15 Coding of Movement Intentions

Hansjörg Scherberger, Rodrigo Quian Quiroga,
and Richard A. Andersen

CONTENTS

15.1 INTRODUCTION

Movement intentions are planning signals of the brain that convey goals of upcoming movements. They emerge from sensory information that has entered the brain through various perceptual channels, or from internal states of the brain. Most often, motor intentions originate neither from purely external nor from entirely internal signals, but they are elicited from a combination of both.

The posterior parietal cortex and the premotor cortex play a central role for the coding of movement intentions. As we will see, both regions contain specific areas that are involved in the planning of motor behavior. They establish an inter-areal network whose premotor part is connected strongly to frontal areas and thereby linked to motor control (Rizzolatti and Luppino, 2001; Lemon, 2008), while the posterior parietal cortex is linked to sensory input, thus representing a large variety of spatial and object-related information (Andersen and Buneo, 2002; Buneo and Andersen, 2006). The transformation of sensory and internal signals into motor goals or movement intentions is a central role of this network. Though many details are still unclear, it appears that the posterior parietal cortex and the premotor cortex are both subdivided into several distinct sub-regions that are specialized for particular motor functions. Furthermore, this transformation of sensory information into motor actions is constantly updated, as we know from many psychophysical and lesion experiments (Clower et al., 1996; Wise et al., 1998; Kurata and Hoshi, 1999).

This chapter highlights the role of the posterior parietal and premotor cortices in motor planning, including movement specificity, action and target selection, reward modulation, and the coding of

information in various coordinate frames. Furthermore, it discusses the potential use of these intentional signals for neural decoding in the context of neural prosthetics.

15.2 ANATOMY OF POSTERIOR PARIETAL AND PREMOTOR CORTEX

The location of the posterior parietal and premotor cortices, including some identified subregions of particular relevance, are depicted in Figure 15.1. The posterior parietal cortex is located anterior to the visual cortex and posterior to the primary somatosensory cortex. It integrates sensory information from primary sensory areas and generates a representation of objects and space of the outside world, which is then further processed for the generation of specific actions. For example, neurons in the lateral intraparietal (LIP) area encode visual stimuli that are processed for the planning of saccadic eye movements (rapid eye movements to particular locations). In contrast, neurons in the parietal reach region (PRR), located more medial and posterior along the intraparietal sulcus, encode the goal and the trajectories of upcoming arm-reaching movements (Andersen et al., 1997; Andersen and Buneo, 2002; Scherberger and Andersen, 2003; Mulliken et al., 2008a,b). More anteriorly and laterally, neurons in the anterior intraparietal (AIP) area represent the shape and orientation of graspable objects and are specifically active for the planning and execution of hand-grasping movements (Sakata et al., 1995; Baumann et al., 2009).

Similarly, neurons in the premotor cortex integrate higher-order sensory and also motor information to generate specific movement intentions. The premotor cortex is located anterior to the primary motor cortex and posterior to the prefrontal cortex. Like posterior parietal cortex, the premotor cortex contains specialized sub-areas for eye-, arm-, and hand movements (Rizzolatti et al., 1997; Rizzolatti and Luppino, 2001). The frontal eye field (FEF) contains neurons that encode saccadic eye movements. More medially, the dorsal premotor area (PMd) is dedicated to encoding reaching movements, while more laterally the rostral portion of the ventral premotor cortex (also called area F5) is specifically active for the preparation and execution of hand-grasping movements. Given the close coordination of eye-, arm-, and hand movements in everyday life, it is not surprising that the premotor areas are anatomically intimately interconnected (Matelli and Luppino, 2001).
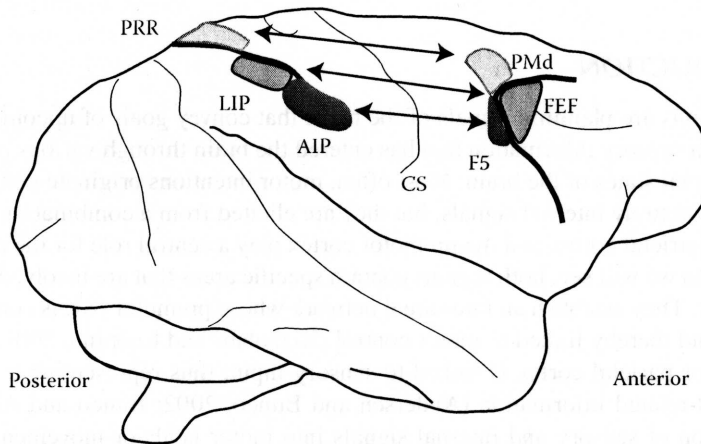

FIGURE 15.1 Posterior parietal and premotor brain areas of the macaque brain involved in coding movement intentions. Specific subareas in parietal and premotor cortex code different functions. Posterior parietal cortex areas: parietal reach region (PRR; arm reaching, light gray) lateral intraparietal area (LIP; eye movements, medium gray), and anterior intraparietal area (AIP; hand grasping, dark gray). Premotor cortex areas: dorsal premotor cortex (PMd; arm reaching, also light gray) frontal eye field (FEF; eye movements, also medium gray), and premotor area F5 (hand grasping, also dark gray). Functionally related areas share direct and reciprocal anatomical projections (bidirectional arrows). CS, central sulcus; anterior–posterior, anterior–posterior direction in the saggital plane.

They also receive strong projections from more anterior aspects of the frontal lobe, where cognitive and motivational signals can be retrieved (Rizzolatti et al., 1988; Belmalih et al., 2009).

Importantly, the different eye-, arm-, and hand-movement-related premotor areas are directly and reciprocally connected to their corresponding areas in the posterior parietal cortex: PMd with PRR, FEF with LIP, and F5 with AIP (Figure 15.1; bidirectional arrows). These connections constitute an action-specific network for sensorimotor transformation across premotor and posterior parietal cortex, which is able to combine high-level information in order to generate movement intentions (Desmurget and Sirigu, 2009).

15.3 PLANNING OF SPECIFIC ACTIONS

To understand how specific cortical regions of the primate brain represent particular movements and contribute to the generation of movement intentions, electrophysiological single-neuron recordings have been performed in awake, behaving monkeys. For these studies, animals are first trained to perform a specific behavioral task and then the activity of individual neurons is recorded using movable or permanently implanted microelectrodes while the animals perform the trained behavior. This methodology for recording neuronal activity from the brain of behaving monkeys has been well established for nearly 50 years (Cordeau et al., 1960; Evarts, 1965; Mountcastle et al., 1975).

15.3.1 Eye and Reach Movement Planning

An important example of such a behavioral task is a delayed response task, in which the instruction (cue) to perform a specific action is presented well before the start (go) signal indicates the time of moment initiation. An example of a delayed response task, in which animals performed rapid eye movements (saccades) to peripheral targets, is illustrated in Figure 15.2a. Generally, monkeys are trained to look at a red light-emitting diode (LED) and to touch the location of a green LED. In the delayed-saccade task, the monkey first looks at and touches a central fixation light (red and green LED). Then, a red target-cue light flashes briefly (~300 ms) at one of eight possible locations in the peripheral visual field. The animal must then wait for about 1 s until the central fixation light extinguishes. At that time he can look at the target (by making a saccade), but he must still continue to touch the center. Thus, during the waiting time between the brief flash of the red target light and the extinction of the central-fixation light, the animal must remember the location of the target and plan the saccade, but must withhold its execution. If the monkey is successful in the trial (i.e., if he waits the required time and then looks at the target while still touching the center), he receives a reward consisting of a small amount of juice, whereas no reward is given when the trial is not completed successfully. In either case, the animal can initiate the next trial by looking again at the central fixation light when it reappears after some delay (~1 s).

Similarly, a delayed-reach task can be constructed in an analogous fashion. For such an arm-reaching task, the sequence of events is the same, except that the cue instruction is given with a green LED, and the animal plans and executes a reach to the target while continuing to look at the center-fixation light. For any given trial, the monkey is informed about the type of action (i.e., delayed-saccade vs. delayed-reach) by using two different target colors (i.e., red for saccade, green for reach). In this way, individual delayed-saccade and delayed-reach trials can be randomly interleaved.

