A COMMON REFERENCE FRAME FOR MOVEMENT PLANS IN THE POSTERIOR PARIETAL CORTEX

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Orchestrating a movement towards a sensory target requires many computational processes, including a transformation between reference frames. This transformation is important because the reference frames in which sensory stimuli are encoded often differ from those of motor effectors. The posterior parietal cortex has an important role in these transformations. Recent work indicates that a significant proportion of parietal neurons in two cortical areas transforms the sensory signals that are used to guide movements into a common reference frame. This common reference frame is an eye-centred representation that is modulated by eye-, head-, body- or limb-position signals. A common reference frame might facilitate communication between different areas that are involved in coordinating the movements of different effectors. It might also be an efficient way to represent the locations of different sensory targets in the world.

SACCADIC EYE MOVEMENT
A very rapid, ballistic eye movement (with speeds of up to 800 degrees per second).

Goal-directed behaviour can be considered as a dynamic link between a sensory stimulus and a motor act. Between the transduction of sensory stimuli into biochemical energy and the muscle contractions that are needed to move a motor effector, several intermediate processes must be carried out. These processes include changes in the locus of attention[1,2], response selection[3–6], coordinate transformations[7–12] and a decision to 'act' on the sensory stimulus[13–16].

Neural correlates of many of these intermediate events are reflected in activity in the posterior parietal cortex (PPC)[3,7–9,13–15,17]. In this review, we examine the involvement of the PPC in the coordinate transformations that are used in movement planning. We propose that an element of the transformation process is for a population of neurons to represent space in a common reference frame in at least two areas of the PPC. The advantage of such an abstract representation could be to facilitate the coordination of various aspects of goal-oriented behaviour, such as hand–eye coordination. It also has the computational advantage of maintaining a distributed representation of many different reference frames that can be read by other brain areas, depending on the requirements of the ongoing behaviour. We first review the role of the PPC in movement planning, and then examine its role in reference-frame transformations.

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Movement planning in the parietal cortex

A large component of PPC activity seems to be correlated with movement planning. Cells that code preferentially a specific type of movement plan are organized into functional subdivisions within the PPC[3,18–21]. Three areas have been identified as being specialized for different types of movement plan (FIG. 1). The lateral intraparietal area (LIP) is situated in the lateral wall of the intraparietal sulcus and is specialized for SACCADIC EYE MOVEMENTS. The parietal reach region (PRR) is specialized for reaching and includes the medial intraparietal area (MIP) in the medial wall of the intraparietal sulcus, and the dorsal aspect of the parieto-occipital area (PO). The anterior intraparietal area (AIP) lies along the anterior portion of the intraparietal sulcus and is involved in grasp planning.

The role of areas LIP and PRR in movement planning was elucidated by recording neural activity while monkeys participated in two interleaved tasks:

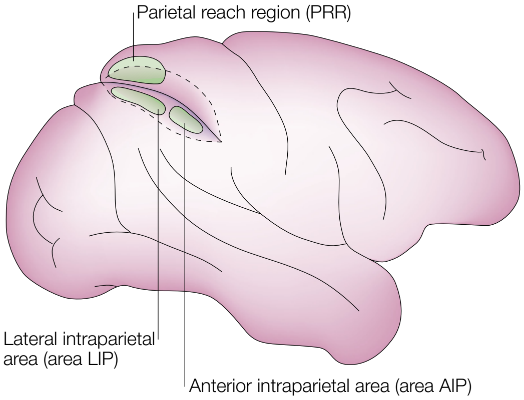


Figure 1 | **Diagram of a lateral view of the macaque cortex.** The figure shows the inside of the intraparietal sulcus, and the locations of the lateral intraparietal area, a portion of the parietal reach region and the anterior intraparietal area in the posterior parietal cortex.

a delayed-saccade task and a delayed-reach task[3]. The delayed-saccade task required monkeys to make saccades to the remembered locations of visual targets, whereas the delayed-reach task required monkeys to perform the same task but with reaches. If LIP and PRR neurons are involved in mediating spatial attention, then they should respond similarly on both tasks. On the other hand, if they are involved in movement planning, they should respond preferentially in one of the delay tasks. The results of this study are consistent with the latter hypothesis: during the delay period that precedes the movement, LIP neurons responded preferentially before saccades, whereas PRR neurons responded preferentially before reaches.

