6.12 Dorsal and Ventral Streams in the Sense of Touch

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Glossary

haptics The study of touch and tactile sensations, especially as a means of communication. Haptic sensations are derived primarily from active touch, in which proprioceptive and cutaneous inputs are combined to define object properties.

intention Direction of the mind or attention to a particular action, goal, or effort. Intention also implies understanding the meaning, significance, import, purpose, design, or aim of an action. In its strongest usage, intention describes the volition or determination to carry out a particular action.

kinematics The science concerned with movements of the parts of the body.

kinaesthesia (kinesthesis) The sense of muscular effort and perception of movement that accompanies a voluntary motion of the body. This sense is mediated by end organs located in muscles, tendons, and joints stimulated by bodily movements and tensions.

prehension The action of taking possession of and grasping or holding something. The term is also applied to mental comprehension, the action of grasping with the mind.

proprioception The sense or perception, usually at a subconscious level, of the movements and posture of the body and especially its limbs, independent of vision. This sense is mediated by sensory nerve terminals in muscles and tendons (muscle spindles) and the fibrous capsule of joints combined with input from the vestibular apparatus.

stereognosis The appreciation and recognition of the form of solid objects by means of touch.

tactile agnosia The inability to recognize objects by touch, in the presence of intact cutaneous and proprioceptive hand sensation. This deficit is caused by a lesion in the contralateral parietal lobe, and is also termed astereognosis.

6.12.1 Introduction

One of the key concepts to illuminate our understanding of sensory processing in the cerebral cortex was set forth in a seminal paper by Ungerleider L. G. and Mishkin M. (1982). They proposed that visual information from the retina enters the cortex in the primary visual area, V1, is transmitted to V2 cortex, and then split into two parallel pathways directed to the temporal and parietal lobes. These pathways analyze the same sensory information in different ways that came to be known as the what and where streams.

The ventral stream – transmitted through the inferotemporal cortex – is the putative 'what' pathway. These cortical areas analyze the visual signals to derive cognitive information about the size, shape, and color of the stimulus. These intrinsic properties allow us to recognize such stimuli as distinct objects, persons, or places. The dorsal stream – transmitted through the parietal lobe – forms the where pathway. It analyzes the extrinsic properties of the image, defining the spatial and temporal properties of the stimulus with respect to the observer and the environment.

Later studies of these pathways by Milner A. D. and Goodale M. A. (1995) suggested a more sophisticated view, based on their clinical studies of patients with lesions localized to the parietal or temporal cortex. They proposed that the ventral stream forms a vision-for-cognition pathway that allows us to name objects, contributing to semantic memory. The dorsal stream forms a vision-for-action network that provides spatial information for guiding behavior. The parietal pathway creates a pragmatic representation of the world needed for immediate action, and for the formation of procedural memories underlying skilled behavior. The Milner–Goodale hypothesis can be summarized as what and how networks.

Mishkin M. (1979) also proposed a similar dual organization of the somatosensory pathways for touch and proprioception. In his formulation, the somatosensory ventral stream originates in the projections from the primary somatic sensory cortex (S-I) to the second somatic sensory area (S-II cortex), including the neighboring zones along the upper bank of the Sylvian (lateral) fissure and the parietal operculum. The ventral network has strong anatomical links through the insular cortex to the medial temporal lobe and hippocampus (Friedman, D. P. *et al.*, 1986; Felleman, D. J. and Van Essen, D. C., 1991), providing a cortico-limbic circuit for object memory acquired through touch.

The somatosensory dorsal stream is conveyed through the posterior parietal cortex (PPC), particularly the region bordering the intraparietal sulcus (IPS) in humans and monkeys. The dorsal stream represents the actions of the subject when interacting with the environment, as gleaned by touch and proprioception. The PPC projects primarily to the premotor areas of the frontal lobe, providing a pathway for initiating and controlling motor behavior. These frontal–parietal networks play a key role in voluntary movement, particularly the skilled behaviors of the hand and arm: reaching, grasping, and tool use.

In this chapter, I review the anatomical, physiological, and clinical evidence for a dorsal stream pathway in the sense of touch. The discussion is focused on actions of the hand and arm, as physiological studies have concentrated on the role of PPC in reach and grasp behaviors. The properties of the ventral stream network in the sense of touch are described in the chapters by Leah Krubitzer, Steven Hsiao, and Ranulfo Romo in this volume.

6.12.2 Anatomical Localization of the Posterior Parietal Cortex

The cortical areas surrounding the IPS in monkeys are referred to collectively as the posterior parietal cortex. PPC is normally subdivided anatomically into a rostral division – the superior parietal lobule (SPL) – and a caudal zone – the inferior parietal lobule (IPL). The SPL and IPL in monkeys were named areas 5 and 7 by Brodmann K. (1909). Vogt C. and Vogt O. (1919) subdivided the SPL into caudal and rostral regions (areas 5a and 5b), and the IPL into areas 7a and 7b. Later anatomists further subdivided the SPL into areas PE, PEc, and PEa, and the IPL convexity into areas PF, PFG, PG, and Opt (von Economo, C. and Koskinas, G. N., 1925; von Bonin, G. and Bailey, P., 1947; Pandya, D. N. and Selzer, B., 1982; Gregoriou, G. G. *et al.*, 2006) (Figure 1). Anatomical distinctions were also made for the regions buried within the wall of the IPS (areas MIP, LIP, AIP, and VIP) and those bordering the parietal operculum (PFop and PGop).

More recent physiological, cytoarchitectural, myeloarchitectural, and connectionist studies have resulted in further fractionation of this region into 17 distinct areas concerned primarily with vision and/or somatic sensation (Lewis, J. W. and Van Essen, D. C., 2000a; 2000b; Van Essen, D. C. *et al.*, 2001). Visual areas are situated primarily in the IPL, and along the midline at the parietal–occipital (PO) junction; these include areas 7a, LIPv, LIPd, VIPm, VIPl, PO (V6A), PIP, V3, V3A, MDP, and LOP. Somatosensory areas are situated primarily in the SPL, and in the rostral and lateral regions of the IPL (areas 5d, 5v, MIP, AIP, 7b, and 7t) (Figure 2). To add to the confusion of terminology, the regions of the SPL in the human brain called BA5 and BA7 do not coincide with their namesakes in the macaque cortex; their properties as revealed in functional imaging studies suggest instead that they correspond to areas PE, PEa, and PEc in the macaque (Galletti, C.

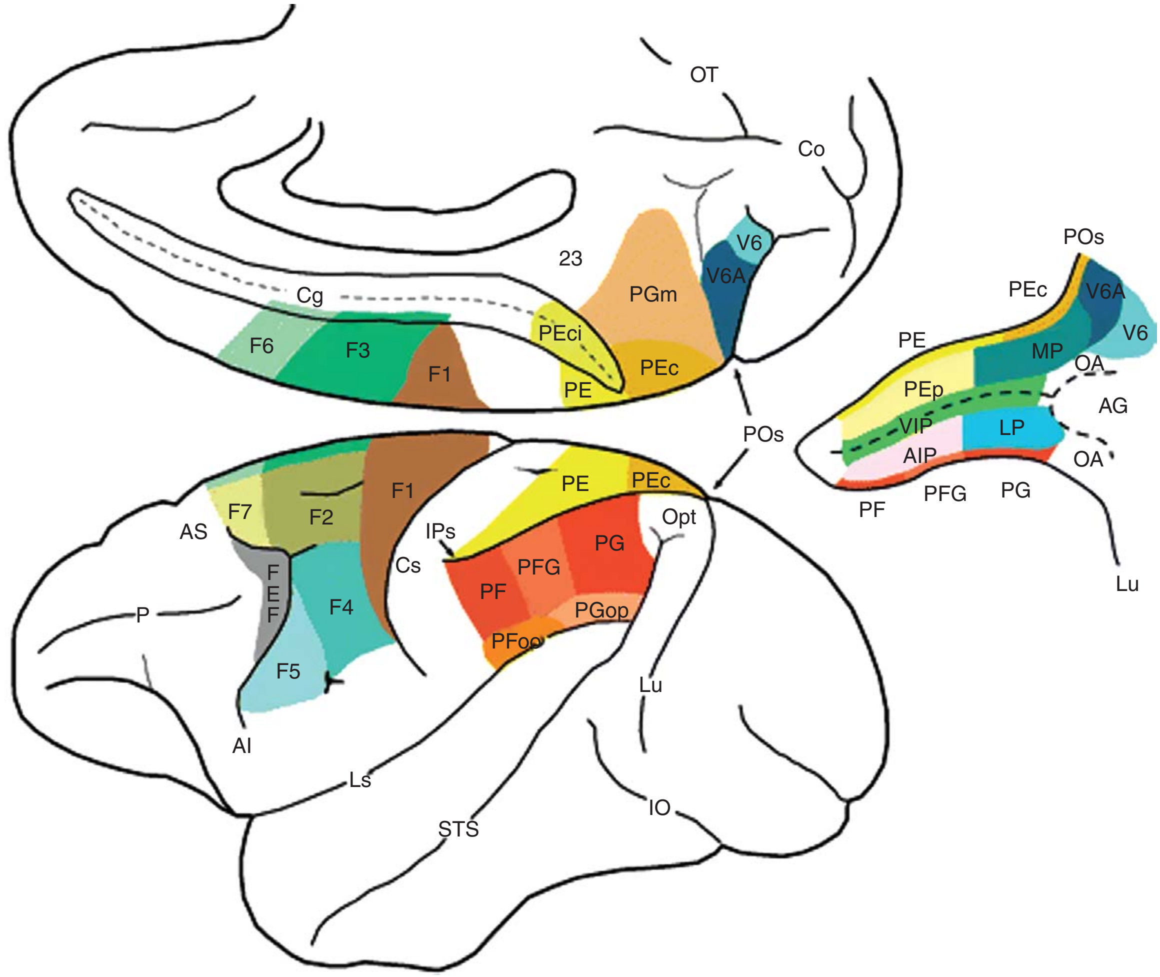

Figure 1 Lateral and medial views of the macaque cerebral cortex showing the anatomical locations of the posterior parietal cortex (areas PE, PEc, PO, PF, PFG, PG, Opt, PFop, and PGop) and frontal motor areas (areas F1, F2/F3, F7/F6, F4, F5, and FEF). The inset shows the areas lying within the intraparietal sulcus (IPS). Reproduced from Rizzolatti, G. and Matelli, M. 2003. Two different streams form the dorsal visual system: anatomy and functions. Exp. Brain Res. 153, 146–157; figure 1).

et al., 1997; Binkofski, F. *et al.*, 1999a). Similarly, the human BA39 and 40 are functionally related to the macaque areas 7a and 7b.

The anatomical connections of somatosensory areas of the PPC are schematized in Figure 3. The principal somatosensory input to area 5 originates from S-I cortex, particularly from area 2 (Jones, E. G. and Powell, T. P. S., 1969; 1970; Pearson, R. C. A. and Powell, T. P. S., 1985). These feed-forward projections are somatotopic. The hand representation in S-I projects to the lateral end of the IPS in areas 5d and 5v that is involved in grasping behaviors (Mountcastle, V. B. *et al.*, 1975; Gardner, E. P. *et al.*, 1999; 2002; 2007a). The arm and shoulder regions project to more medial and caudal regions in the SPL – designated the parietal reach region (PRR) – that are involved in reaching (reviewed in Caminiti, R. *et al.*, 1996; Andersen, R. A. *et al.*, 1997; Kalaska, J. F. *et al.*, 1997; Caminiti, R. *et al.*, 1998; Burnod, Y. *et al.*, 1999; Andersen, R. A. and Buneo, C. A., 2002). The face representation projects to area VIP, located at the fundus of the IPS at its rostral end; this region may be involved in hand–mouth coordination during feeding (Colby, C. L. *et al.*, 1993; Duhamel, J. R. *et al.*, 1998; Colby, C. L. and Goldberg, M. E., 1999).

Tracer injection studies reveal extensive interconnections between different subregions of the SPL and IPL. For example, the primary output targets of neurons in the hand region of area 5 are the more caudal regions of the SPL involved in reaching (Seltzer, B. and Pandya, D. N., 1980; Pandya, D. N. and Selzer, B., 1982; Lewis, J. W. and Van Essen, D.