After the animal has learned these tasks, neural activity is recorded from the brain with microelectrodes while the monkey performs delayed-saccade and delayed-reach trials. Figure 15.2b shows the activity of sample neurons in the posterior parietal areas LIP (top row) and PRR (bottom row) during the two tasks (Snyder et al., 1997). In the saccade task, the LIP neuron shows elevated activity during the target-cue, the delay period, and the movement epoch of the saccade; in the reach task, the same neuron shows elevated activity only during the cue epoch, indicating that the LIP neuron is specifically active for saccades during the planning and movement epochs, but not for reach planning and movements. In contrast, the PRR neuron shows the opposite effect: it is only transiently
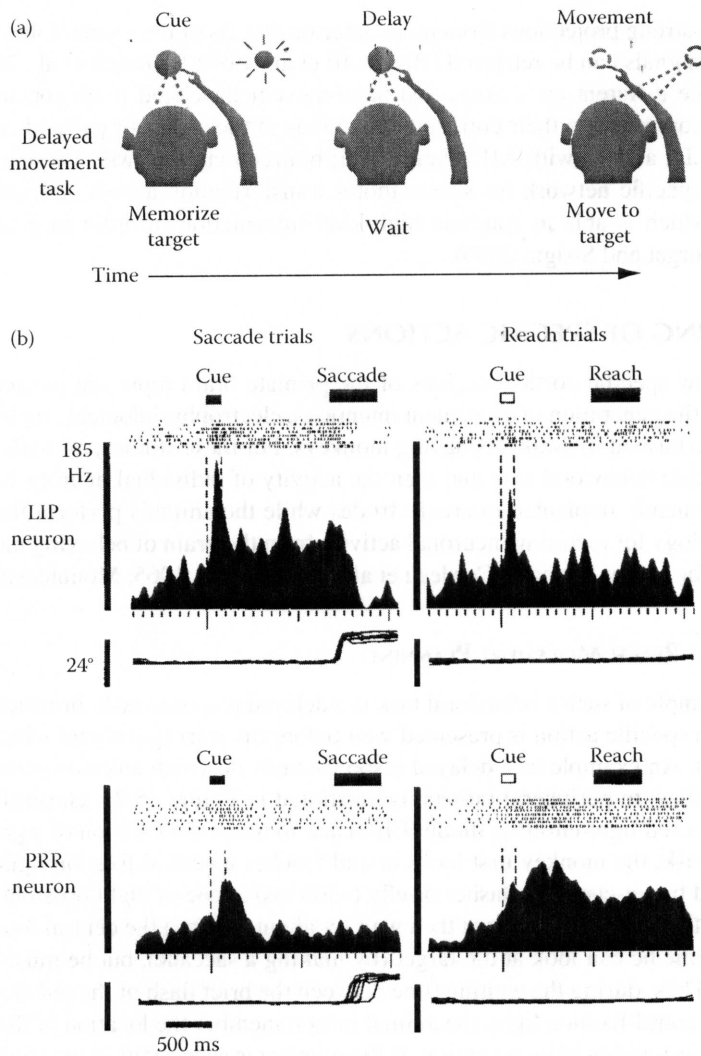
FIGURE 15.2 Saccade and reach movement coding in posterior parietal cortex. (a) Delayed-movement task with task epochs "Cue, 'Delay,' and Movement," which separate sensory from motor components of the behavior. Animals planned a movement to a briefly flashed visual target, waited in complete darkness for a go-signal, and then executed the action (here a saccade) to the remembered target location. (b) Intention-specific spiking activity in LIP and PRR during a delayed-saccade task and a delayed-reach task. An LIP neuron (top row, left) showed elevated activity during the delay period (150–600 ms after the cue) before a saccade, but not before a reach movement (top row, right). In contrast, a PRR neuron (bottom row, left) showed no saccade-related delay activity, but was strongly active in the delay period before a reach movement (bottom row, right). Each panel shows a spike raster (all trials aligned on cue presentation, every third action potential shown) and the corresponding spike density histogram. Short horizontal bars: timing of target flash (filled bar: saccade cue; open bar: reach cue); long horizontal bars: approximate time of motor response (saccade or reach). Thin horizontal lines at the bottom of each panel: vertical eye position. Vertical scale bars: neuronal firing rate (Hz) and vertical eye position (degrees). (c) Directional tuning of a PPR cell with a right/down preferred direction. For each reach direction (white arrows), a spike density histograms is plotted (as in b) to illustrate the neural activity for this reach direction. ((a,c) Modified from Scherberger H, Andersen RA. 2003. In: *The Visual Neurosciences*, pp 1324–1336. Cambridge, MA: MIT Press, by permission of the MIT Press. (b) Modified from Snyder LH, Batista AP, Andersen RA. 1997. *Nature* 386:167–170, by permission from Macmillan Publishers Ltd.)
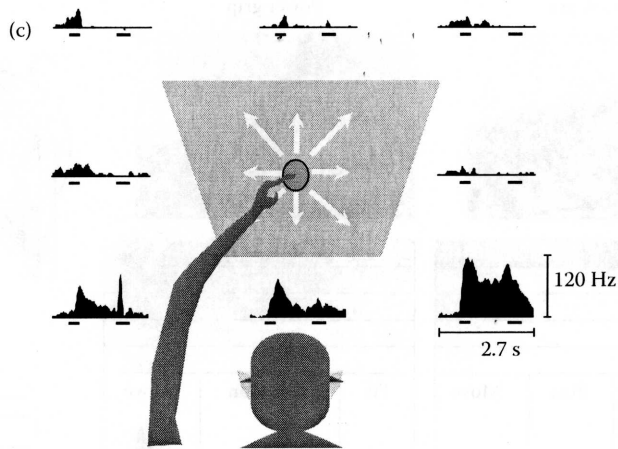
FIGURE 15.2 Continued.

active to the cue during the saccade task, and is strongly active during the cue, delay, and movement epochs of the reach task. From these representative examples, one can conclude that neurons in LIP and PRR are more active for saccades and arm movements, respectively (Snyder et al., 1997). The activity of these neurons during the delay epoch suggests that they play a role in planning of the movement, and that they are involved in the sensorimotor transformation of behaviorally relevant sensory stimuli into a representation that encodes a specific movement plan.

As the example set of LIP and PRR neurons in Figure 15.2b illustrates, specific areas in posterior parietal cortex are selectively active for particular types of actions (Rizzolatti and Luppino, 2001; Andersen and Buneo, 2002). But how do they encode these actions? Figure 15.2c shows the activity of a PRR neuron during the delayed-reach task for movements from the central fixation point to eight different peripheral targets. The example neuron is strongly active in the cue, delay, and movement epochs when the animal reaches to the right-down target, but it is essentially silent when he moves to the opposite (left-up) target and is intermediately active when he moves to targets at other downward locations. Such a movement directional preference is typical for posterior parietal and premotor neurons. Many neurons have an individual preference (Mountcastle et al., 1975; Weinrich et al., 1984), and the overall neuronal population represents movements to all directions. Thus, each individual neuron in the population is essentially voting for (is tuned to) a particular movement direction, and the overall movement is determined by the combined activity of a larger number of neurons.

15.3.2 GRASP MOVEMENT PLANNING

Despite the fact that hand movements of primates are quite complex, the neural mechanisms for the planning of hand-grasping movements seem to be organized very similarly to those of eye and arm movements (Sakata et al., 1995; Murata et al., 1997; Baumann et al., 2009; Fluet et al., 2010). Figure 15.3a shows the activity of a sample neuron in posterior parietal area AIP during a delayed-grasping task, in which the animal grasped a handle using either a precision grip or a power grip (Baumann et al., 2009). Typically, monkeys would use a power grip to hold a branch on a tree and a precision grip to pick up a raisin from the ground. In this experiment, the handle was also positioned in various orientations. During the cue epoch, a spotlight illuminating the handle revealed its orientation, while the color of an LED instructed the animal which grip to use (precision or power grip). In the subsequent delay epoch, the animal could prepare the grasping movement, but had to wait until the dimming of the central fixation light to actually perform the grasp. Thus, this is a delayed reach-to-grasp task.

