the dorsal surface of the postcentral gyrus. CS, central sulcus; IPS, intraparietal sulcus; L, a sagittal section of the postcentral gyrus indicating the electrode track (Tr) and the recording sites of this (an arrow) and other neurons (short bars). A dotted line is drawn through layer IV.

in area 2 or dIPS, respectively. In area 2, 202/379 neurons, and in dIPS, 24/68 neurons responded to skin (including hair and nail) stimulation. Among them we describe response characteristics of five neurons that were activated differentially by the contact of the hand to common objects. They were out of 11 neurons which had an intriguing feature in common, being not activated by the contact of the hand to the monkey's own body. Six or five of them were found in area 2 or dIPS, respectively. Four of them responded to passive skin stimulation but the rest did not respond to any mode of passive stimulus.

The first example is shown in Fig. 1. The receptive field of this neuron was on the palmar skin when tested with punctate skin stimuli but the response was weak. In contrast, the passive contact of a bottle brush or a piece of rabbit fur evoked brisk and reproducible responses (Fig. 1A,B). The contact of the experimenter's beard was also effective (Fig. 1C), but this neuron was never activated when the monkey's right hand was touched with the left hand dorsum, knees, or other parts of the monkey's own body (Fig. 1D,E). Rubbing with the coarse surface of sandpaper or carpet material was not effective (Fig. 1F). Pressing the palm skin gently onto smooth and hard surfaces such as an acrylic plate induced a weak inhibitory response (Fig. 1G). Stronger inhibition was induced when the palmar skin was kneaded by the experimenter's fingers (Fig. 1H), indicating that activation of subcutaneous or more deeply located receptors may be responsible for the inhibition. Similar results were obtained when the monkey was actively exploring objects. Active grasping of a bottle brush or fur gave brisk responses while grasping of a small piece of hard-baked biscuit brought about an inhibition of the background activity (Fig. 1I,J).

Fig. 2 shows the responses of a pair of neurons (a and b) which showed nearly the opposite selectivity for material. The receptive field of neuron 'a' was limited to the contralateral hand dorsum. It was activated by contact with a hard acrylic plate in isolation or as a part of the monkey's primate chair (Fig. 2Aa,Ba) and inhibited with a brush (Fig. 2Ca) or toilet paper. The contact with the monkey's own hairy skin of the ipsilateral hand dorsum was ineffective (Fig. 2Da).

The lower records of Fig. 2 shows the activity of neuron 'b' which was recorded at the same site. It was activated by contact with a bottle brush (Fig. 2Cb) or toilet paper, but not activated by contact with a hard acrylic plate or the monkey's primate chair (Fig. 2Ab,Bb). Un-

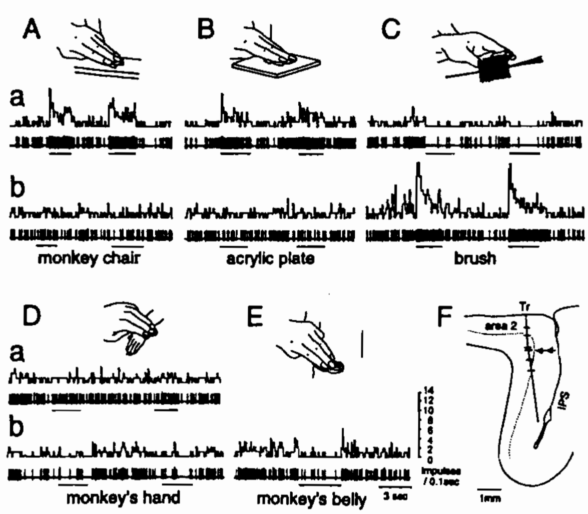

Fig. 2. Two area 2 neurons 'a' and 'b', selective to either hard or soft objects, respectively. They were recorded at the cortical sites close to each other, and the responses were nearly opposite to each other when the dorsal surface of the hand was contacted with various objects. (A) The acrylic table of the monkey's chair; (B) an acrylic plate held by an experimenter; (C) a bottle brush; (D) the monkey's own dorsal surface of the hand; (E) the monkey's own belly; (F) a sagittal section of the postcentral gyrus indicating the electrode track and the recording sites of these and other neurons. Abbreviations and symbols are as in Fig. 1.