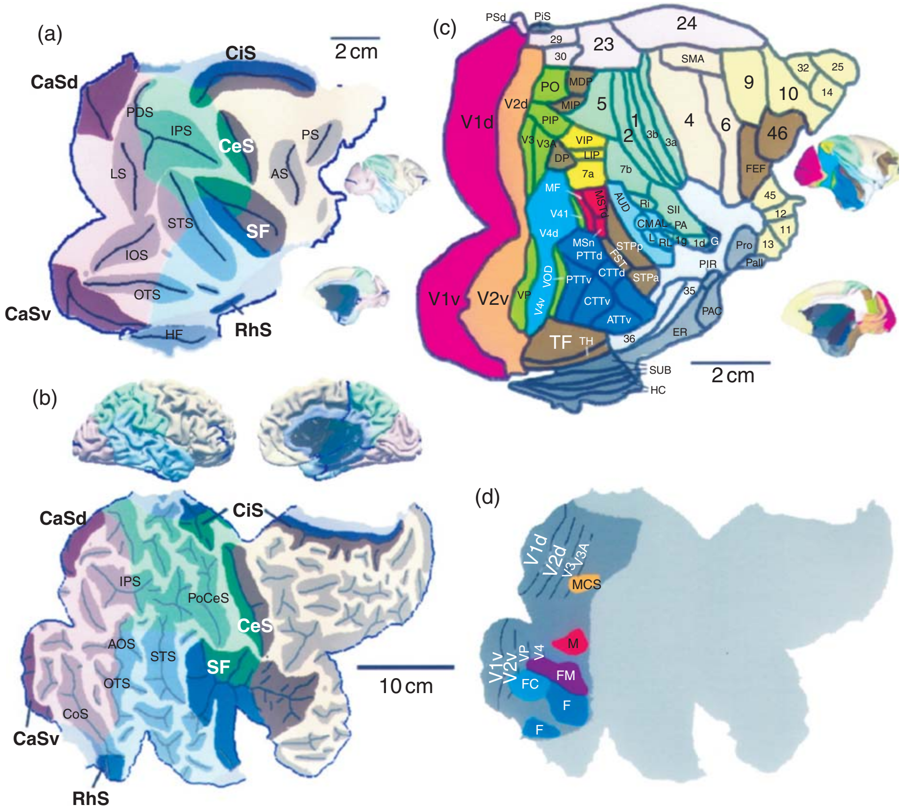

Figure 2 Flat maps showing the spatial relationship between somatosensory, visual, auditory, and motor areas of the cerebral cortex in macaques (a and c) and humans (b and d). The surface is colored to delineate the different cortical lobes. *Shaded regions* on the flat map indicate cortex buried within various sulci (AS, arcuate sulcus; CaS, calcarine sulcus (dorsal and ventral); CeS, central sulcus; CiS, cingulate sulcus; HF, hippocampal fissure; IOS, inferior occipital sulcus; IPS, intraparietal sulcus; LS, lunate sulcus; OTS, occipito-temporal sulcus; POS, parieto-occipital sulcus; PS, principal sulcus; RhS, rhinal sulcus; SF, Sylvian fissure; STS, superior temporal sulcus). Cortical areas in the macaque are labeled according to the partitioning scheme of Felleman D. J. and Van Essen D. C. (1991). Posterior parietal visual areas along the midline are colored chartreuse green (PO, PIP, V3, and V3A), and those buried in the IPS (AIP and VIP) and adjacent bank of the IPL (7a) are colored yellow. Somatosensory areas (3a, 3b, 1, 2, 5, 7b, SII, Ri, and Ig) are shown in pale green. Brown areas between the parietal visual and somatosensory regions (MDP, MIP, and DP) form portions of the parietal reach region (PRR). Dark blue regions in the temporal lobe indicate the ventral visual areas; no distinction is made in this figure between dorsal and ventral somatosensory areas. Reproduced from Van Essen, D. C. and Drury, H. A. 1997. Structural and functional analyses of human cerebral cortex using a surface-based atlas. J. Neurosci. 17, 7079–7107; figure 13).

C., 2000b), providing anatomical pathways to coordinate reach and grasp during goal-directed hand behaviors. Neurons in the hand representation of area 5 project to mirror-image sites in the contralateral hemisphere, providing circuitry for bilateral coordination of the left and right hands (Jones, E. G. *et al.*, 1978; Padberg, J. *et al.*, 2005). This is the first site of bilateral hand interactions in the dorsal pathway, as the hand representation in S-I is apparently acallosal (Jones, E. G. *et al.*, 1978; 1979; Caminiti, R. and Sbriccoli, A., 1985; Shanks, M. F. *et al.*, 1985; Padberg, J. *et al.*, 2005).

Neurons in the hand representation of area 5 also provide prominent somatosensory inputs to areas AIP and 7b in the IPL (Neal, J. W. *et al.*, 1986; 1987; Cavada, C. and Goldman-Rakic, P., 1989a), thereby linking tactile and visual information needed for grasping. The connections between SPL and IPL neurons are reciprocal, allowing exchange of tactile and visual information between cortical areas. Area 7b also receives somatosensory inputs from S-II cortex (Disbrow, E. *et al.*, 2003).

Area 5 also has strong projections to motor areas of the frontal lobe, particularly to the premotor cortex. Medial regions of area 5 that represent the arm project primarily to the dorsal premotor cortex (PMd or F2), while the lateral regions representing the hand and face project to ventral premotor cortex

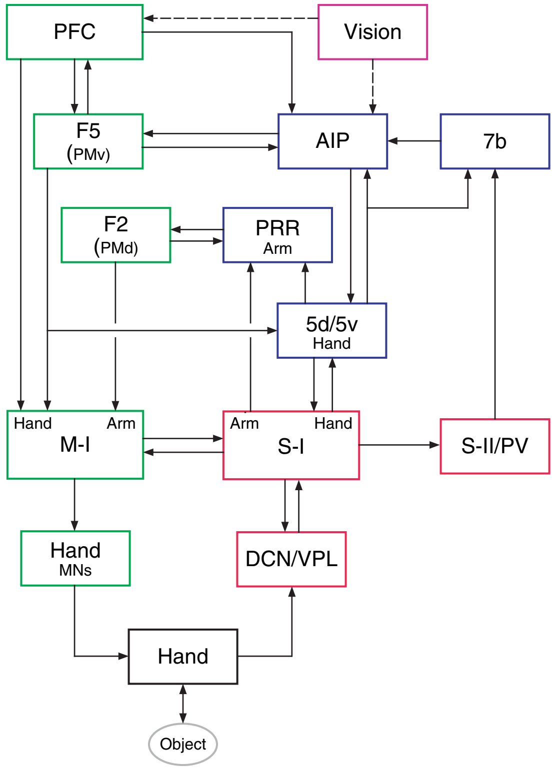

Figure 3 Simplified block diagram of the input–output circuits for grasping. Somatosensory areas (red): DCN/VPL (dorsal column nuclei and ventral posterolateral nucleus of the thalamus), S-I (primary somatosensory cortex, areas 3a, 3b, 1, and 2), S-II/PV (secondary somatosensory and parietal ventral cortex). Posterior parietal areas (blue): 5d/5v (rostral end of superior parietal lobule), PRR (parietal reach region, caudal end of superior parietal lobule), AIP (anterior intraparietal area of inferior parietal lobule), and 7b (lateral convexity of the inferior parietal lobule). Frontal motor areas (green): PFC (prefrontal cortex), F5 (ventral premotor cortex), F2 (dorsal premotor cortex), and M-I (primary motor cortex). Other important frontal motor areas that project to M-I, such as the supplementary motor area (SMA) and cingulate motor area (CMA), are not shown, nor are the corticomotor pathways to spinal interneurons from M-I and F5. Visual areas (violet): For simplicity, the visual pathways from the retina to areas AIP, PRR, and PFC have been compressed into a single box that includes important visuomotor centers of PPC such as areas LIP, CIP, 7a, and V6A; the dashed arrows denote polysynaptic pathways. Reproduced from Gardner, E. P., Ro, J. Y., Babu, K. S., and Ghosh, S. 2007b. Neurophysiology of prehension: II. Response diversity in primary somatosensory (S-I) and motor (M-I) cortices. J. Neurophysiol. 97, 1656–1670; figure 10).

(PMv or F5/F4) (Petrides, M. and Pandya, D. N., 1984; Matelli, M. *et al.*, 1986; Cavada, C. and Goldman-Rakic, P., 1989b; Kurata, K., 1991; Ghosh, S. and Gattera, R., 1995; Johnson, P. B. *et al.*, 1996; Wise, S. P. *et al.*, 1997; Matelli, M. *et al.*, 1998; Luppino, G. *et al.*, 1999; Matelli, M. and Luppino, G., 2001; Tanne-Gariepy, J. T. *et al.*, 2002; Rizzolatti, G. and Matelli, M., 2003).

Neurons in the IPL also receive somatosensory information, but it arrives not from the primary somatic sensory cortex, but from area 5 and S-II cortex. Actions of the arm are represented primarily in area 7a, and those of the hand in more lateral zones, particularly areas AIP and 7b. However, visual inputs exert a stronger influence on these neurons than the somatosensory modality (reviewed in Felleman, D. J. and Van Essen, D. C., 1991; Fogassi, L. and Luppino, G., 2005; Jeannerod, M. *et al.*, 1995; Andersen, R. A. *et al.*, 1997; Rizzolatti, G. *et al.*, 1997; Sakata, H. *et al.*, 1997; Colby, C. L. and Goldberg, M. E., 1999; Van Essen, D. C. *et al.*, 2001; Andersen, R. A. and Buneo, C. A., 2002; Buneo, C. A. and Andersen, R. A., 2006). Hand manipulation neurons in areas AIP and 7b receive visual inputs from area LIP (Lewis, J. W. and Van Essen, D. C., 2000b; Nakamura, H. *et al.*, 2001), project to ventral premotor cortex (PMv or F5), and receive reciprocal connections from these frontal motor areas (Matelli, M. *et al.*, 1986; Rizzolatti, G. *et al.*, 1987; Matelli, M. *et al.*, 1988; Cavada, C. and Goldman-Rakic, P., 1989b; Preuss, T. M. and Goldman-Rakic, P. S., 1991; Fogassi, L. and Luppino,G., 1995; Rizzolatti, G. *et al.*, 1997; Ghosh, S. and Gattera, R., 1995; Luppino, G. *et al.*, 1999; Matelli, M. and Luppino, G., 2001; Rizzolatti, G. and Luppino, G., 2001).

6.12.3 Physiological Studies of Posterior Parietal Cortex

The anatomical connections of PPC suggest that this region is a higher-order somatosensory and visual area important for feature detection for one or both modalities (Gardner, E. P., 1988; Felleman, D. J. and Van Essen, D. C., 1991; Van Essen, D. C. *et al.*, 2001). Its connections to the frontal motor areas also provide sensory feedback networks for guiding movements. Early physiological studies seemed to support the notion of serial hierarchical processing of tactile input in PPC for the purpose of exteroception and object recognition (Iwamura, Y. and Tanaka, M., 1978; Darian-Smith, I. *et al.*, 1984; Koch, K. W. and Fuster, J. M., 1989; Felleman, D. J. and Van Essen, D. C., 1991; Ageranioti-Bélanger, S. A. and Chapman, C. E., 1992; Iwamura, Y. *et al.*, 1993, 1995). Neurons recorded along the rostral bank of the IPS were shown to have complex tactile receptive fields that distinguish the roughness of textures (Ageranioti-Bélanger, S. A. and Chapman, C.

E., 1992), the spatial frequency and/or orientation of gratings scanned by the fingers (Darian-Smith, I. *et al.*, 1984), and the shape of objects touched by the hand (Iwamura, Y. and Tanaka, M., 1978; Iwamura, Y. *et al.*, 1995), or aid recognition of the surface features of objects previously grasped in the hand (Koch, K. W. and Fuster, J. M., 1989). Other neurons recorded in this region receive proprioceptive signals from multiple joints that aid perception of integrated body postures (Duffy, F. H. and Burchfiel, J. L., 1971; Sakata, H. *et al.*, 1973). Although many of these physiological studies attributed recording sites in the superior bank of the IPS to area 2, anatomists such as Pandya D. N. and Selzer B. (1982), Pons T. P. *et al.* (1985), and Lewis, J. W. *et al.* (1999) have included this region in Brodmann's area 5, calling it area PEa or 5v. Interestingly, most of the complex tactile responses reported in the physiological studies cited above were evoked by active hand movements that were rewarded, such as grasping objects or palpating surfaces.