FIGURE 15.3 Grasp-related activity in parietal and premotor cortex. (a) Activity of a typical AIP neuron during a delayed-grasping task. A monkey grasps a rotatable handle (far right) either with a precision-grip (left column) or a power-grip (right column). Spike rasters and average firing rates are presented in different gray-scales for each of the five handle orientations (key at far right). The neuron is maximally active (i.e., tuned) for the right-most handle orientation (+50°; black line) and for power grips. (b) Percentage of orientation and grip-type tuned neurons in the AIP population (571 single neurons) during the course of the task (two-way ANOVA, $p < 0.01$; sliding window of 200-ms width, centered on each data point). Gray line: percentage of cells tuned for handle orientation; black line: same for grip-type tuning. Data curves are aligned to the end of the cue ($t = 0$; arrowhead marker) up to 0.6 s, after which they are aligned to the movement start (dotted line). Realignment is indicated by a gap in the curves at 0.6 s. (c) The same analysis as in (b), but for a population of 420 neurons from F5. (Modified from Baumann M et al. 2009. *J Neurosci* 29:6436–6448; Fluet MC, Baumann MA, Scherberger H. 2010. *J Neurosci* 30:15175–15184.)

The firing rate of the AIP neuron in Figure 15.3a increased sharply after the start of the cue epoch, and most strongly for power grips with handle orientation of +50°. The neuron was also tuned (more selectively) to the +50° orientation for the precision grip, but with a lower response strength compared to the power grips. Thus, this neuron was sensitive to the handle orientation as well as the grip type. In the overall population of the ~550 AIP neurons recorded from two monkeys, many neurons were sensitive to various handle orientations and/or grip types. Figure 15.3b shows the results of a 2-way ANOVA analysis with factors grip type and orientation within a 200-ms sliding window that was moved across the task. Many AIP neurons represented the handle orientation from the cue epoch onward. In contrast, the number of neurons representing grip type increased during the task and peaked during movement execution. In premotor cortical area F5, which is closely related both anatomically and functionally to posterior parietal area AIP, similar grasp-related activity was also observed (Figure 15.3c) (Fluet et al., 2010). The main difference was that object orientation was encoded less prominently in F5 than AIP. Furthermore, other experiments have shown that AIP and F5 are sensitive to the visual presentation of objects even when no grasping actions are prepared (Murata et al., 2000; Raos et al., 2006).

These few examples already illustrate that the posterior parietal and premotor cortices can be regarded as a network that integrates sensory and cognitive signals for the generation of actions. While particular areas represent specific types of actions, individual neurons in these areas represent signals for the planning and execution of particular movements, as well as sensory stimuli related to the planning of these actions.

15.4   DECISION MAKING FOR ACTIONS

From everyday behavior, we know that movements are not slavishly driven by external stimuli. We often select an action from a multitude of possible options, and we can act even in the absence of external stimuli. Under such natural circumstances, the posterior parietal and premotor cortex could represent aspects of the sensory stimuli, of the motor plan, or both.

15.4.1   ACTION SELECTION

To investigate the autonomous selection of appropriate actions, a free-choice task was designed in which animals could freely select the type of action, either a reach movement or a saccade, to acquire a specific target (Cui and Andersen, 2007). Figure 15.4a illustrates this free-choice action selection paradigm. Animals first fixated and touched a central fixation position before a peripheral target was briefly cued with the simultaneous illumination of a red and a green LED light. This cue informed the animal about the location of the upcoming movement, but was uninformative about the required type of action, either a reach movement or a saccade. After the cue period, in 25% of the trials only the green LED was extinguished and the red LED was left on, which instructed the animal to make a saccade to the target. In another 25% of the trials, the green LED was left on instructing the monkey to make a reach movement to the target, and in the remaining 50% of the trials both peripheral LEDs were extinguished, which left the animal a free choice between acquiring the target either with a saccade (and keeping the hand at the center), or with the hand (and keeping the eyes fixating the center). Importantly, in these effector choice trials the animal could freely select between both types of actions. However, to prevent a systematic bias of the animal's choice, the monkey was rewarded according to a competitive game played with the computer, in which a reward was delivered only if the choice of the monkey matched the computer's choice that was biased against the animal's choice sequence in the preceding trials.

In neural recordings, single cell activity was investigated in LIP and PRR while animals performed this set of tasks. Figure 15.4b shows spiking activity of two example neurons from LIP and PRR for the free choice trials. In both neurons, the activity was initially elevated during the cue epoch independently of the later choice. The early elevation of activity in both LIP and PRR is due to the design of the task.
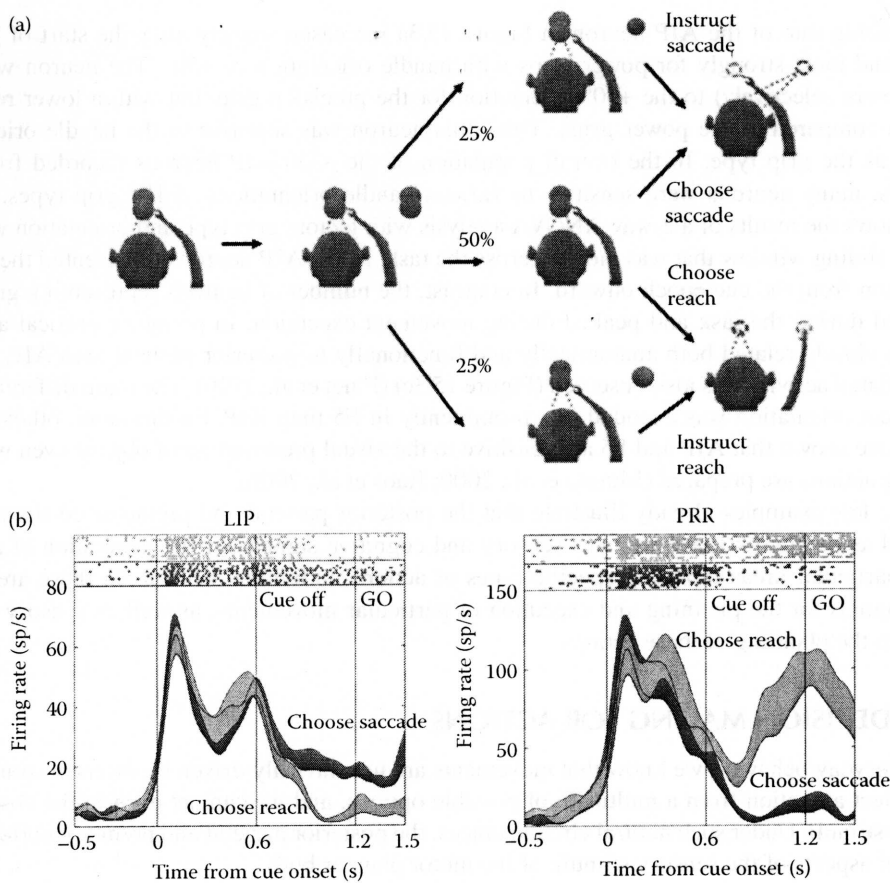
FIGURE 15.4   Activity in parietal areas LIP and PRR during an action selection task. (a) Action selection task, in which a monkey first fixated and touched a pair of red and green LEDs, before a pair of red and green LEDs was presented in a peripheral location during a first instruction period, which indicated to the animal the target location, but not which movement to make (saccade or reach). In 50% of all trials, both peripheral LEDs were extinguished after this first instruction period, which indicated a free choice to the animal to acquire the peripheral target with either a reach movement or a saccade in order to receive a reward. However, in 25% of all trials, only the green LED was extinguished, and the red LED remained on, which instructed the animal to make a saccade to the target, while in the remaining 25% of all trials, the red LED was extinguished and the green LED remained on, thus indicating to the monkey that a reach movement to the instructed target location was required to receive a reward. (b) Example neuron from LIP (left panel) and from PRR (right panel) during the effector choice task. Both neurons show elevated activity during the instruction (cue) period for both reach and saccade selections. In the LIP neuron, activity stayed elevated during the delay epoch (after the cue) only when the animal selected a saccade action to acquire the target, whereas for reach action selections the activity dropped back to baseline. In contrast, the activity of the PRR neuron remained elevated in the epoch only for reach movements, but dropped to baseline for saccade choices. This indicates that LIP and PRR are specific for saccade and reach selection, respectively. (c) Population response of choice probabilities for the LIP population ($n = 100$; light curve) and the PRR population ($n = 91$; dark curve). Each curve depicts the average choice probability (and 95% confidence interval) calculated by ROC analysis with a 200 ms time interval in steps of 20 ms. Values larger than 0.5 indicate selectivity for saccades while values smaller than 0.5 indicate selectivity for reaches. Clearly, LIP and PRR population activity are action selective after the end of the cue period. (Modified from *Neuron* 56, Cui H, Andersen RA. Posterior parietal cortex encodes autonomously selected motor plans 552–559, Copyright 2007, with permission from Elsevier.)
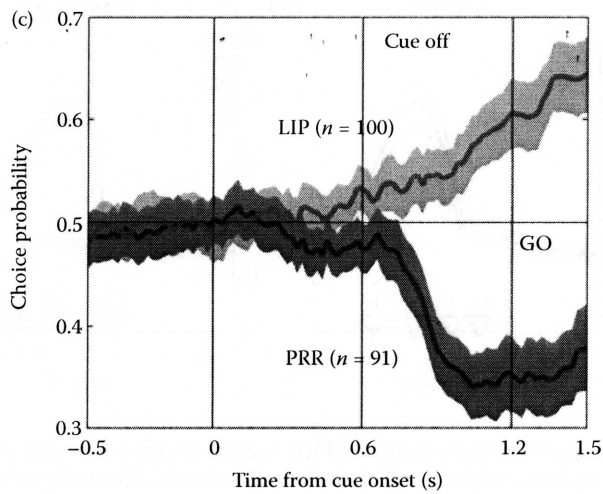
FIGURE 15.4 Continued.