The role of area AIP in grasp planning was shown in a series of studies by Sakata and colleagues[18–21]. In one set of experiments[20], monkeys were trained to grasp objects of different shapes, sizes and orientations. After training was completed, muscimol, an agonist of the inhibitory neurotransmitter GABA (γ-aminobutyric acid), was injected into area AIP before the monkeys performed the task. While area AIP was inactivated, the monkeys were able to make well-coordinated reaches, but were unable to shape their hands properly to grasp objects. Neurophysiological studies[18,19,21] confirmed the role of AIP in grasp planning by showing that AIP neurons are selective for certain types of grasp. For instance, in one study[18], AIP activity was recorded while monkeys participated in a delayed-grasp task. A monkey was shown an object, the illumination of the object was extinguished and, after a brief delay, the monkey grasped the object. During the delay period, AIP neurons responded selectively for preferred objects to be grasped. This selective delay-period activity is analogous to the reach and saccade planning activity that is found in PRR and LIP neurons[3], respectively, and is consistent with the idea that AIP neurons participate in the programming of grasps.

Although we have stressed the role of the PPC in movement planning, PPC neurons carry other signals besides those related to planning. These signals have been illustrated in a variety of studies and include cognitive intermediates of the sensorimotor transformation, such as attention[17], salience[22] and decision variables[13–15]. Indeed, many of these intermediates can be seen during different epochs of a behavioural task[13–15,23], indicating that the variables being encoded in the firing rates of PPC neurons change as the sensory, cognitive and motor demands of the task evolve[24]. A critical analysis of these different signals is outside the scope of this review (but see REFS 25–28 for a more in-depth discussion of these important topics).

As the PPC receives visual, auditory and somatosensory input[5,29–32], it is reasonable to propose that regions of the parietal cortex, such as areas LIP and PRR, might participate in the planning of movements to targets of different sensory modalities. Indeed, neurons in areas LIP and PRR are modulated during tasks that use either auditory or visual cues to indicate the locations of planned movements[8,9,24,33–35].

Reference frames and transformations

A reference frame can be defined as a set of axes that describes the location of an object. For instance, imagine that you are sitting at your kitchen table and looking at a cup of hot coffee on the table. The location of the coffee cup can be described in several different reference frames. Relative to your eyes, the cup is straight ahead. On the other hand, relative to your left arm, which is by your side, the coffee is to the right. The cup's location can also be described in a reference frame that depends on the external world rather than the location of your body; for example, relative to its position on the table.

Being able to compute the location of an object in different reference frames is not just a theoretical exercise. It is crucial for the successful completion of different types of behaviour[10,12,36,37]. For instance, if you want to know whether your coffee is cool enough to drink, you could look at the cup and note whether there is any steam rising from it. To perform this behaviour, it is important to know the location of the cup relative to the foveae of your eyes so that you can direct them towards the cup. Once the coffee is cool enough, you might want to reach out and grasp the cup. This behaviour requires knowledge of the location of the cup relative to your arm.

Although we have focused on describing various reference frames for the location of visual stimuli, reference frames are also important considerations for stimuli in other sensory modalities, such as auditory stimuli. For example, if we want to direct our gaze towards the sound of a creaking door with rusty hinges, knowledge of the location of the sound relative to our head and eyes is important. Similarly, if we want to reach towards the sound, we need to know the location of the sound relative to our limbs.