Our view of PPC was changed dramatically by the pioneering studies of Vernon Mountcastle and Juhani Hyvärinen and their collaborators (Hyvärinen, J. and Poranen, A., 1974; Mountcastle, V. B. *et al.*, 1975; Leinonen, L. *et al.*, 1979; Hyvärinen, J., 1981; 1982a; 1982b). They found that neurons in areas 5 and 7 in the macaque cortex did not respond to the traditional types of tactile stimuli used to study S-I, such as pressure pulses or vibration. In a later historical review, Mountcastle V. B. (1995) described these cells as "neurons that were active if and only if the animal 'had a mind' to deal with the stimulus in a behaviorally meaningful way!" They responded to goal-directed actions of the hand and arm "aimed at securing for the animal an object he desires, such as food when he is hungry; or, as in our experimental paradigm, contacting a switch or pulling a lever that provides fluid when he is thirsty" (Mountcastle, V. B. *et al.*, 1975). Mountcastle and coworkers distinguished two classes of neurons in PPC: arm projection neurons involved in reaching to targets in immediate extrapersonal space and hand manipulation neurons engaged in hand movements such as grasping or foraging for objects with the fingers. Both types were influenced by visual information, particularly neurons recorded in area 7. Reaching and grasping behaviors activated neurons in different portions of PPC, as arm projection neurons were recorded at more medial sites in areas 5 and 7 than hand manipulation neurons. These actions are also segregated anatomically into medial and lateral zones in human parietal cortex, as revealed in functional imaging studies (Chieffi, S. and Gentilucci, M., 1993; Grafton, S. T. *et al.*, 1996; Binkofski, F. *et al.*, 1998; 1999a; Ehrsson, H. H. *et al.*, 2000; 2001; Culham, J. C. *et al.*, 2003; Connolly, J. D. *et al.*, 2003; Ehrsson, H. H. *et al.*, 2003; Shikata, E. *et al.*, 2003; Culham, J. C., 2004; Frey, S. H. *et al.*, 2005; Culham, J. C. and Valyear, K. F., 2006).

The studies by Mountcastle, Hyvärinen, and their collaborators played a seminal role in subsequent investigations of PPC that have focused on reaching movements of the arm, grasping actions of the hand, and goal-directed eye movements to salient targets. They led to the development of new behavioral tasks that tested not only sensory discrimination and motor behaviors, but also the role of memory, intention, and planning of such actions. The correlation of neuronal firing patterns with hand actions also provided an impetus for detailed analyses of the kinematics of reach and grasp behaviors. Collectively, these studies implicate PPC in sensorimotor transformations that couple perceptions to actions needed to direct the hand to objects of behavioral interest such as food and acquire them for consumption.

6.12.3.1 Reaching as a Model System for Analyzing Sensorimotor Integration

Neurons in the SPL appear to play an important role in perception of the body, and its relation to external space during reaching, pointing, and grasping. Reaching is primarily a visuomotor action in which the subject projects the arm toward a target object to touch or grasp it (reviewed in Jeannerod, M., 1994; Jeannerod, M. *et al.*, 1995; Paulignan, Y. and Jeannerod, M., 1996). Reaching occurs in a smooth trajectory in which the peak velocity of the wrist occurs at 40% of the movement time in humans (Jeannerod, M., 1984) and 50% in monkeys (Georgopoulos, A. P. *et al.*, 1982; Roy, A. C. *et al.*, 2000). Ipsilateral reaches take proportionately less time than those to contralateral sites at the same distance. Reaches toward small objects take longer than those toward large ones (Wing, A. M. *et al.*, 1986; Marteniuk, R. G. *et al.*, 1990; Paulignan, Y. and Jeannerod, M., 1996; Roy, A. C. *et al.*, 2000; Roy, A. *et al.*, 2002), presumably because a small object requires more precise aim and finger placement for accurate grip.

Reach and grasp are temporally synchronized but controlled by distinct networks of neurons in parietal cortex (Chieffi, S. and Gentilucci, M., 1993; Grafton, S. T. *et al.*, 1996; Binkofski, F. *et al.*, 1998; 1999; Ehrsson, H. H. *et al.*, 2000; 2001; 2003; Astafiev, S. V. *et al.*, 2003; Culham, J. C. *et al.*, 2003; Rizzolatti, G. and Matelli, M., 2003; Shikata, E. *et al.*, 2003; Frey, S. H. *et al.*, 2005; Hu,

Y. *et al*., 2005; Tunik, E. *et al*., 2005). Reach targets are encoded by neurons in the shoulder representation of area 5, the PRR including areas MIP, 7a, PEc, and the PO zone (areas V6, V6A, and 7m) on the medial surface of the hemisphere. These regions have been studied using a variety of reaching tasks (Kalaska, J. F. *et al*., 1983; Crammond, D. J. and Kalaska, J. F., 1989; Snyder, L. H. *et al*., 1998a; 1998b; Kalaska, J. F. *et al*., 1990; Galletti, C. *et al*., 1993; Kalaska, J. F. and Crammond, D. J., 1995; Lacquaniti, F. *et al*., 1995; Caminiti, R. *et al*., 1996; Ferraina, S. *et al*., 1997; Kalaska, J. F. *et al*., 1997; Rizzolatti, G. *et al*., 1997; Caminiti, R. *et al*., 1998; Batista, A. P. *et al*., 1999; Battaglia-Mayer, A. *et al*., 2000; Batista, A. P. and Andersen, R. H., 2001; Ferraina, S. *et al*., 2001; Andersen, R. A. and Buneo, C. A., 2002; Galletti, C. *et al*., 2003; Fattori, P. *et al*., 2004; Fogassi, L. and Luppino, G., 2005; Buneo, C. A. and Andersen, R. A., 2006).

The notion that goal-directed reaches are mediated through area 5 was first analyzed by Kalaska J. F. *et al.* (1983) and Georgopoulos, *et al.* (1884). They developed a behavioral paradigm – called the center-out task – that has been widely used to study reaching and other goal-directed behaviors such as eye movements (Georgopoulos, A. P. *et al*., 1982). In this task, monkeys are trained to grasp a handle, place it at a central start point, and then displace it to one of eight targets surrounding the origin (Figure 4, *upper panels*). Each trial requires the animal to reach in a specific direction to a visually defined endpoint. They found that most neurons in area 5 respond to a broad range of reach directions, with maximum firing in one preferred direction, and minimum rates along the opposite path. The directional tuning curves of firing rates for the eight different directions can be approximated by a sine wave (Figure 4, *lower panel*), allowing them to derive preferred reach directions for each cell studied. Although the individual neurons do not by themselves provide a strong directional signal, collectively the population of neurons precisely specifies the reach direction on each trial. This notion was further extended to three dimensions in later studies (Georgopoulos, A. P. *et al*., 1988; Schwartz, A. B. *et al*., 1988; Lacquiniti *et al*., 1995). Kalaska and colleagues (1990) later discovered that the tuning of area 5 neurons to particular reach directions reflects the movement kinematics, that is, the particular muscle groups needed to direct the arm in specific directions. Area 5 firing rates are independent of the amount of muscle force needed to pull or push the handle toward the specified target.

The time course of neural responses during reaches also has important implications concerning the sensorimotor role of PPC. The onset of neuronal responses in area 5 coincides with the start of reach and overlaps motor activity in primary motor cortex (M-I) and in the dorsal premotor cortex (PMd) (Kalaska, J. F. *et al*., 1983; Crammond, D. J. and Kalaska, J. F., 1989; Kalaska, J. F. *et al*., 1990; Burbaud, P. *et al*., 1991; Kalaska, J. F. and Crammond, D. J., 1995). In addition, Seal J. *et al.* (1982) and Seal J. and Commenges D. (1985) found that area 5 neurons in deafferented monkeys respond to reaching movements in the absence of somatosensory feedback, suggesting that an efference copy of motor commands from the frontal lobe is also transmitted to PPC (Mountcastle, V. B. *et al*., 1975). These findings led to the proposal that area 5 receives convergent central and peripheral signals that allow it to compare central motor commands with peripheral sensory feedback during task performance. These circuits provide a network for planning intended movements and updating ongoing actions as they proceed. Kalaska and colleagues (1997) described this role as a "sequence of sensorimotor coordinate transformations between a signal of spatial location and a pattern of muscle activity."

6.12.3.2 Role of Posterior Parietal Cortex in Motor Planning and the Neural Representation of Space

Further clues about the sensorimotor function of PPC have been derived from instructed delay tasks when the animal was able to plan reaches or saccades to cued spatial targets. In these studies, the motor plans or intentions of the animal are distinguished from subsequent actions during motor performance of the task. During delayed reaching tasks, neurons in areas 5 and PRR show strongly enhanced firing rates prior to the onset of movement that are tuned to the location of the visual target and that specify potential actions that can be performed there (Crammond, D. J. and Kalaska, J. F., 1989; Andersen, R. A., 1995; Kalaska, J. F. and Crammond, D. J., 1995; Kalaska, J. F., 1996; Batista, A. P. and Andersen, R. H., 2001). The initial hand position modifies the strength of responses of neurons in area 5 (Crammond, D. J. and Kalaska, J. F., 1989; Kalaska, J. F. and Crammond, D. J., 1995), but not those in PRR (Andersen, R. A. *et al*., 1997; Batista, A. P. and Andersen, R. H., 2001; Buneo, C. A. and Andersen, R. A., 2006), suggesting that these regions respond to different aspects of the sensory cue. These studies support the notion that PPC activity reflects the intention to execute a specific motor program.

Premovement activity during the instructed delay period has been variously described as motor intentions (Andersen, R. A. *et al*., 1997; Andersen, R. A. and