Initially the animal does not know whether the trial will be an instructed or free choice trial so he forms potential plans to both. Interestingly, using the same task but recording in area 5d, another reach-related area in posterior parietal cortex, it was found that area 5d neurons do not code the potential plan but only the final chosen plan, suggesting that this area is downstream of PRR (Cui and Andersen, 2011).

When the animal is given the indication to make a free choice, early on the activities in LIP and PRR separated depending on the effector choice of the animal (Figure 15.4b). In the LIP cell, activity remained elevated only in cases in which the animal chose to make a saccade to the target, but not for selecting a reach movement, whereas for the PRR cell the opposite was true: activity remained high only for reach movement selections and returned back to baseline for saccades. This activity pattern was confirmed in the neuronal population of about 100 LIP neurons and 90 PRR cells, as demonstrated in the mean ROC score in a sliding window analysis for both neuronal populations (Figure 15.4c). In this analysis, an ROC score of 0.5 indicates predictability at chance level, while values significantly larger than 0.5 indicate selectivity for a saccade and less than 0.5 indicates selectivity for a reach. Clearly, starting with the delay period, the LIP population became selective for saccades while the PRR population became similarly selective for reach movements.

These findings indicate that both LIP and PRR are not only playing a role in assigning behavioral relevance for a sensory stimulus, but they are also prospectively involved in action selection and movement preparation under identical stimulus conditions, that is, when selection is driven entirely by internal signals.

15.4.2 Target Selection

Besides choosing appropriate actions, it is common to select a particular target out of a multitude of potential alternatives. Also in these circumstances, the posterior parietal and premotor cortex represents sensory stimuli and the final motor plan, suggesting a direct involvement in the target selection process.

Figure 15.5 shows the activity of a population of PRR neurons during a free-choice task (Scherberger and Andersen, 2007), in which two monkeys could freely select one of two stimuli as a reach target (e.g., targets to the left and right of a fixation point). This experiment also included control trials in which only a single target was offered (Figure 15.5b). In these single-target trials, PRR neurons were strongly active for reach movements to the preferred target and inhibited for movements in the opposite direction, indicating tuning of these neurons to their respective preferred
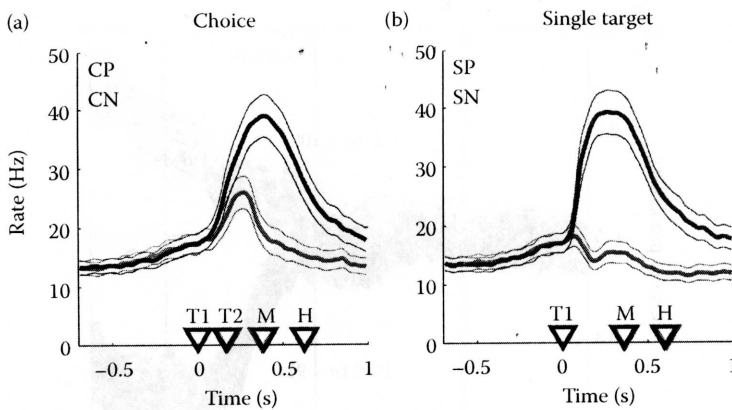
FIGURE 15.5 Spiking activity of a population of PRR neurons during target selection for arm reaching. (a) Population activity during choice trials, in which the animal selected either the preferred (CP, dark curve) or the nonpreferred choice target (CN, light curve). The peri-stimulus time histogram indicates the mean spike rate (thick line) and 95% confidence area (thin lines). Time markers on the abscissa indicate the mean times of appearance of the first (T1) and second target (T2) and the mean times of the beginning (M) and end (H) of the movement. T2 appears with some delay to T1 to compensate for the animal's selection bias to T2 (a long delay makes the animal's choice of T1 more likely), and a staircase procedure was used to set the delay such that both targets were selected equally often. Within a block of trials, T1 and T2 were spatially constant and equidistant targets on opposite sides of a fixation position. Trials are aligned on the appearance of the first target (T1). (b) Neural activity of the same cell population for single-target trials to the preferred (SP, dark curve) and nonpreferred targets (SN, light curve). (Modified from Scherberger H, Andersen RA. 2007. *J Neurosci* 27:2001–2012.)

direction. However, when both targets were presented and the animal was free to choose (Figure 15.5a), neurons were active throughout the movement when the animal selected the preferred target (as defined by the single-target trials). In contrast, when the nonpreferred target was selected, neurons were only briefly active after target presentation and then quickly fell to its pre-target baseline.

This result demonstrates that neurons in posterior parietal cortex are initially activated by sensory stimuli that represent potential movement plans, but then are strongly modulated by the animal's choice and eventually, that is, at the time of movement execution, only reflect the intended movement (Platt and Glimcher, 1999; Schall and Thompson, 1999; Gail and Andersen, 2006; Scherberger and Andersen, 2007). Similar activity patterns were also found for neurons in premotor cortex (Cisek and Kalaska, 2005). Furthermore, as we see below (Figure 15.9a), activity is modulated by the expected reward for an intended action. Therefore, the posterior parietal and premotor cortex can be regarded as a network that integrates sensory and cognitive (e.g., intention-related) signals for actions.

15.5   ATTENTION VERSUS INTENTION CODING

From the evidence mentioned above, it is clear that neurons in the posterior parietal cortex encode different movement intentions. In particular, neurons in PRR are involved in the planning of arm reaches and neurons in LIP are involved in the planning of saccades. However, it has also been argued that the responses of these neurons are not related to movement planning but rather to attention to the target location (Robinson et al., 1978; Bisley and Goldberg, 2003). According to this "attention-only" view, differential responses to reaches and saccades may be due to the different attentional loads of these two tasks. While such an explanation might fit if both LIP and PRR showed the same selectivity for a particular effector movement, it does not explain why they have different selectivities; that is, LIP preferring eye movement plans and PRR reach movement plans.