However, calculating these different frames of reference is not trivial, because sensory information is often collected in a reference frame that is different from that of the eventual motor act. Auditory stimuli are initially coded in a head-centred reference frame that is computed on the basis of interaural level and difference cues, and monaural spectral cues[38–40]. By contrast, the motor system codes actions in reference frames that depend on the motor effectors[41–44]. Eye movements, for example, are coded in a reference frame that is based on the difference between current and desired eye positions[43,44], whereas reaches are coded in a reference frame that is based on the differences between current and desired arm positions[41,45]. Consequently, to guide an effector towards the location of a sensory stimulus, the representation of the location of the sensory stimulus must be transformed into a representation that is appropriate for the motor act.

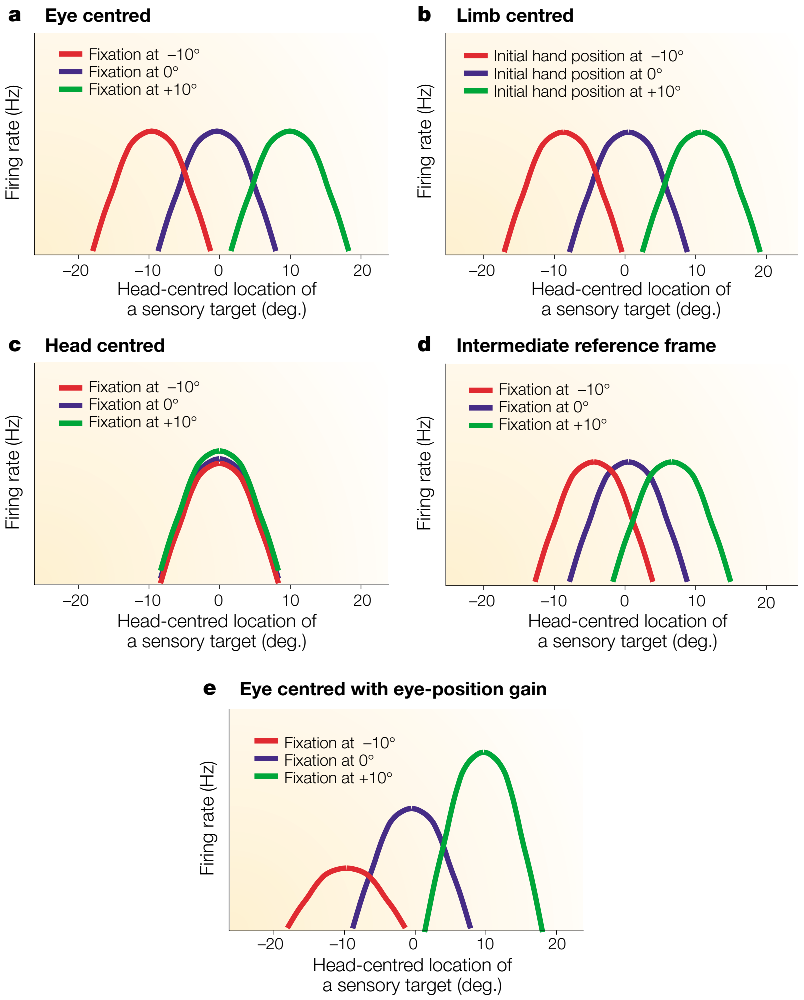


Figure 2 | **Schematic of different frames of reference.** The locations of sensory targets along the abscissa are plotted relative to the observer's head. Hypothetical response profiles are represented by bell-shaped curves. **a** | If a neuron encodes the location of a sensory target in an eye-centred reference frame, the peak location of the response profile should shift with eye position. For example, a +10° shift of eye position would shift the peak of the response profile by +10°. **b** | If a neuron encodes the location of a sensory target in a limb-centred reference frame, the peak location of the response profile should shift with initial hand position. **c** | If a neuron encodes the location of a sensory target in a head-centred reference frame, the peak location of the response profile should not shift with eye position (response profiles offset for clarity). **d** | If a neuron encodes the location of a sensory target in an intermediate reference frame, the response profile should shift with eye position, but the shift should be smaller than the change in eye position. In this example, a 10° shift of eye position shifts the peak of the response profile by only 5°. **e** | If a neuron encodes the location of a sensory target in an eye-centred reference frame that is modulated by eye-position gain, the peak of the response profile should shift with eye position, and the magnitude of the response should change with eye position. In this example, a +10° shift of eye position shifts the response profile by +10° and increases the magnitude of the response by 50%. By contrast, a –10° shift in eye position shifts the peak response by –10° and decreases the magnitude of the response by 50%.