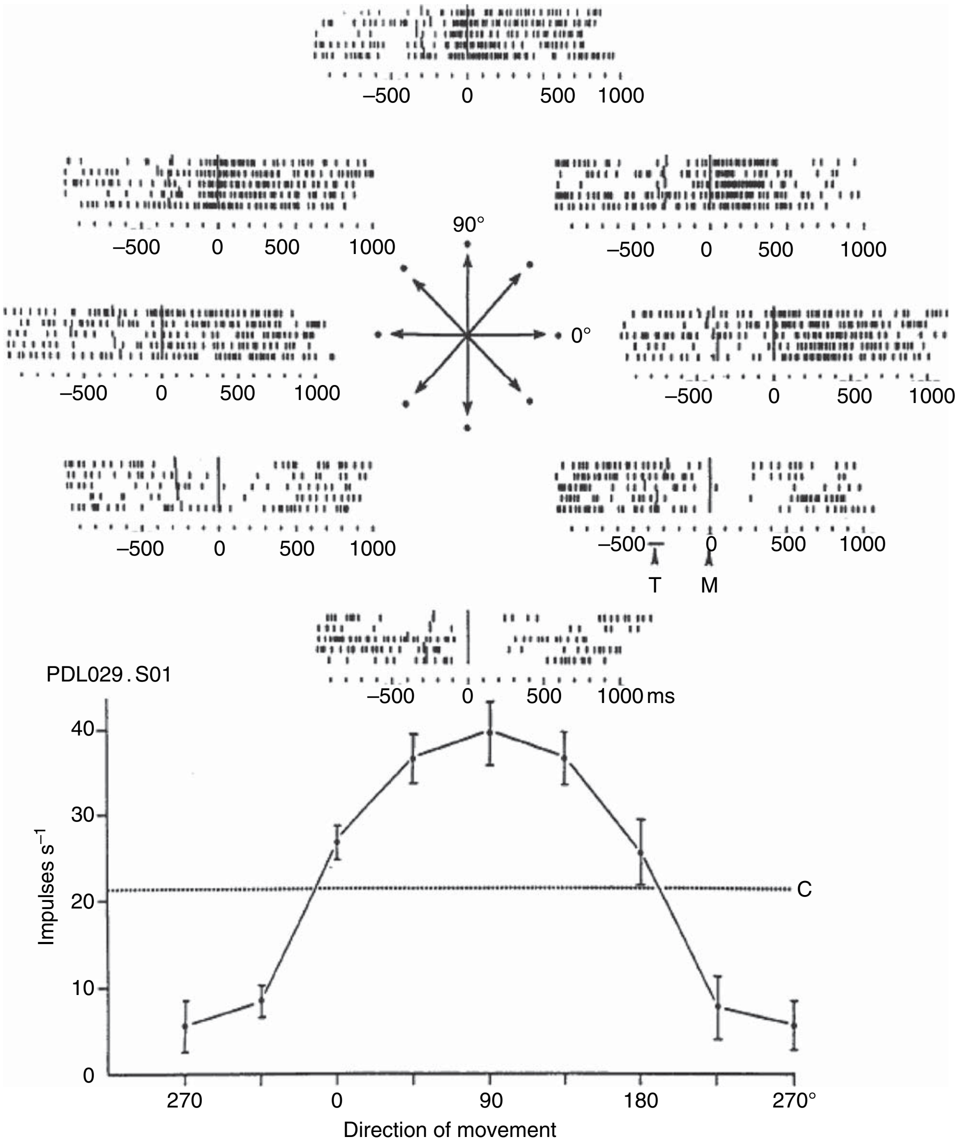

Figure 4 Tuning of responses of an area 5 neuron to the direction of reach in the center-out task. Upper panels: Rasters illustrating five trials in the stated directions aligned to the start of reach (M); the neuron responded most vigorously to upward movements (90°) and was inhibited by movement in the opposite direction (270°). Note that neural responses precede the start of movement, and continue until the hand reaches the specified target. Lower panel: Mean firing rate during the movement time; the neuron responded to movement over most of the range tested. *C*, mean firing rate during the control period before the target cue light was illuminated. Reproduced from Kalaska, J. F., Caminiti, R., and Georgopoulos, A. P. 1983. Cortical mechanisms related to the direction of two-dimensional arm movements: relations in parietal area 5 and comparison with motor cortex. Exp. Brain Res. 51, 247–260; figure 3).

Buneo, C. A., 2002; Buneo, C. A. and Andersen, R. A., 2006), spatial attention (Colby, C. L., 1998; Duhamel, J. R. *et al.*, 1998; Colby, C. L. and Goldberg, M. E., 1999; Bisley, J. W. and Goldberg, M. E., 2003), or perceptual decision-making (Platt, M. L. and Glimcher, P. W., 1999; Shadlen, M. N. and Newsome, W. T., 2001; Glimcher, P. W., 2003; Dorris, M. C. and Glimcher, P. W., 2004; Sugrue, L. P. *et al.*, 2004; 2005). We refer to this early activity as motor planning, because it reflects high-level cognitive plans for movement without the implication of emotional commitment to such behaviors.

Motor plans for reaching require transformation of a visual signal concerning the target position in the workspace into a motor signal that selects the appropriate muscle groups needed to transport the hand to the specified place. The intended goal of the reach is often described as a motor error signal, that is, the difference between the starting hand and arm position, and the desired goal (reviewed in Buneo, C. A. and Andersen, R. A., 2006). Actions of the arm are represented in a variety of coordinate systems along the SPL including eye-centered (Figure 5), head-centered, arm-centered, and hand-centered reference frames, or combinations of these expressed as gain fields (Crammond, D. J. and Kalaska, J. F., 1989; Pause, M. and Freund, H.-J., 1989; Galletti, C. *et al.*, 1993; Kalaska, J. F. and Crammond, D. J., 1995; Lacquaniti, F. *et al.*, 1995; Caminiti, R. *et al.*, 1996; Andersen, R. A. *et al.*, 1997; Ferraina, S. *et al.*, 1997; Kalaska, J. F. *et al.*, 1997; Caminiti, R. *et al.*, 1998; Colby, C. L., 1998; Snyder, L. H. *et al.*, 1998a; 1998b; Batista, A. P. *et al.*, 1999; Burnod, Y. *et al.*, 1999; Ferraina, S. *et al.*, 2001; Battaglia-Mayer, A. *et al.*, 2003; 2006; Buneo, C. A. and Andersen, R. A., 2006). This is a hotly debated and somewhat controversial subject. In a recent review, Buneo C. A. and Andersen R. A. (2006) proposed that PPC contains both a "representation of target and hand position in eye coordinates, and a representation of motor error in hand-centered coordinates." They seem to recognize that different coordinate systems are arrayed along the IPS but that their relative importance may depend on the specific task requirements. Multiple coordinate frames are useful for achieving flexibility when reaching is the prelude to subsequent hand actions such as grasping, pointing, pulling, pushing, or turning that require a variety of motor synergies.

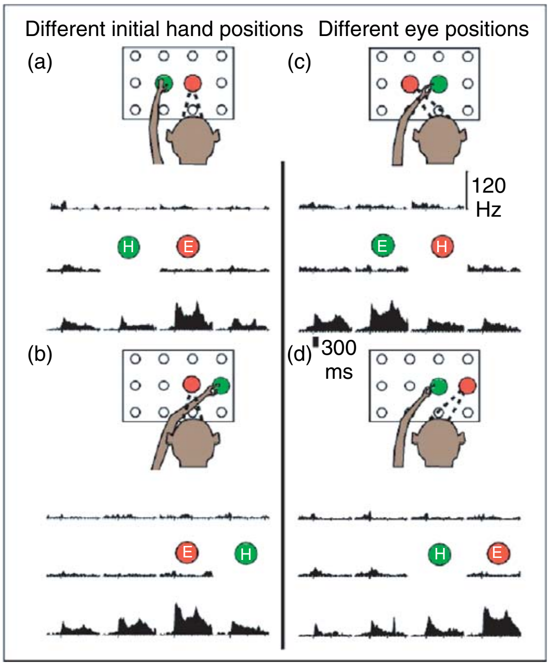

Figure 5 Sensitivity of a neuron in the parietal reach region (PRR) to eye and hand position during the instructed delay period of a reach task. The initial hand position and the point of visual fixation are represented by green and red circles, respectively, in the behavioral cartoons. The animal is instructed to reach to one of the other 11 positions when the GO signal occurs while maintaining fixation of gaze on the red circle. The spike density histograms below the cartoons illustrate the averaged response to the cue; in each case the strongest response occurred when the animal was instructed to reach to the location below the center of gaze, regardless of the starting point of the hand or the direction of reach. The authors conclude that the neuron encodes the required movement in terms of the target location on the retina. Modified from Andersen, R. A. and Buneo, C. A. 2002. Intentional maps in posterior parietal cortex. Annu. Rev. Neurosci. 25, 189–220; figure 5).

Spatial maps may play a critical role in the dysmetrias and neglect syndromes characteristic of damage to PPC (reviewed in Hyvärinen, J., 1982b; Pause, M. *et al.*, 1989; Milner, A. D. and Goodale, M. A., 1995; Ghika, J. *et al.*, 1998; Pouget, A. and Driver, J., 2000; Freund, H.-J., 2001; Goodale, M. A. and Westwood, D. A., 2004; Battaglia-Mayer, A. *et al.*, 2006). Ben-Hamed and Duhamel reported that the population of neurons in area VIP of each hemisphere responded to stimulation of the entire visual field, both ipsilateral and contralateral, but the relative distribution of neurons responding at each eccentricity was skewed, with peak numbers ~15° contralateral to the recording side (Figure 1 in Pouget, A. and Driver, J., 2000). This coincides with the location of the fingertips when the arm is extended forward of the body. From a bilateral perspective, the greatest number of neurons represents the workspace between the shoulders, with equal representation at the midline for left and right sides, and a gradual bias toward the contralateral side that accelerates lateral to the shoulder. The large population monitoring the intramanual space endows it as the preferred site of skilled bimanual actions. If one hemisphere is disabled, the skewed representation of visual space biases reaches and attention toward the contralateral side. This model predicts hypometric reaches toward ipsilateral targets, because fewer than 10% of cells in the intact hemisphere represent eccentricities >20° in that space. Similarly, modulation of visual gain fields by eye and head position could further skew neuronal responses to contralaterally displaced reach targets (Andersen, R. A. *et al.*, 1985; Snyder, L. H. *et al.*, 1998a; 1998b).

6.12.3.3 Grasping and Hand Manipulation Neurons in Posterior Parietal Cortex

Prehension is an object-oriented behavior that is fundamental to skilled actions of the hand. As Lederman S. J. (1994) notes, "the grasp would appear to be a privileged movement pattern of the human hand, inasmuch as it provides varied somatosensory inputs that may be used to guide both motoric and perceptual functions." Skilled grasping behaviors are strongly influenced by both visual and somatosensory information. Visual information about the object's size, shape, and orientation is required during reaching for proper orientation of the hand and for preshaping of the fingers prior to acquisition (Jeannerod, M., 1984; 1994; Milner, A. D. and Goodale, M. A., 1995; Paulignan, Y. and Jeannerod, M., 1996; Connolly, J. D. and Goodale, M. A., 1999; Castiello, U., 2005). The grip aperture of the fingers is proportional to object size and is maximum at 75% of the movement time as the hand decelerates near the target (Jeannerod, M., 1986; Chieffi, S. and Gentillucci, M., 1993; Jeannerod, M., 1994; Jeannerod, M. *et al.*, 1995; Lemon, R. N. *et al.*, 1995; Roy, A. *et al.*, 2002; Hu, Y. *et al.*, 2005). Hand preshaping to object size and shape is characteristic of normal primate hand function and is disrupted by lesions of PPC (LaMotte, R. H. and Acuña, C., 1978; Gallese, V. *et al.*, 1994; Jeannerod, M. *et al.*, 1994; Milner, A. D. and Goodale, M. A., 1995; Fogassi, L. *et al.*, 2001; Tunik, E. *et al.*, 2005). Johansson and coworkers (Jenmalm, P. and Johansson, R. S., 1997; Jenmalm, P. *et al.*, 2000; Johansson, R. S. *et al.*, 2001) demonstrated that visual information helps guide the choice of grasp points on an object to promote stability and efficient manipulation. The development of grasp forces is determined initially by visual identification of the object and retrieval of implicit memory information concerning its physical properties (Johansson, R. S. and Westling, G., 1984; Gordon, A. M. *et al.*, 1993).

Grasping is also influenced by somatosensory information from previous encounters with objects. Through experience we learn how and where to grasp objects, and the rate and amount of force required to lift and manipulate them. Roland Johansson and Göran Westling have shown that when we grasp objects, we do so delicately applying just enough force to secure it in the hand without slippage (reviewed in Johansson, R. S., 1996). The tactile information transmitted by receptors in the hand as objects are handled allows us to develop skills and learn new behaviors that can be used as templates for future action.

Johansson R. S. (1996) proposed that prehension is governed by two control mechanisms operating in parallel: anticipatory parameter control and sensory-driven event control (see chapter by Johansson and Flanagan, this volume). Anticipatory parameter control is used for motor planning of prehension. Subjects anticipate what an object should feel like in the hand when it is viewed and formulate a grasp program. Visual and somatosensory inputs are combined with sensorimotor memories to construct an internal model of the hand shape and grip forces needed for prehension and manipulation of the object. These modalities set a context in which ascending tactile information is interpreted after the object is touched. Anticipatory parameter control also involves the conjoint application of grip and load forces to the object in order to execute a smooth lift without the application of excessive grip force. Discrete event, sensory-driven control describes the sensory information that signals completion of one action such as grasping to allow rapid transition to another behavior such as manipulation. It also includes error signals when a mismatch occurs between expectation and execution of the task, requiring corrective responses. For example, tactile afferents in the hand can detect slippage due to unexpected contours, textures, or weight that require adjustment in hand position or force. Anticipatory parameter control provides an efficient mechanism of sensorimotor control, because long-loop feedback to the cortex is not needed for the initiation of sequential actions. It allows rapid movement execution by relying on experience to control the timing of muscle activation in the hand. Sensory feedback monitors how the task proceeds; this information strengthens grasp motor programs when implemented properly and initiates corrective actions if errors such as slippage occur.