Insight regarding whether the posterior parietal cortex encodes movement intention or only the locus of attention can be further gained by considering the activity of the whole population of PRR and LIP cells, for example when using the decoding methods described in Chapter 10 (Quian-Quiroga et al., 2006). The two leftmost columns of Figure 15.6a,b show the decoding of saccades and reaches, using a population of 47 PRR and 32 LIP cells, respectively. According to the attention-only hypothesis, it should not be possible to predict the particular movement plan (a reach or a saccade) but rather only the target location, which is where attention is focused. However, for the PRR cells the predictions of reach directions were nearly perfect, with an average hit rate of 0.9). With the PRR neurons the prediction of saccades was much poorer, with an overall hit rate of 0.51. Using the same decoding algorithm, we can also predict the target location (irrespective of whether they were reaches or saccades), as shown in the rightmost column of Figure 15.6a,b. Interestingly,
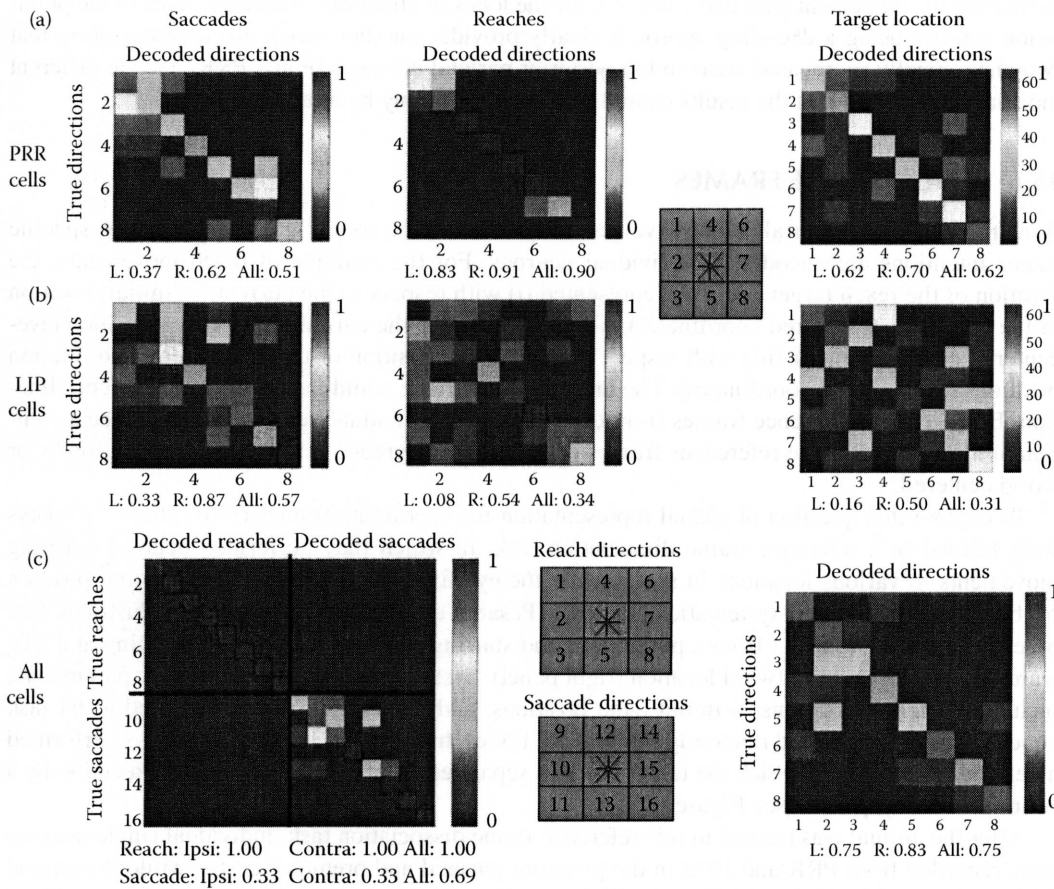

FIGURE 15.6 (**See color insert.**) Decoding of reaches, saccades, and locus of attention. (a,b) Decoding of saccades (left), reaches (middle), and locus of attention (right matrix) using a population of PRR cells (a) and LIP cells (b). Each panel shows a confusion matrix with numbers below indicating the average hit rate for predicting targets in the left hemifield (L; targets 1, 2, and 3), the right hemifield (R; targets 6, 7, and 8), and for all targets (All: 1–8; average across the matrix diagonal). Note that for PRR cells, the prediction of reaches is much better than of saccades or the locus of attention. Conversely, for LIP cells the prediction of saccades is better than of reaches or the locus of attention. (c) Prediction of both reaches and saccades to all eight directions using the whole population of PRR and LIP neurons. Note that reach and saccade predictions are nearly perfect (left matrix) and better than predictions of the locus of attention from the same population (right matrix). (Modified from Quian-Quiroga R. et al. 2006. *J Neurosci* 26:3615–3620.)

the prediction of the target location (hit rate: 0.62) was also much lower than the one for reaches. With the population of LIP neurons a similar pattern was observed. In this case, the prediction of saccades to the contralateral (right) location was high (hit rate: 0.87) and the prediction of reaches (0.54) and target location (0.50) was much lower. Note that LIP response fields favor the contralateral visual field whereas PRR neurons tend to have response fields more evenly distributed between the contralateral and ipsilateral visual fields.

Figure 15.6c shows the prediction of reaches and saccades to all eight directions using the whole population of LIP and PRR neurons. We observe that the decoding of reaches was perfect for all directions and that in no case was a saccade confused with a reach or vice versa. The prediction of saccades was perfect for the contralateral field (directions 14, 15, 16) and at chance for the ipsilateral field, given that LIP neurons encode largely information from the contralateral sites. Interestingly the prediction of each movement plan was better than the one of the locus of attention (0.85 and 0.75, respectively), even though the chance level was lower in the former case (1 out of 16 possibilities for predicting the movement plan and 1 out of 8 for the locus of attention). These analyses of the population activity using a decoding approach clearly provides another metric for demonstrating that two anatomically segregated areas in the posterior parietal cortex, LIP and PRR, encode different movement plans and that the results cannot be explained simply by attention.

15.6   COORDINATE FRAMES

A central problem of neural coding involves the question of the coordinate frame in which specific motor intentions are encoded in individual neurons. For the example of reach movements, the position of the reach target could be represented (i) with respect to the current (or initial) position of the hand (hand-centered coordinates), (ii) with respect to the current eye fixation position (eye-centered coordinates), or (iii) with respect to the relative position of the initial hand and fixation positions (hand-in-eye coordinates). The last reference frame could facilitate hand–eye coordination. Besides these reference frames (i–iii), the coding of individual neurons could also be a combination of some of these references frames or additional reference frames such as head, body, or world centered.

To explore this question of spatial representation for coordinate frames (i–iii) above, monkeys were trained in a reference frame dissociation task, in which they performed delayed reaching movements to various locations in space while the eye fixation position and the starting position of the reaching hand was systematically varied (Pesaran et al., 2006). Figure 15.7a illustrates four potential reach movements from a particular hand starting position, with the eye fixating at a leftward (left panel) or a rightward location (right panel). Systematic variations of all task parameters, including 4 target positions, 4 initial hand positions, and 4 eye fixation positions, led to 64 task conditions that were tested randomly interleaved. For each of these conditions, monkeys performed a delayed reach task, in which the target cue was separated in time from movement execution by a waiting, or delay, period (see Figure 15.2a).

After the animal was trained in this reference frame dissociation task, individual single neurons were recorded from PRR and PMd in the posterior parietal and premotor cortex while the animal performed the task. Figure 15.7b and c illustrates the neural activity of an example neuron from each area. For each neuron, the three grayscale-coded response (gradient) fields illustrate the average firing rate of the neuron during the planning epoch (after movement instruction until movement start) for the three pairwise combinations of target position (T), eye position (E), and initial hand position (H).

For the PRR neuron, the neural response was largely independent of the initial hand position (H) in the hand–eye and target–hand response fields, whereas the influence of the eye (E) and target (T) position was coupled in the target–eye response field such that essentially the difference between both signals (T–E) is most relevant (highest activity along a diagonal line). Furthermore, a singular-value decomposition (SVD) analysis revealed that the target–eye response was inseparable, while
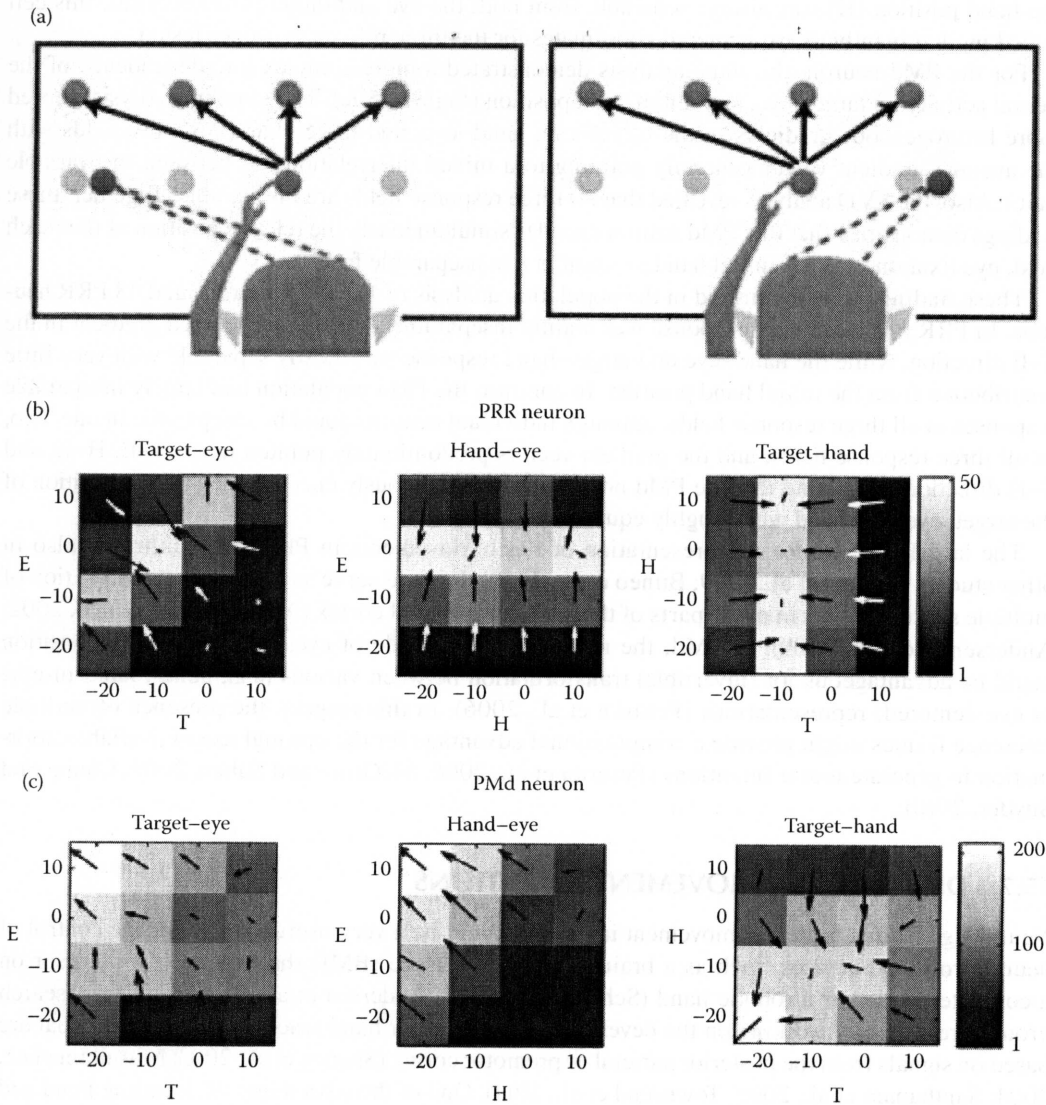
(a)