The PPC has an important role in these reference-frame transformations. Below, we provide evidence that is consistent with the idea that areas LIP and PRR transform target location into a common reference frame.

A common reference frame in LIP and PRR

Neurons in LIP have long been known to code the location of visual targets in an eye-centred reference frame[46–48]. In this reference frame, neurons signal the relative distance between the monkey's eye position and the position of a visual target (FIG. 2a). For example, an LIP neuron might respond maximally to a visual target that is located at the monkey's fixation point, regardless of the absolute position of the monkey's eyes.

Before proceeding further, it is important to differentiate between an eye-centred reference frame and a retinotopic reference frame. An eye-centred reference frame, as noted above, is one that depends on the location of the eyes in the head. A retinotopic reference frame is one that depends on the retinal location that is activated by a visual stimulus. Although these two reference frames are often used interchangeably, they are not always the same. Double-saccade tasks, for example, show how the location of the second visual target is coded relative to current and desired eye positions (eye-centred reference frame), and not on the basis of the locus of stimulation of the retina (retinotopic reference frame)[49–51]. Our definition of an eye-centred reference frame is appropriate for the studies discussed below, because it does not require retinal activation and allows us to compare the reference frame for both auditory and visual stimuli.

Do neurons in LIP code auditory stimuli in a similar eye-centred reference frame? As LIP neurons are involved in the planning of eye movements to the locations of both auditory and visual targets[35], it is reasonable to believe that they would code auditory-target locations in a reference frame that is comparable to the one used to code visual-target locations. This hypothesis was tested by training monkeys to saccade to the remembered locations of auditory targets from different initial eye-fixation locations[9]. If LIP activity is coded in an eye-centred reference frame, then the auditory-target location that maximally activates a neuron should shift as the monkey's initial fixation point shifts (FIG. 2a). On the other hand, if neural responses are not in an eye-centred reference frame, then the sound location that activates a neuron would not be expected to vary with changes in eye position.

Data were analysed during the delay period of the saccade task, which followed offset of the auditory stimulus, but preceded the eye movement to the remembered location. During the delay period, a significant proportion of LIP neurons (44%) codes the locations of sounds in an eye-centred frame of reference[9]. This finding is similar to the classic observation by Jay and Sparks[52] that neurons in