Studies of the neurophysiology of prehension using single unit recordings in monkeys indicate that PPC responses are predictive rather than reactive to touch receptor stimulation during prehension (Mountcastle, V. B. *et al.*, 1975; Leinonen, L. *et al.*, 1979; Taira, M. *et al.*, 1990; Sakata, H. *et al.*, 1995; Murata, A. *et al.*, 1996; Sakata, H. *et al.*, 1997; Gardner, E. P. *et al.*, 1999; Murata, A. *et al.*, 2000; Ro, J. Y. *et al.*, 2000; Debowy, D. J. *et al.*, 2001; Gardner, E. P. *et al.*, 2002; Fogassi, L. and Luppino, G., 2005; Gardner, E. P. *et al.*, 2007a). Other studies demonstrate that sensory-driven control is mediated primarily by neurons in S-I (Iwamura, Y. and Tanaka, M., 1978; Hikosaka, O. *et al.*, 1985; Wannier, T. M. *et al.*, 1986; Wannier, T. M. *et al.*, 1991; Iwamura, Y. *et al.*, 1995; Iwamura, Y. and Tanaka, M., 1996; Brochier, T. *et al.*, 1999; Gardner, E.

P. *et al.*, 1999; Salimi, I. *et al.*, 1999; Ro, J. Y. *et al.*, 2000; Debowy, D. J. *et al.*, 2001; Gardner, E. P. *et al.*, 2002; 2007b; Jenmalm, P. *et al.*, 2006).

Mountcastle V. B. *et al.* (1975) described neurons in areas 5 and 7 activated during exploratory hand movements such as foraging for raisins in small containers. They named these cells 'hand manipulation' neurons but did not document their firing patterns beyond a textual description. They noted that hand manipulation neurons in area 7 responded to both visual and tactile modalities when the stimuli occupied the same spatial location. These cells fired during visual fixation or tracking of desired objects such as food but responded at highest rates during projection of the arm toward the object or manipulation of it in the hand. The eye–hand coordination neurons were situated in the posterior bank of the IPS in the most anterior portion of area 7, a region that is now called the anterior intraparietal (AIP) area. Leinonen L. *et al.* (1979) described similar hand manipulation neurons in the adjacent convexity of the IPL (area 7b) that were active as monkeys tried to acquire raisins or other food morsels from the experimenter and ceased firing as the food was grasped and brought to the mouth.

The first systematic studies of hand manipulation neurons in monkeys were performed by Hideo Sakata and coworkers, who developed a prehension task to study neural responses in area AIP (Taira, M. *et al.*, 1990; Sakata, H. *et al.*, 1995; Murata, A. *et al.*, 1996; Sakata, H. *et al.*, 1997; 1999; Murata, A. *et al.*, 2000). They trained the animals to grasp and pull handles of different shapes located on a turntable in the middle of the workspace. In order to test the visual sensitivity of these neurons, and to measure its effect on hand movements, the task included an instructed delay period in which the animal viewed an object (FIX, Figure 6) before a GO cue signaled the start of the movement period. Some of the task trials were also conducted in the dark where only tactile and proprioceptive signals were available to aid task performance. Sakata and colleagues subdivided the population of hand manipulation neurons into five classes according to their relative sensitivity to vision and somatosensory modalities. The most common class was visuomotor 'object-type' neurons (28%) that were similar to the eye–hand coordination neurons originally reported by Mountcastle V. B. *et al.* (1975). These neurons combined visual and tactile inputs, displaying higher overall firing rates during manipulation in light – in which the animal viewed the object and the hand grasping it – than in the dark when neither hand nor object was visible (Figure 6a). It is unclear whether the enhanced responses resulted from somatosensory input from the hand, efference copy of the motor commands for hand preshaping and grasping, or visual stimulation as the hand entered foveal receptive fields. Responses during the visuomotor and motor tasks were higher than during object fixation, when the object was displayed and viewed but not grasped. Fourteen percent of the neurons tested responded only to the conjunction of vision and hand actions during manipulation in the light (visual nonobject, Figure 6d), showing no response to object presentation during fixation, nor during manipulation in the dark. Another 16% had purely visual inputs, responding only when the object was visible, without increasing their firing rates during reach or grasping actions (visual object, Figure 6c). The remaining 42% of cells did not have overt visual responses; they responded only during the reach and grasp stages of the task (visuomotor nonobject or motor, Figure 6b and e).

The firing rates of hand manipulation neurons were also tuned to broad categories of object shapes tested in this task (Murata, A. *et al.*, 2000). Visuomotor neurons displayed the same preferences during viewing and grasping objects, suggesting that they might provide relevant information about the size, shape, and composition of objects needed to grasp them. However, Murata and coworkers concluded that AIP neurons signaled the type of manipulatory action performed by the hand, rather than object properties, because the neurons did not distinguish between objects of different shape that were grasped using the same or similar hand postures.

Likewise, neurons in areas F5 and F2vr (the primary projection targets of area AIP) responded primarily to the grasp posture of the hand rather than the object form (Murata, A. *et al.*, 1997; Raos, V. *et al.*, 2004; 2006). Raos V. and coworkers (2006) noted that "although the object-related visual responses of AIP neurons reflect the objects' common geometrical features, the object-related visual responses of F5 neurons reflect the chosen grip." These circuits create 'pragmatic representations' of objects in which their intrinsic properties are encoded in terms of the hand postures normally used to grasp them. Since neurons in area AIP respond both to direct view of an object to be grasped and to the actual performance of grasp, they are postulated to be involved in the sensorimotor transformation of the visual representation of object features into the hand posture needed for grasping (Jeannerod, M. *et al.*, 1995; Sakata, H. *et al.*, 1997; Fagg, A. H. and Arbib, M. A., 1998; Rizzolatti, G. and Luppino, G., 2001; Fogassi, L. and Luppino, G., 2005).

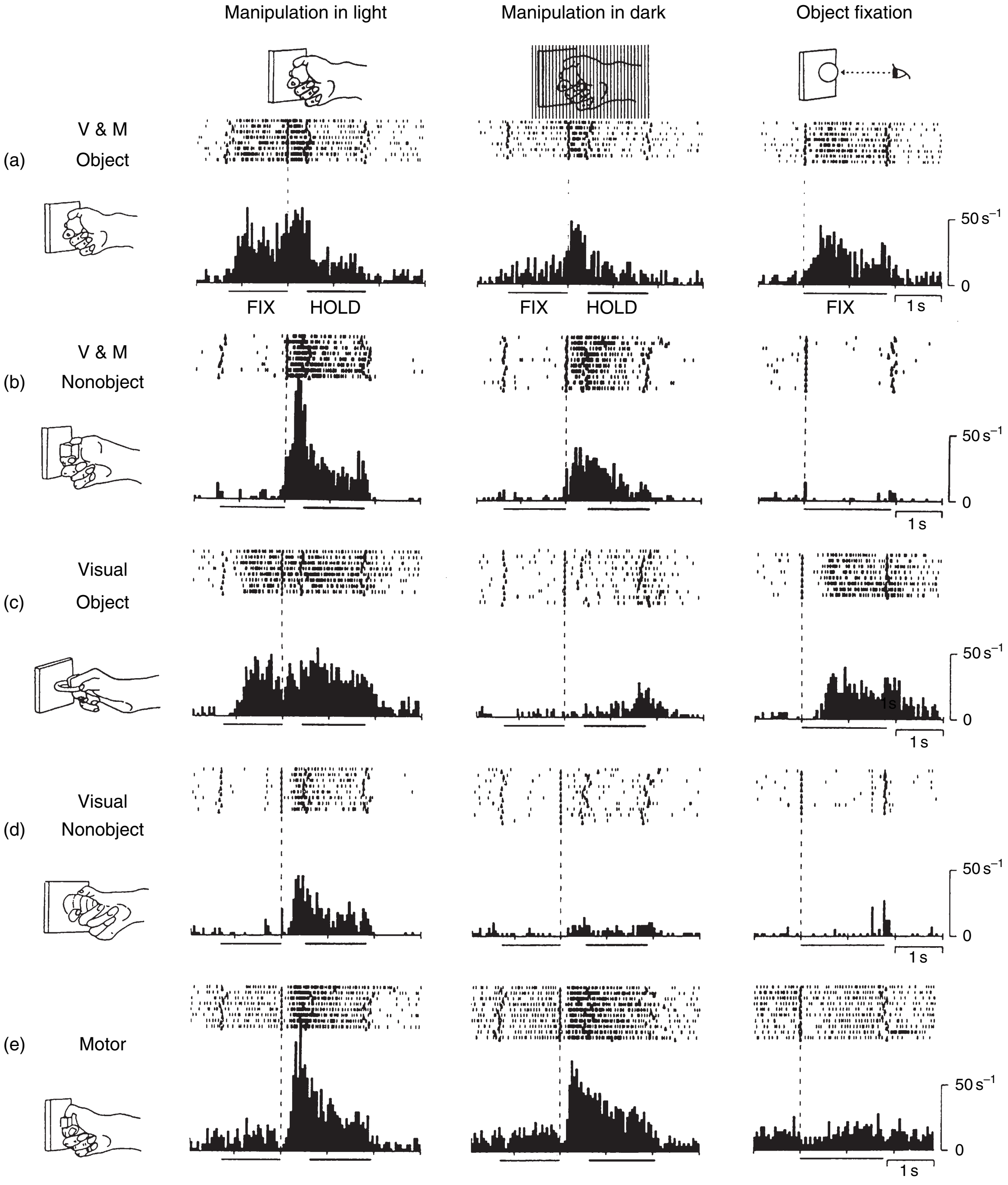

Figure 6 Classes of hand manipulation neurons recorded in area AIP during a prehension task. Responses illustrated in the rasters and peristimulus–time histograms (PSTHs) are aligned to the onset of reach; different neurons are illustrated in each row. At the start of each trial, the animal had to maintain gaze on the test object for ~2 s while pressing a button with the test hand (FIX). The animal was trained to reach toward the test object after a GO signal, grasp and pull it, and maintain the pull posture during the HOLD period. All of these neurons fired at highest rates during reach and grasp actions, and most continued to respond during holding, although at lower rates. Object-type neurons responded to viewing the object during the FIX period; nonobject-type responded only to hand actions but not to visual stimulation. Motor type neurons responded equally well to manipulation in light and in darkness. Reproduced from Murata, A., Gallese, V., Luppino, G., Kaseda, M., and Sakata, H. 2000. Selectivity for the shape, size and orientation of objects for grasping in neurons of monkey parietal area AIP. J. Neurophysiol. 83, 2580–2601; figure 2).

Hand manipulation neurons in area 5 also signal how an object is grasped. Using digital video methods to quantify hand kinematics, Esther Gardner and colleagues found that area 5 neurons responded to the actions of the hand during object acquisition and manipulation (Ro, J. Y. *et al.*, 1998; Gardner, E. P. *et al.*, 1999; Ro, J. Y. *et al.*, 2000; Debowy, D. J. *et al.*, 2001; 2002; Gardner, E. P. *et al.*, 2002; 2007a). Activity in area 5 spanned the period from the start of reach through object manipulation (Figures 7b and 8). Responses began before the hand was stimulated directly by the object when approach was initiated. Firing rates peaked during hand preshaping or at contact and declined after the object was securely grasped in the hand. Neural activity during lifting and holding was weaker than during acquisition and concluded when the object was released from the hand.