(b)   PRR neuron

(c)   PMd neuron

FIGURE 15.7 Coordinate frame of reach-related premotor and parietal neurons. (a) Reference frame dissociation task. Animals perform reach movements on a reach board to four possible target locations (top row of each panel) from four possible starting points (bottom row) and with the eyes fixating in one out of four possible fixation positions (left panel: leftmost fixation position; right panel: rightmost fixation position). (b) Activity of an example cell form PRR during the reference frame dissociation task. Grayscale-coded response fields illustrate the average firing rate during the planning epoch (after instruction until movement start) for the target–eye, hand–eye, and target–hand response fields. Small arrows within each response field indicate the local gradient vector in the response field. The influence of the eye (E) and target (T) position was coupled, such that the difference of both signals (T–E) was most relevant. These results are consistent with an eye-centered representation of reach targets in PRR without a major contribution of the initial hand position. (c) The same analysis for an example neuron from PMd revealed a complex interdependence of the neural activity on target, eye, and initial hand position. The gradient field was heterogeneous with mixed interrelationships between the variable pairs, which indicates a coding of reach target positions relative to the eye fixation, initial hand position, and the relative position of the fixation and hand position. (Modified from Pesaran B, Nelson MJ, Andersen RA. 2006. *Neuron* 51:125–134.)

the hand position (H) was always separable from both the eye and target position. Thus, this cell coded predominantly in eye-centered coordinates for the three reference frames tested.

For the PMd neuron, the same analysis demonstrated a more complex interdependence of the neural activity on target, eye, and initial hand position (Figure 15.7c). The gradient analysis showed more heterogeneous gradients in the target–eye, hand–eye, and target–hand response fields with the average gradient vector generally pointing to a mixed interrelationship between the variable pairs. Also, the SVD analysis revealed that all three response fields are inseparable. Together, these findings demonstrate that this PMd neuron encodes simultaneously the relative position of the reach goal, eye fixation, and the initial hand position in a nonseparable fashion.

These findings were confirmed in the population analysis of 111 PMd neurons and 48 PRR neurons. In PRR, the target–eye response was mainly inseparable and had an averaged gradient in the T–E direction, while the hand–eye and target–hand response was mostly separable with very little contribution from the initial hand position. In contrast, the PMd population had largely inseparable responses in all three response fields, although individual neurons could be inseparable in one, two, or all three response fields, and the gradient vectors predominantly pointed in the T–E, H–E, and T–H direction, indicating that the PMd population simultaneously encodes the relative position of the target, eye, and hand with roughly equal strength.

The largely eye-centered representation of reach movements in PRR was confirmed also in other studies (Batista et al., 1999; Buneo et al., 2002). It could serve as a unified representation of multiple sensory inputs in many parts of the posterior parietal cortex (Andersen and Buneo, 2002; Andersen and Cui, 2009). In PMd, the relative position code of eye, hand, and target position could be advantageous for (invertible) transformation between various (e.g., hand-, hand-in-eye, or eye-centered) representations (Pesaran et al., 2006). In this respect, the presence of multiple reference frames might provide a computational advantage for the optimal use of available information to generate motor intentions (Pesaran et al., 2006; McGuire and Sabes, 2009; Chang and Snyder, 2010).

15.7 DECODING OF MOVEMENT INTENTIONS

Neural signals that represent movement intentions could be a very useful source for the control of neural prosthetic devices, such as a brain–machine interface (BMI) that can control a cursor on a computer screen or a robotic hand (Scherberger, 2009; Andersen et al., 2010). Several research groups are currently working on the development of BMIs for hand reaching and grasping that are based on signals from the posterior parietal or premotor cortex (Shenoy et al., 2003; Musallam et al., 2004; Santhanam et al., 2006; Townsend et al., 2011). One of the advantages of decoding hand and arm control signals from movement intentions, rather than from primary motor areas that are more directly involved with movement execution (Hochberg et al., 2006; Velliste et al., 2008), is the fact that motor intention signals provide additional and complementary information about the goal of the movement (Musallam et al., 2004; Scherberger, 2009). Furthermore, understanding which kind of signals can be decoded from a cortical area (and how well) will contribute considerably to our understanding of specific cortical functions. The investigation of neural decoding is therefore interesting also from a neural coding point of view.

15.7.1 DECODING OF GRASP INTENTIONS

Figure 15.8a shows the principle design of a BMI experiment for execution of a hand-grasping task that predicts grasp intentions from neuronal activity in AIP and F5. As shown above, these areas are involved in the generation of hand-grasping intentions and they receive both sensory (particularly visual) and internal information. To test the hypothesis that signals from these areas can be used for decoding, a total of 80–128 microelectrodes were implanted permanently in AIP and F5 (Townsend et al., 2011). Neuronal activity was then recorded and analyzed in real time, and
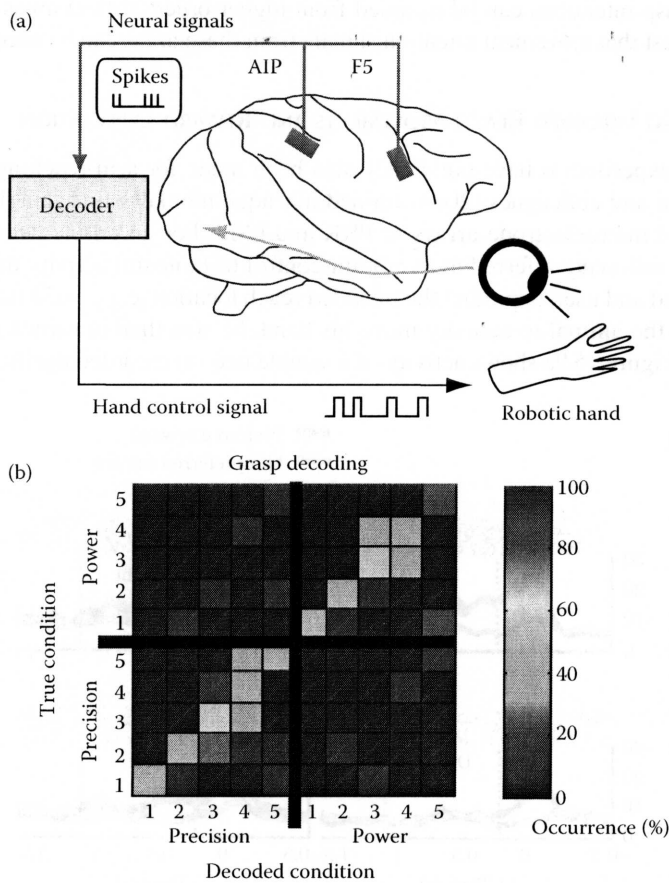
FIGURE 15.8 Decoding hand-grasping intentions from macaque parietal (AIP) and premotor (F5) cortex. (a) Decoding schematic. Movement intentions are recorded in the posterior parietal cortex (AIP) and the premotor cortex (F5) using permanently implanted electrode arrays (gray pads). Neural signals are then processed externally and used to predict movement intentions. (b) Confusion matrix indicating the performance in decoding the grip type (power vs. precision) and the grip orientation (1 of 5 handle orientations) from 128 permanently implanted electrodes in AIP and F5. Data show the results of one online decoding session with about 100 decoding trials. If decoding was perfect, all trials would align on the diagonal (lower left to upper right). Here, the diagonal shows an average performance of 62% across all 10 conditions. (Modified from Townsend BR, Subasi E, Scherberger H. 2011. *J Neurosci* 31:14386–14398.)