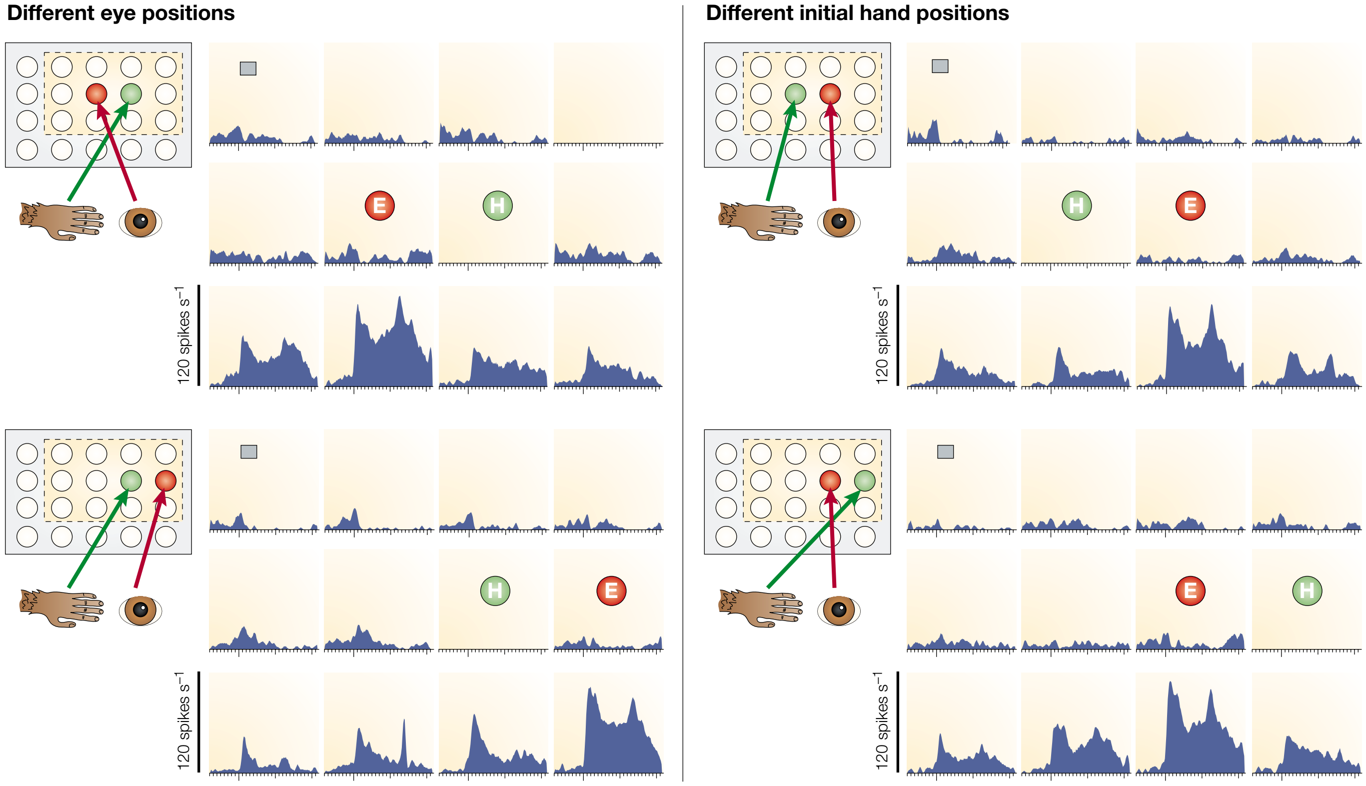
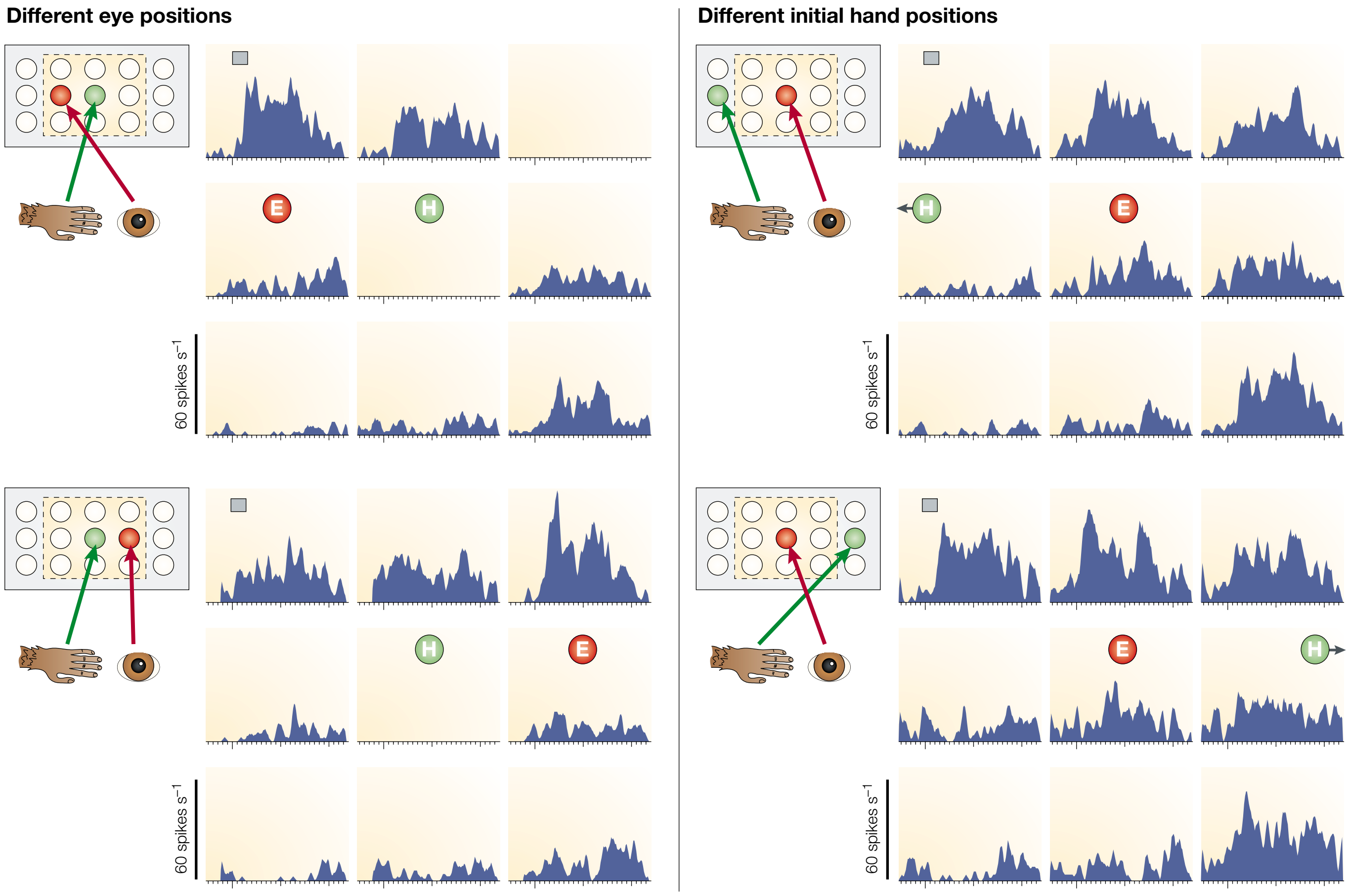