Selectivity of neuronal firing rates for particular objects occurred most often after contact and during grasping and lifting actions. For example, the neuron in Figure 9e responded most vigorously to grasp and lift of a large round object (stages 3 and 4) but showed little distinction in firing rates between the test objects during approach or at contact. Most neurons

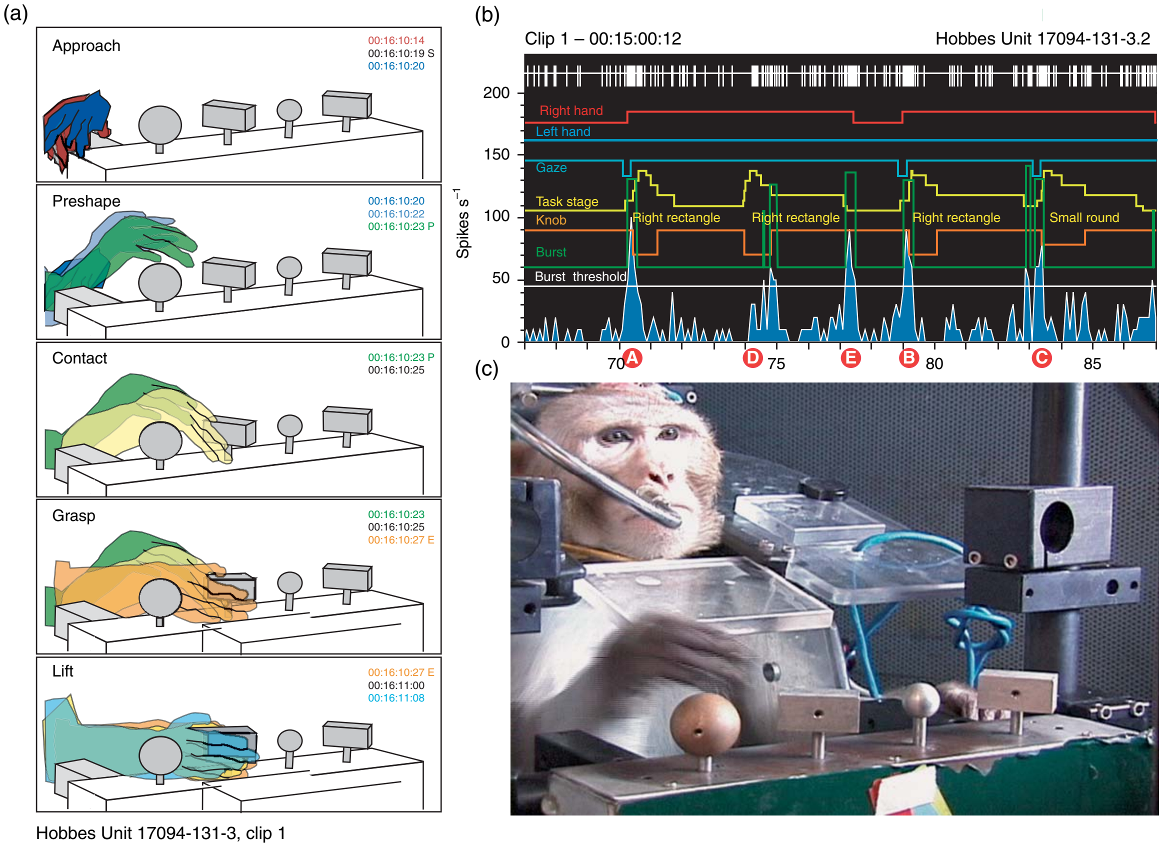

Figure 7 Hand kinematics and neural responses in area 5 during a prehension task. The animal was trained to grasp and lift one of four knobs designated by icons on a video monitor. (a) Kinematic actions of the hand during sequential stages of the task traced from digital video images of a single trial. Labels describe the action performed in the top image of each set. (b) Burst analysis graphs of continuous neural and behavioral activity recorded during the task. Neural responses evoked during the trial in Panel (a) are marked by the red A below the graph. Each burst in this 20 s record coincides with the initiation of a task trial (A–D), or grasp of the chair frame (E). Green burst trace: Periods of firing 1 SD above the mean rate for the entire analysis period. *Yellow task stage trace*: Each stepped pyramid marks a single trial. Upward deflections denote the start of stages 1–4 (approach, contact, grasp, and lift); downward deflections mark the onset of stages 5–8 (hold, lower, relax, and release). *Orange knob trace*: Downward pulses indicate knob location in the workspace and duration of hand contact. Other traces illustrate spontaneous actions of the two hands (red and blue) and gaze fixation on the target object (cyan, downward deflection). (c) Video image captured at the peak of burst A; maximum activity occurred during hand preshaping prior to contact. Modified from Gardner, E. P., Babu, K. S., Reitzen, S. D., Ghosh, S., Brown, A. M., Chen, J., Hall, A. L., Herzlinger, M. D., Kohlenstein, J. B., and Ro, J. Y. 2007a. Neurophysiology of prehension: I. Posterior parietal cortex and object-oriented hand behaviors. J. Neurophysiol. 97, 387–406; figures 4 and 5).

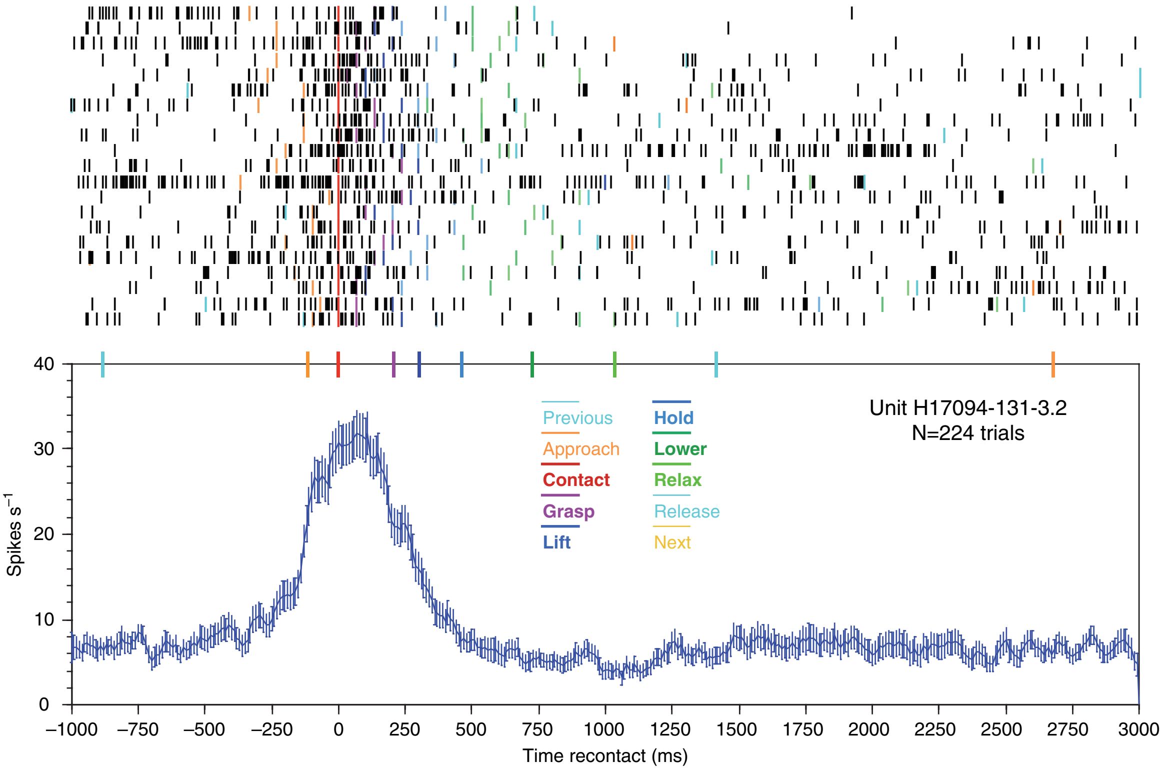

Figure 8 Raster and spike density plot of neural responses during the prehension task aligned to hand contact with the objects; error bars show SEM during each time epoch. Same neuron as in Figure 7. Colored lines on rasters and markers above the spike density graph indicate the onset times of the task stages relative to contact. Responses began ~250 ms before contact at the start of approach and peaked at contact. Modified from Gardner, E. P., Babu, K. S., Reitzen, S. D., Ghosh, S., Brown, A. M., Chen, J., Hall, A. L., Herzlinger, M. D., Kohlenstein, J. B., and Ro, J. Y. 2007a. Neurophysiology of prehension: I. Posterior parietal cortex and object-oriented hand behaviors. J. Neurophysiol. 97, 387–406; figure 7).

in area 5 displayed weak and subtle distinctions between objects as in Figure 9f. The slight preference of this neuron for the smallest object during grasping appears to reflect the tightly flexed posture of the fingers (Figure 9a–d).

The similarity of the hand postures used to grasp these objects and the overlap in evoked firing patterns throughout most of the task suggest that neurons in area 5, like those in area AIP, represent grasp actions of the hand rather than the particular shape of the grasped object. The persistence of neural activity after contact indicates that neurons in area 5 also monitor the success or failure of object acquisition. Dynamic error correction occurred when an incorrect object was touched, and it was reflected in immediate alteration of responses of area 5 neurons (Gardner, E. P. *et al.*, 2007a).

The strong responses observed during approach suggest that the motor commands for hand preshaping and grasping may originate in area 5 and as well as in AIP. Alternatively, area 5 neurons may receive an efference copy of motor commands from the ventral premotor cortex (area F5) that is itself activated from visuomotor signals originating in area AIP. Like reach neurons in the more medial regions of area 5, hand manipulation neurons in the SPL may provide a body schema of hand actions that allow them to compare the predictions of feed-forward grasping plans with feedback sensory information from the hand.

We were somewhat surprised by the weak selectivity for object shape in the area 5 population, as Iwamura and coworkers had reported shape-specific responses in the anterior bank of the IPS during spontaneous grasp of objects such as fruits, rulers, or blocks (Iwamura, Y. and Tanaka, M., 1978; Iwamura, Y. *et al.*, 1985; 1995; Iwamura, Y. and Tanaka, M., 1996). However, it is possible that the selectivity for shape described in their studies may actually reflect the animal's intentions or interest in the test objects. It is clear from Mountcastle's original observations that the intentions motivating grasp of food are different from those directed toward inedible wooden objects. Alternatively, the

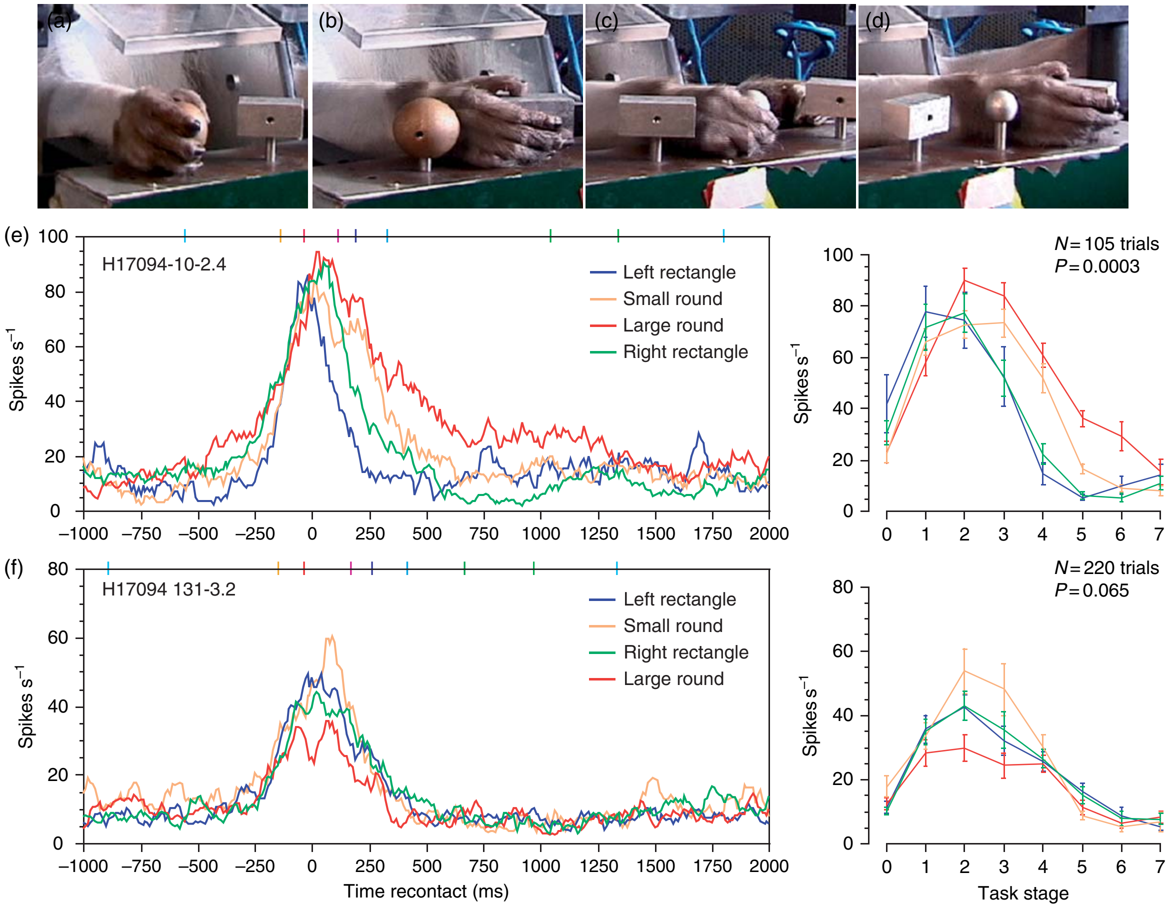

Figure 9 Shape selectivity of two different area 5 neurons during performance of the prehension task. (a–d) Video images of the grasp posture used for each knob captured during recordings from Unit H17094-131-3. (e–f) *Left panels*: Superimposed spike density plots evoked by the four test objects. Right panels: Average firing rates per task stage evoked by each object. The neuron in (e) responded most vigorously to grasp of the large round knob, particularly during lift and hold. The neuron in (f) preferred the small round knob and had the weakest response to the large one; responses to the two rectangles were similar, as these objects were grasped with the same posture.

apparent shape selectivity reported in the Iwamura and Tanaka studies may reflect the diverse hand postures and distinctive muscle activation patterns used to grasp their test objects (Brochier, T. *et al.*, 2004).