subjected to a maximum-likelihood estimator that predicted the grip type (power vs. precision) and the hand orientation (1 of 5) from the activity during the delay epoch of the delayed-grasping task. The decoded grasp was then presented to the animal as a picture of a hand grasping an object, and for each correctly decoded grasp, the animal received a reward immediately without having to actually perform the movement.

Figure 15.8b shows the results of a representative decoding session, which had an overall decoding performance of ~60% (chance level: 10%). This figure illustrates a confusion matrix, a 10×10 matrix consisting of the 10 possible grasp instructions vs. the 10 grasp-decoding results for each instruction and summarizes how each of the 10 grasp instructions was decoded. Most trials fell on the diagonal, indicating correct predictions. Decoding errors occurred mainly for closely related grip orientations, while the grip type was almost never confused. Further offline analysis using different classification algorithms lead to similar results (Subasi et al., 2010). These results provide a first proof

of concept that grasp intentions can be decoded from higher-order cortical areas like AIP and F5, and therefore suggest that movement intention signals from these areas can be used for BMI control.

15.7.2   Decoding Intended Reach Movements and Reward Expectation

Similar decoding experiments have previously also been made for arm-reaching movements. For example, Musallam and colleagues (2004) trained macaque monkeys first in a delayed-reach task and then implanted microelectrode arrays in PRR and PMd. For an online decoding of grasping movements, in the following referred to as a brain-control task, neural activity during the memory period was analyzed and used to predict the intended reach location (e.g., 1 of 4 targets) in real time. Without requiring the animal to actually move his hand, he was then rewarded for correct movement predictions. Figure 15.9a shows activity of a sample neuron recorded during the brain-control
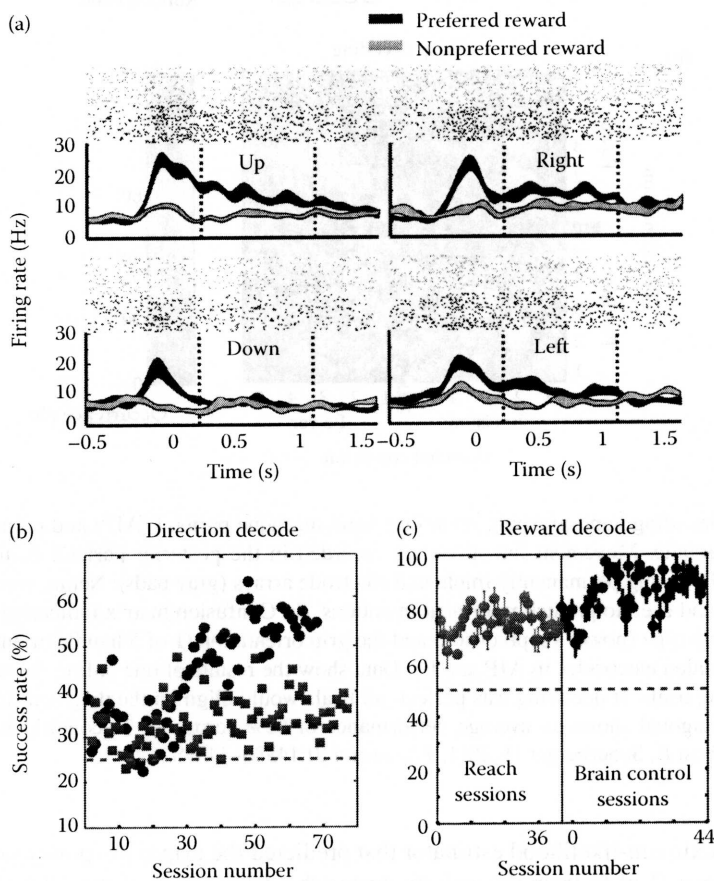

FIGURE 15.9   Cognitive control signals for neural prosthetics. (a) Activity of a PRR neuron during the brain-control task with instructions to the up, right, left, and down directions that were rewarded with either orange juice (black) or water (gray). This neuron was more active for trials when the preferred reward (orange juice; black) was expected. (b) Overall success rate for decoding the intended movement from four possible targets in subsequent recording sessions in two animals (black and gray dots). Chance level: 25% (horizontal dotted line). Both animals improved their performance over time. (c) Success rate in the offline decoding of expected reward (preferred vs. nonpreferred) in 36 reach (gray) and 44 brain-control (black) sessions across three animals. Error bars: standard deviation obtained by cross-validation. Dotted line: chance level (50%). (Musallam S. et al. 2004. Cognitive control signals for neural prosthetics. *Science* 305:258–262. Reprinted with permission of AAAS.)

task. It shows a preferred reach direction up and to the right, and an increased activity from baseline after cue onset and throughout the memory period (delineated by vertical dotted lines).

However, in this experiment, the neural response was strongly modulated when different target-cue sizes were used to signal to the animal the type of reward (orange juice vs. water) to be expected for successful trial completion. Trials in which the animal knew in advance that it would receive a preferred reward (orange juice) produced a significantly stronger response (black spike rasters and curves) than trials in which the animal expected a less-preferred reward (water; gray spike rasters and curves). This was true independent of whether the preferred reward was indicated with the smaller or larger cue size. Similarly, activity was stronger when the expected amount of reward (volume) or the reward probability was increased. This demonstrates that posterior parietal and premotor neurons encode not only the intended target location but also the expected value associated with the intended action.

Across a series of daily real-time decoding sessions, the online decoding performance for the reach direction gradually improved over weeks and months of the ongoing experiment. Figure 15.9b shows the overall success rate for predicting the correct target position (1 out of 4 possible positions) from 10 to 30 recording channels (single neurons and multi-units) in about 70 daily sessions of two animals.

Furthermore, the expected reward value (high or low) was also predicted from the neuronal population in a subsequent offline analysis. Figure 15.9c depicts the success rate for the offline decoding of the expected reward value across three animals (dashed line: chance level 50%). Interestingly, the mean decoding performance was significantly larger (85%) when the animals performed the brain-controlled task as compared to the standard delayed reach task (75%), in which they had to execute the reach movement in order to receive the reward. Together, these decoding experiments clearly demonstrate the potential usefulness of these signals for neural decoding.

15.8 SUMMARY

As we have seen, the posterior parietal and the premotor cortices play important roles for generating intentional movements. These areas are intimately connected to the sensory system in the posterior parietal and occipital cortex, which provides them with bottom-up, multi-modal perceptual information. The posterior parietal and premotor cortices comprise distinctive subregions that are specialized for specific movement types. At the same time, they are strongly connected to frontal areas related to top-down information like motivation and reward. Based on this sensory and cognitive information, the posterior parietal and the premotor cortex are both intimately involved in the selection of appropriate actions and targets, and in the coordinate transformation of action-specific target information from sensory-based representations into coordinates that are more readily accessible for movement execution.

In everyday life, we can grasp a cup of coffee while reading a newspaper or while talking. Motor planning capabilities therefore need to be able to operate in parallel, and without constant conscious supervision. Patients with lesions in posterior parietal cortex often have deficits in performing such functions, either at all or without excessive cognitive effort (Perenin and Vighetto, 1988; Goodale and Milner, 1995). The posterior parietal and premotor cortices lie at the heart of sensorimotor transformation and action-related decision making. This could be explored with, and exploited for BMI applications. Future research will need to investigate the mechanisms of how these neuronal networks operate both within and in between these cortical areas.