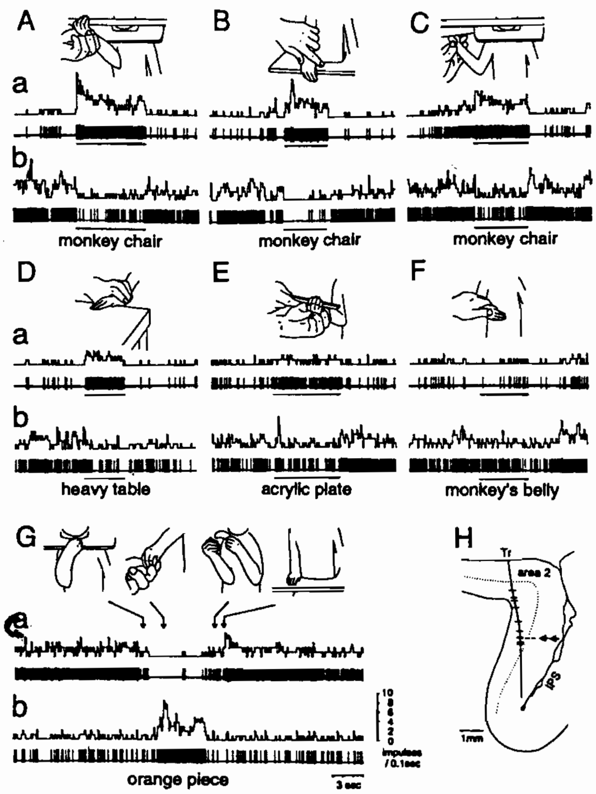

Fig. 3. Two neurons 'a' and 'b', selective to either immobile or mobile objects, respectively. They were recorded at the same time in the anterior bank of the intraparietal sulcus, and the responses were nearly opposite to each other when the hand was contacted with various objects. (A–C) Various parts of the monkey's chair; (D) another heavy table in front of the monkey; (E) an acrylic plate held by an experimenter; (F) the monkey's own belly; (G) an inhibitory or excitatory response evoked by active grabbing of a slice of orange from the human hand (note the difference in the level of the spontaneous discharges in the pre-reaching period when the monkey rested his right hand on a part of the monkey's chair); (H) a sagittal section of the postcentral gyrus indicating the electrode track and the recording sites of these and other neurons. Abbreviations and symbols are as in Fig. 1.

like the neuron shown in Fig. 1, its background activity was slightly inhibited by the contact of the hand dorsum with the monkey's own body (Fig. 2Db,Eb).

Fig. 3 shows the responses of another pair of neurons. Neuron 'a' (upper records of Fig. 3), fired most briskly when the monkey's contralateral hand, either the palmar or dorsal side, was brought in contact with any part of the monkey's chair including parts invisible to the monkey (Fig. 3Aa–Ca). The possibility that this neuron was activated by visual stimulus was thus excluded. It was also activated when the monkey's hand was in contact with another heavy wooden table placed in front of the monkey (Fig. 3Da). The response was weaker when a hard acrylic plate, the same material as the table on the monkey's chair, was held by an experimenter (it was thus unstable) and contact was made with the monkey's hand (Fig. 3Ea). No response was evoked by contact with the monkey's own belly (Fig. 3Fa). The activity of this neuron was inhibited when the monkey actively reached and picked up a slice of orange from the experimenter's hand (Fig. 3Ga). The inhibition lasted as long as the monkey kept the orange piece in the same hand, and returned to the original high level when the monkey rested its empty contralateral hand on the monkey's chair again.

The activity of the partner neuron 'b' was inhibited by contact of the hand with the monkey's chair or a stabilized table (Fig. 3Ab–Db), but the neuron fired most briskly when the monkey reached, grabbed and held food in hand (Fig. 3Gb). Thus we concluded that neuron 'a' was activated by contact of the hand with stabilized objects while neuron 'b' was activated by contact of the hand with mobile objects.

We found an additional six neurons that shared this intriguing character, with unresponsiveness to the body in common. We failed to conclude to what object each of these neurons was selective. However, the responses of one of them might be worthy of note; the active or passive contact of the hand with any part of the monkey's chair, the monkey's own body, or food offered by the experimenter did not evoke any response. In contrast, the contact of any other objects brought passively to the hand evoked brisk and reproducible responses irrespective of their material or shape. When tested out of sight, the contact of the hand with an orange piece activated this neuron. However, once the monkey started to grope the object (thus realizing what it was), the neuron became silent. We interpreted that this neuron may serve to differentiate tactually unfamiliar objects from familiar ones, such as the monkey's own body, the monkey's primate chair and food.

The strong selectivity of the present neurons might be accounted for if sensory inputs of multiple sources converge on them. Indeed, neurons with a variety of receptive fields characteristics, cutaneous, deep, and the proximal arm origins, are intermingled in this region of the cortex [10]. We have reported that response characteristics of even area 1 neurons [7] were sometimes complex, some being activated by touch and inhibited by pressure. The neurons described here might further integrate somatosensory and perhaps also non-somatosensory signals to acquire such complex response characteristics.

To what object each neuron was selective varied, but the unresponsiveness to the monkey's own body was common among them. It would require a mechanism to cancel excitatory signals from the hand by those from other body parts which are stimulated at the same time. Gibson [2] wrote, 'The haptic system is an apparatus by which the individual gets information about both the environment and his body. He feels an object relative to the body and the body relative to an object.' He wrote also 'The body percept is a set of possible dispositions or pose-standing, or lying relative to the substratum and to gravity.' It was thus not unexpected to find a set of neurons that responded to stabilized objects including the monkey's chair to which the monkey's head was fixed. The unresponsiveness to the body and the monkey's chair was also observed in the polysensory region of the temporal cortex [11].

All of the present neurons were found in the caudal part of the postcentral gyrus, area 2 near to or rather deep in the anterior bank of the intraparietal sulcus. Earlier clinical observations in human and cortical ablation studies in animals have indicated that the tactile discrimination of common objects, shapes, or texture is impaired after lesions in the postcentral gyrus, rather than the parietal association cortices [1,12–14]. Moffett et al. [12] pointed out that in tactile discrimination tasks there exists a functional focus along the posterior margin of area 2 and the anterior extremity of the intraparietal sulcus; a small removal from this focal area gives rise to more severe impairment than a removal of comparable size from elsewhere within the posterior parietal region. The sites of recording of the present neurons fell in the same cortical region. This region thus may be critical for discrimination of not only shape and texture but also material of objects by touch and groping.

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