Hand manipulation neurons in areas 5 and 7 differ in their sensitivity to visual inputs. As noted above, 58% of the neurons recorded in area AIP responded to viewing as well as grasping objects, and most responded more vigorously during the task when both the hand and objects were visible. Mirror neurons recorded more caudally in area 7b responded to observation as well as performance of grasping, suggesting that they signal action recognition as well as motor planning (Rizzolatti, G. *et al.*, 2001; Rizzolatti, G. and Craighero, L., 2004; Fogassi, L. *et al.*, 2005).

Visual receptive fields in area 5 are rare and, when present, seem linked to view of the animal's own hand rather than to view of the object. Iriki A. and coworkers (1996; 2001) reported that such neurons respond to salient objects (such as food morsels) approaching the hand and fire at peak rates when the object is in range for grasp regardless of where the gaze is directed. These fields may extend beyond the hand when the animal uses a tool to rake in distant food morsels. Maravita A. and Iriki A. (2004) proposed that area 5 neurons may contribute to the animal's own body schema, the conscious perception of one's own actions.

Functional magnetic resonance imaging (fMRI) studies in humans have revealed similar areas for grasping in the human cerebral cortex (Figure 10). The first of these studies by Binkofski, F. *et al.* (1998) demonstrated that patients with lesions that included the anterior intraparietal sulcus had impairments of grasping behaviors whereas patients with PPC lesions sparing this

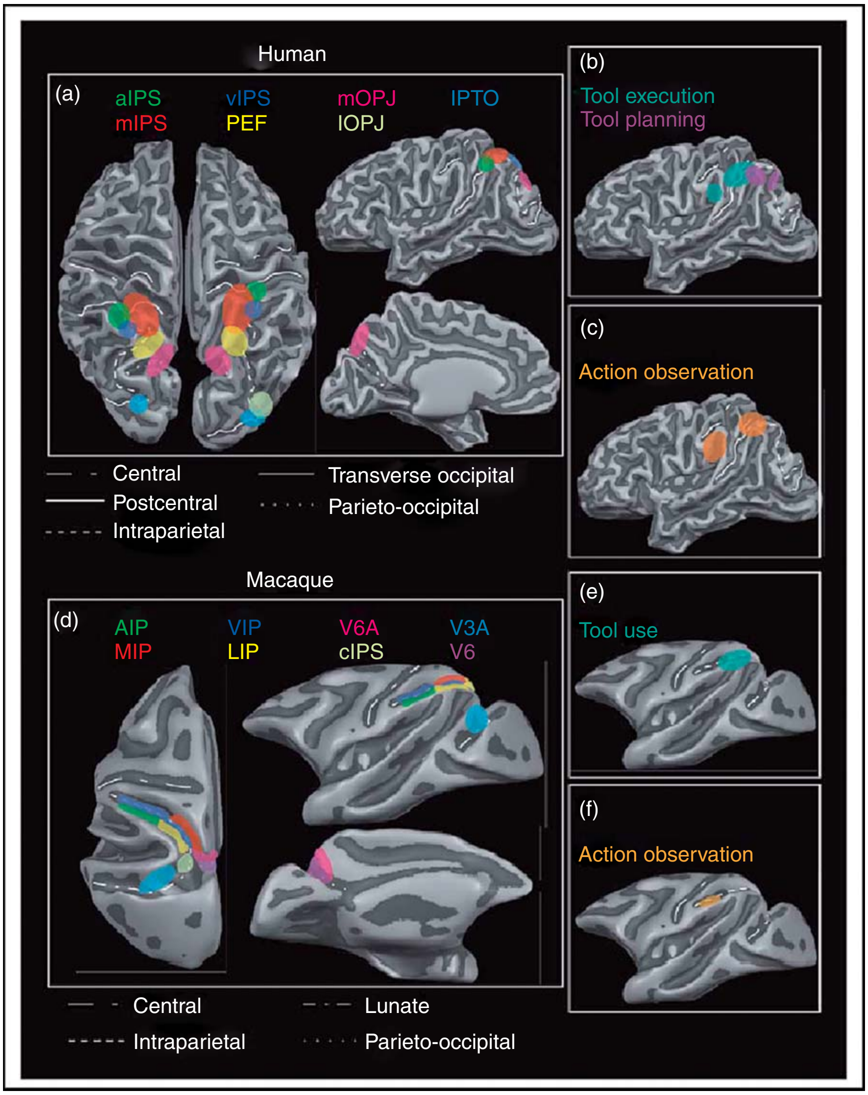

Figure 10 Inflated brain maps of the macaque and human brain showing regions of posterior parietal cortex (PPC) involved in various skilled tasks. Reproduced from Culham, J. C. and Valyear, K. F. 2006. Human parietal cortex in action. Curr. Opin. Neurobiol. 16, 205–212; figure 1).

region did not. The deficits in hand preshaping included slower hand opening during reach, and unusually large apertures betweeen the thumb and index finger of the contralesional hand before contact, compared to age-matched control subjects, and to their own ipsilesional hand. fMRI scans of neurologically normal adults in this same study revealed a focus of activation in the lateral bank of the anterior intraparietal sulcus (aIPS) when they grasped and manipulated rectangular blocks. The activation sites in the aIPS during grasping have been confirmed in subsequent studies comparing grasping and reaching behaviors (Culham, J. C., *et al.*, 2003; Frey, S. H., *et al.*, 2005). These same brain areas are also activated by viewing grasping actions performed by other individuals (Buccino, G., *et al.*, 2001; Fogassi, L., *et al.*, 2005; Shmuelof, L. and Zohary, E., 2005, 2006). More detailed descriptions of areas in the human brain involved in grasping are provided in several excellent reviews recently published (Culham, J. C., and Valyear, K. F., 2006; Culham, J. C., *et al.*, 2006; Grefkes, C., and Fink, G. R., 2005; Tunik, E., *et al.*, 2007).

In summary, hand manipulation neurons in areas 5 and 7 participate in sensorimotor networks involved in grasp planning, prediction of sensory stimulation, and monitoring of appropriate execution of the desired actions. Firing patterns of these neurons appear to reflect the internal motor commands needed to accomplish task goals, as well as the sensory events resulting from self-generated movement. The onset of firing seems best correlated with the preparation of specific actions. The external tactile stimulation of the hand by the grasped object appears to reinforce the motor plans by signaling the accomplishment of the desired action when successful or provides an error signal for corrective maneuvers when it fails.

6.12.4 Bilateral Coordination of the Hands

Neurons in both the dorsal and ventral stream pathways for touch respond to tactile stimulation of both the contralateral and ipsilateral hands. Anatomical studies indicate that callosal connections within the hand representation do not occur in S-I but first appear in S-II (reviewed in Disbrow, E. *et al.*, 2003) and in PPC (Jones, E. G. *et al.*, 1978; Padberg, J. *et al.*, 2005). Bilateral receptive fields on the hands of monkeys have been found in S-II cortex (Whitsel, B. L. *et al.*, 1969; Robinson, C. J. and Burton, H., 1980a; 1980b; Burton, H., 1986; Disbrow, E. *et al.*, 2003; Fitzgerald, P. J. *et al.*, 2004; 2006) and in PPC (Mountcastle, V. B. *et al.*, 1975; Leinonen, L. *et al.*, 1979; Koch, K. W. and Fuster, J. M., 1989; Iwamura, Y. *et al.*, 1994; Iwamura, Y., 2000; Iwamura, Y. *et al.*, 2002; Padberg, J. *et al.*, 2005), and on midline structures in S-I (Taoka, M. *et al.*, 1998; Iwamura, Y., 2000).

The functional role of distal bilateral receptive fields is unclear and has not been tested rigorously in monkeys. Using digital video, we analyzed how hand kinematics are related to neuronal spike trains recorded in area 5 as monkeys performed trained prehension tasks and spontaneous behaviors engaging both hands (Gardner, E. P. *et al.*, 2001). Many of the cells analyzed responded equally to grasp by either hand. These bimanual neurons represented equivalent actions of the right and the left hand in a common cell population. For example, the neurons shown in Figure 11 responded equally to grasp of a raisin with the ipsilateral left hand (burst D) and the contralateral right hand (burst E). The responses to precision grip were similar to those evoked in the same neurons during the trained task (Figure 7). Like the hand manipulation neurons described by

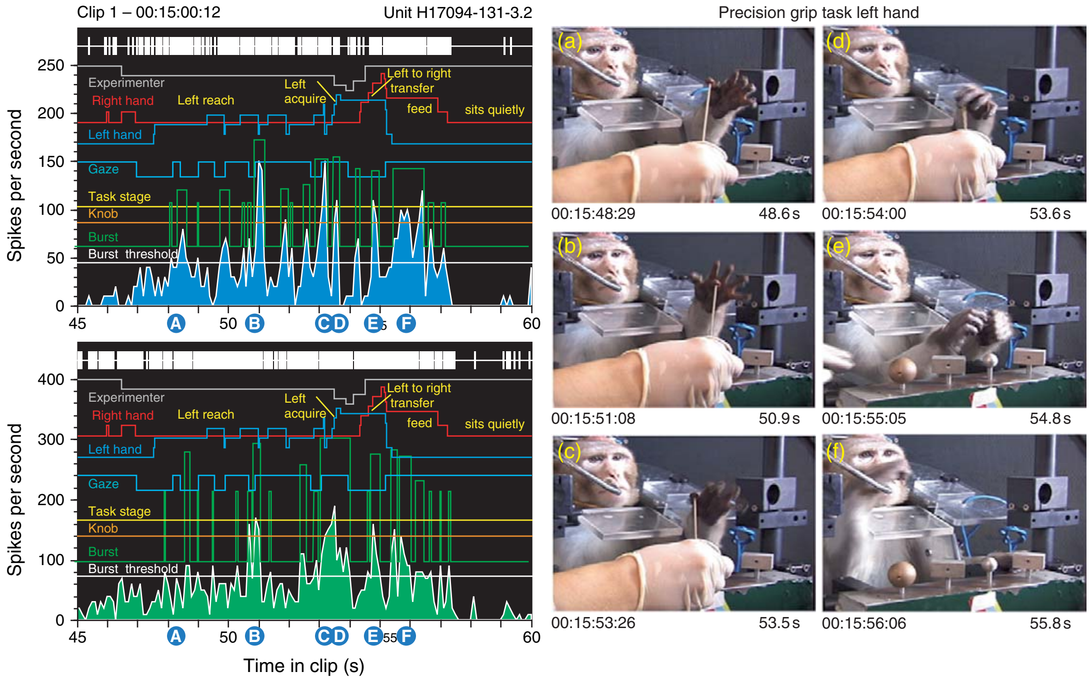

Figure 11 Responses of two simultaneously recorded area 5 neurons to acquisition of a raisin with the ipsilateral (left) hand. Natural grasping actions of the right and left hands (red and blue traces) are represented in the burst analysis records using the same format as the task stages in Figure 7. Each attempt to grasp the raisin was accompanied by a burst of impulses (A–D). Video images captured at the times marked by letters below the burst analysis graphs; note that when reaching toward a moving target, the animal opened the fingers using a baseball glove-like posture to maximize contact area on the hand. Once the stick was immobilized, the animal plucked the raisin using a precision grip between the thumb and digits 2 and 3.