REFERENCES

Andersen RA, Buneo CA. 2002. Intentional maps in posterior parietal cortex. *Annu Rev Neurosci* 25:189–220.
Andersen RA, Cui H. 2009. Intention, action planning, and decision making in parietal–frontal circuits. *Neuron* 63:568–583.

Andersen RA, Hwang EJ, Mulliken GH. 2010. Cognitive neural prosthetics. *Ann Rev Psychol* 61:169–190, C161–C163.

Andersen RA, Snyder LH, Bradley DC, Xing J. 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu Rev Neurosci* 20:303–330.

Batista AP, Buneo CA, Snyder LH, Andersen RA. 1999. Reach plans in eye-centered coordinates. *Science* 285:257–260.

Baumann MA, Fluet M-C, Scherberger H. 2009. Context-specific grasp movement representation in the macaque anterior intraparietal area. *J Neurosci* 29:6436–6448.

Belmalih A, Borra E, Contini M, Gerbella M, Rozzi S, Luppino G. 2009. Multimodal architectonic subdivision of the rostral part (area F5) of the macaque ventral premotor cortex. *J Comp Neurol* 512:183–217.

Bisley JW, Goldberg ME. 2003. Neuronal activity in the lateral intraparietal area and spatial attention. *Science* 299:81–86.

Buneo CA, Andersen RA. 2006. The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia* 44:2594–2606.

Buneo CA, Jarvis MR, Batista AP, Andersen RA. 2002. Direct visuomotor transformations for reaching. *Nature* 416:632–636.

Chang SW, Snyder LH. 2010. Idiosyncratic and systematic aspects of spatial representations in the macaque parietal cortex. *Proc Natl Acad Sci USA* 107:7951–7956.

Cisek P, Kalaska JF. 2005. Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron* 45:801–814.

Clower DM, Hoffman JM, Votaw JR, Faber TL, Woods RP, Alexander GE. 1996. Role of posterior parietal cortex in the recalibration of visually guided reaching. *Nature* 383:618–621.

Cordeau JP, Gybels J, Jasper H, Poirier LJ. 1960. Microelectrode studies of unit discharges in the sensorimotor cortex: Investigations in monkeys with experimental tremor. *Neurology* 10:591–600.

Cui H, Andersen RA. 2007. Posterior parietal cortex encodes autonomously selected motor plans. *Neuron* 56:552–559.

Cui H, Andersen RA. 2011. Different representations of potential and selected motor plans by distinct parietal areas. *J Neurosci* 31:18130–18136.

Desmurget M, Sirigu A. 2009. A parietal-premotor network for movement intention and motor awareness. *Trends Cogn Sci* 13:411–419.

Evarts EV. 1965. Relation of discharge frequency to conduction velocity in pyramidal tract neurons. *J Neurophysiol* 28:216–228.

Fluet MC, Baumann MA, Scherberger H. 2010. Context-specific grasp movement representation in macaque ventral premotor cortex. *J Neurosci* 30:15175–15184.

Gail A, Andersen RA. 2006. Neural dynamics in monkey parietal reach region reflect context-specific sensorimotor transformations. *J Neurosci* 26:9376–9384.

Goodale MA, Milner AD. 1995. *The Visual Brain in Action*. Oxford: Oxford University Press.

Hochberg LR, Serruya MD, Friehs GM, Mukand JA, Saleh M, Caplan AH, Branner A, Chen D, Penn RD, Donoghue JP. 2006. Neuronal ensemble control of prosthetic devices by a human with tetraplegia. *Nature* 442:164–171.

Kurata K, Hoshi E. 1999. Reacquisition deficits in prism adaptation after muscimol microinjection into the ventral premotor cortex of monkeys. *J Neurophysiol* 81:1927–1938.

Lemon RN. 2008. Descending pathways in motor control. *Annu Rev Neurosci* 31:195–218.

Matelli M, Luppino G. 2001. Parietofrontal circuits for action and space perception in the macaque monkey. *Neuroimage* 14:S27–S32.

McGuire LM, Sabes PN. 2009. Sensory transformations and the use of multiple reference frames for reach planning. *Nat Neurosci* 12:1056–1061.

Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C. 1975. Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *J Neurophysiol* 38:871–908.

Mulliken GH, Musallam S, Andersen RA. 2008a. Forward estimation of movement state in posterior parietal cortex. *Proc Natl Acad Sci USA* 105:8170–8177.

Mulliken GH, Musallam S, Andersen RA. 2008b. Decoding trajectories from posterior parietal cortex ensembles. *J Neurosci* 28:12913–12926.

Murata A, Gallese V, Luppino G, Kaseda M, 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.

Murata A, Fadiga L, Fogassi L, Gallese V, Raos V, Rizzolatti G. 1997. Object representation in the ventral premotor cortex (area F5) of the monkey. *J Neurophysiol* 78:2226–2230.

Musallam S, Corneil BD, Greger B, Scherberger H, Andersen RA. 2004. Cognitive control signals for neural prosthetics. *Science* 305:258–262.

Perenin MT, Vighetto A. 1988. Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain* 111:643–674.

Pesaran B, Nelson MJ, Andersen RA. 2006. Dorsal premotor neurons encode the relative position of the hand, eye, and goal during reach planning. *Neuron* 51:125–134.

Platt ML, Glimcher PW. 1999. Neural correlates of decision variables in parietal cortex. *Nature* 400:233–238.

Quian-Quiroga R, Snyder LH, Batista AP, Cui H, Andersen RA. 2006. Movement intention is better predicted than attention in the posterior parietal cortex. *J Neurosci* 26:3615–3620.

Raos V, Umilta MA, Murata A, Fogassi L, Gallese V. 2006. Functional properties of grasping-related neurons in the ventral premotor area F5 of the macaque monkey. *J Neurophysiol* 95:709–729.

Rizzolatti G, Fogassi L, Gallese V. 1997. Parietal cortex: From sight to action. *Curr Opin Neurobiol* 7:562–567.

Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M. 1988. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp Brain Res* 71:491–507.

Rizzolatti G, Luppino G. 2001. The cortical motor system. *Neuron* 31:889–901.

Robinson DL, Goldberg ME, Stanton GB. 1978. Parietal association cortex in the primate: Sensory mechanisms and behavioral modulations. *J Neurophysiol* 41:910–932.

Sakata H, Taira M, Murata A, Mine S. 1995. Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cereb Cortex* 5:429–438.

Santhanam G, Ryu SI, Yu BM, Afshar A, Shenoy KV. 2006. A high-performance brain–computer interface. *Nature* 442:195–198.

Schall JD, Thompson KG. 1999. Neural selection and control of visually guided eye movements. *Ann Rev Neurosci* 22:241–259.

Scherberger H. 2009. Neural control of motor prostheses. *Curr Opin Neurobiol* 19:629–633.

Scherberger H, Andersen RA. 2003. Sensorimotor transformations. In: *The Visual Neurosciences* (Chalupa LM, Werner JS, eds), pp 1324–1336. Cambridge, MA: MIT Press.

Scherberger H, Andersen RA. 2007. Target selection signals for arm reaching in the posterior parietal cortex. *J Neurosci* 27:2001–2012.

Shenoy KV, Meeker D, Cao S, Kureshi SA, Pesaran B, Buneo CA, Batista AP, Mitra PP, Burdick JW, Andersen RA. 2003. Neural prosthetic control signals from plan activity. *Neuroreport* 14:591–596.

Snyder LH, Batista AP, Andersen RA. 1997. Coding of intention in the posterior parietal cortex. *Nature* 386:167–170.

Subasi E, Townsend B, Scherberger H. 2010. In search of more robust decoding algorithms for neural prostheses, a data driven approach. *Conf Proc IEEE Eng Med Biol Soc* 1:4172–4175.

Townsend BR, Subasi E, Scherberger H. 2011. Grasp movement decoding from premotor and parietal cortex. *J Neurosci* 31:14386–14398.

Velliste M, Perel S, Spalding MC, Whitford AS, Schwartz AB. 2008. Cortical control of a prosthetic arm for self-feeding. *Nature* 453:1098–1101.

Weinrich M, Wise SP, Mauritz KH. 1984. A neurophysiological study of the premotor cortex in the rhesus monkey. *Brain* 107(Pt 2):385–414.

Wise SP, Moody SL, Blomstrom KJ, Mitz AR. 1998. Changes in motor cortical activity during visuomotor adaptation. *Exp Brain Res* 121:285–299.