Leinonen L. *et al.* (1979) in area 7b, these area 5 neurons fired at high rates as the hand tracked movements of the raisin by the experimenter (bursts A, B, and C). Activity declined once the raisin was acquired in the hand (burst D), or when the animal withdrew the hand as the target moved beyond reach. These neurons also responded strongly as the hand brought the raisin to the mouth to eat it (burst F).

Other neurons in area 5 fired most intensely when bilateral actions were coordinated between the left and the right hand, as when food morsels were transferred between them (Figure 12). These

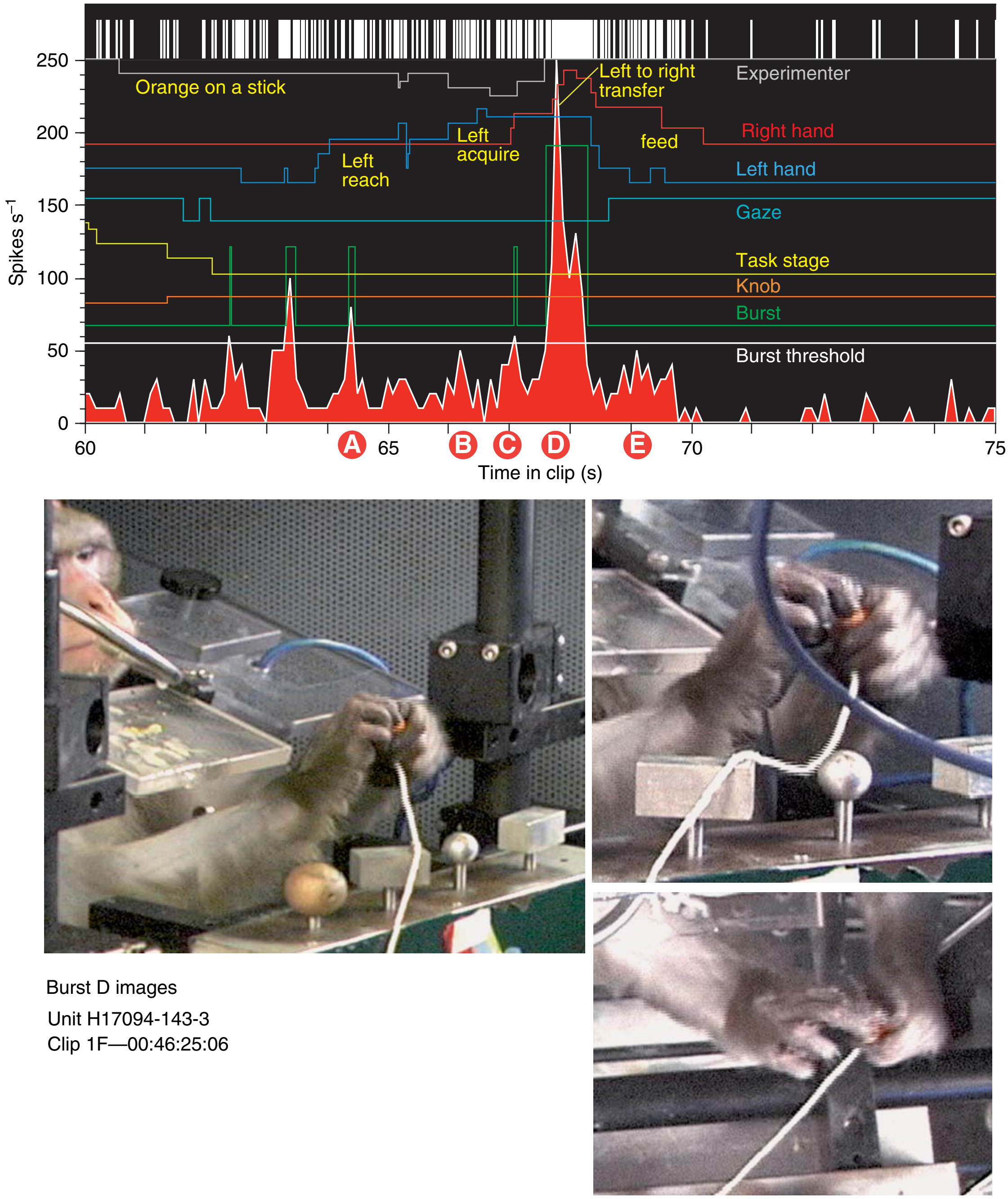

Figure 12 Responses of an intrapersonal-coordinated neuron in area 5 to precision grasp of an orange segment; the strongest responses were obtained when the orange was transferred from the left to the right hand (burst D). Images captured at the time of peak firing on three different cameras.

intrapersonal-coordinated neurons did not just encode equivalent tactile information from either side but preferentially signaled coincident somatosensory data shared between hemispheres during synergistic hand actions. They responded more vigorously to manipulatory actions of the two hands during bimanual transfer than to acquisition or release of food by either hand alone. Kinematic analyses of the hand actions indicated that hand-to-hand transfer integrated two prehensile actions: one hand slowly released grip as the other acquired the object. Bimanual and intrapersonal coordination neurons thus provide somesthetic feedback from both limbs, encoding whether the hands act independently or in concert. Consequently, frontal motor areas receive information, allowing them to coordinate the actions of both hands.

Two complementary mechanisms have been envisaged for bilateral coordination of the left and right hands. Temporal coordination involves a bilateral schema in which each hand is controlled separately in the contralateral hemisphere. Coordinated actions between the hands would need to be synchronized temporally by simultaneous activity in homologous regions on both sides of the brain (Gerloff, C. and Andres, F. G., 2002; Serrien, D. J. and Brown, P., 2002; Swinner, S. P., 2002; Serrien, D. J. *et al.*, 2006). Spatial specialization is a unilateral mechanism in which each hemisphere has neurons activated by bimanual actions (Kermadi, I. *et al.*, 2000; Donchin, *et al.*, 1998, 2002). Specific classes of these bilateral neurons would be engaged when coordinated bimanual activity is required. Although the temporal coordination hypothesis is the traditional view, the spatial specialization hypothesis provides an attractive mechanism for bilateral control for various reasons. In addition to the obvious advantage of providing redundant circuits for recovery from cortical damage, autonomous bilateral control is a prerequisite for hemispheric specialization and unilateral dominance. It also could explain some bilateral interactions observed between the hands during skilled tasks. Grasp forces exerted by each hand are interdependent regardless of whether the hands manipulate the same or different objects (Marteniuk, R. G. *et al.*, 1984; Paulignan, Y. *et al.*, 1989; Geffen, G. M. *et al.*, 1994; Wiesendanger, M. *et al.*, 1996; Ohki, Y. and Johansson, R. S., 1999; Birznieks, I. *et al.*, 2001; Serrien, D. J. and Wiesendanger, M., 2001; Serrien, D. J. *et al.*, 2006); a common output pathway would provide a simple circuit for coordinating grip force during bimanual grasp. PPC is a likely source of such bilateral control, as lesions to the posterior corpus callosum have been associated with losses of coordinated actions between the hands (Eliassen, J. C. *et al.*, 1999; Serrien, D. J. *et al.*, 2001).

6.12.5 Posterior Parietal Cortex and Active Touch

In their original study, Mountcastle V. B. *et al.* (1975) emphasized the difficulty of evoking responses in areas 5 and 7 to light tactile stimuli applied to the hand. However, these neurons were successfully activated when the animal's attention was directed toward the stimuli as a mechanism for reward or during active palpation of surfaces during tactile discrimination tasks. Like the studies of reach and grasp described above, the active touch studies involved goal-directed hand movements. However, the hand actions were directed not toward acquiring objects, but rather to acquiring sensory information needed for reward. Although many of these studies attributed recording sites in the rostral bank of the IPS to area 2, this region is now properly included in area 5 (Pandya D. N. and Selzer B., 1982; Pons, T. P. *et al.*, 1985; Lewis, J. W. *et al.* 1999).

Darian-Smith I. and colleagues (1984) trained monkeys to scan their fingers over gratings using a back-and-forth sinusoidal pattern. About one-third of the cells recorded in their area 5 population responded to the direction of hand movement but failed to signal the spatial properties of the grating surface. Indeed these authors expressed disappointment at the failure to find a greater population of neurons sensitive to the properties of the textured surface. Similarly, Ageranioti-Bélanger S. A. and Chapman C. E. (1992) classified area 5 responses to scans of gratings and smooth surfaces as either texture-related (25%) or movement-related (26%). These neurons were presumed to underlie the analysis of surface texture and the representation of the physical parameters of movement, respectively. Their movement-related cells showed monotonic increases in firing rates precisely timed to the onset and end of hand movement and were independent of whether the surface texture was rough or smooth. In addition, 35% of the texture-related units responded more vigorously during active performance of the scanning movement than to passive stimulation of the fingers with the same surfaces (texture- and movement-related cells); no such units were found in area 3b, and only one was encountered in area 1.

Lastly, they described neurons that were silent during the scanning movement but subsequently fired a burst that was stronger for rough surfaces, suggesting that they signaled the perceptual decision made by the animal.

Studies using procedural memory tasks – in which the animal had to retain visual information about a target's shape or location during a delay period – are consistent with the notion that PPC activity may express the intention to execute a specific motor program. Fifty percent of neurons tested in areas 2, 5, and 7 by Joaquin Fuster and colleagues showed sustained activity during a delayed visual–haptic match-to-sample task related to the surface texture of a viewed object (Koch, K. W. and Fuster, J. M., 1989; Zhou, Y. D. and Fuster, J. M., 1996; 1997; 2000); tactile responses to palpation of the object were of matching sign. These authors proposed that alterations of firing prior to hand contact with an object may represent long-term tactile memory associations with objects previously perceived by touch or by vision. Zhou Y. D. and Fuster J. M. (2000) suggested that, by association, the visual cue might activate the internal representation of the object's tactile features to enable the correct choice. Alternatively, the firing patterns could represent the upcoming exploratory procedures used during palpation by the hand to distinguish the object properties (Klatzky, R. A. *et al.*, 1985; Bodegård, A. *et al.*, 2001).

Object manipulation activates similar regions in the human brain (Binkofski, F., *et al.*, 1999; Bodegård, A. *et al.*, 2001; Grefkes, C., *et al.*, 2002; Stoeckel, M. C., *et al.*, 2004), including area aIPS and the anterior portion of the superior parietal cortex (aSPL) that corresponds to the macaque area 5 hand representation. Activation of aSPL was particularly strong when subjects had to palpate the surfaces to discriminate object dimensions or form, while area aIPS was preferentially activated in cross-modal visual–tactile matching tasks. Neurological tests of stereognosis in humans and psychophysical tests of complex tactile discrimination in humans and animals can be considered goal-directed actions in which the aim is to acquire information about objects, rather than to gain possession of objects as in prehension tasks. The common neurological substrate of both types of behaviors supports hypotheses that the principal function of the dorsal stream involves both the planning of such behaviors and on-line control and adjustment of hand actions to achieve the intended goal.

6.12.6 Conclusions

We have shown in this chapter that goal-directed hand and arm movements seem to play a key role in the responses of neurons in PPC. Although most of the current research has analyzed reaching, pointing, and grasping behaviors, studies of active touch should also be included in analyses of PPC function. The common feature of all of these studies has been the importance of directing actions of the hand to internally generated task goals such as acquiring objects or information about them that are beneficial or desirable to the subject. Repeated experience and practice allows the subject, whether human or monkey, to plan the action efficiently and to monitor successful execution. The feedback circuits between parietal and frontal cortex allow dynamic error correction and updating of existing motor programs. They help guide hand movements to salient targets on an object, whether for efficient grasp or for exploratory palpation. The sensory feedback provided to S-I cortex from the hand may in turn call forth more information by redirecting the hand elsewhere on the object. As such, these circuits enable acquisition of new skills and the maintenance of a repertoire of learned adaptive behaviors of the hand.

Lesions of the hand representation of PPC result in paucity of exploratory and skilled movements of the hand in humans and deficits in stereognosis and other complex tactile recognition tasks (reviewed in Pause, M. *et al.*, 1989; Ghika, J. *et al.*, 1998; Binkofski, F. *et al.*, 2001; Freund, H.-J., 2001; Jäncke, L. *et al.*, 2001). The importance of PPC in monitoring and guiding sensorimotor functions of the hand may explain the neurophysiological basis of such disorders.

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