Figure 3 | **A PRR neuron that encodes reaches to visual targets in an eye-centred reference frame.** A monkey faced a panel that contained touch-sensitive buttons. Within each button was a red and a green light-emitting diode (LED). Red lights indicated where the monkey should look; green lights indicated where the monkey should reach. A trial began with the illumination of both a red and green LED. The monkey looked at the button that was illuminated by the red LED and pushed the button that was illuminated by the green LED. Next, a sensory target (the flash of a green LED) was presented. After a delay, the red and green LEDs were extinguished and the monkey reached towards the remembered location of the sensory target. Each panel contains a schematic that shows the variations of eye position and initial hand position. The circles indicate the relative position of each button assembly and the dotted square outlines a grid of potential sensory-target locations. The red circle indicates the button that the monkey fixated. The green button indicates the button that the monkey initially pressed. Next to each schematic is a parietal reach region (PRR) response profile that was generated from data obtained when the monkey was participating in the variant of the reach task that is shown in the schematic. The spike-density histograms, aligned relative to the onset of the sensory cue, are arranged as a function of target location. The circled 'E' and the circled 'H' indicate the location of the monkey's eye position and initial hand position, respectively. The grey bar indicates the time of cue onset and the duration of the cue. Left, two response profiles that were generated with the same initial hand position but different eye positions. Right, two response profiles that were generated with the same eye position but different initial hand positions. When eye position varied, the peak of the response profile shifted. By contrast, when initial hand position varied, the response profiles did not shift. Tic interval, 100 ms. Modified, with permission, from REF. 7 © 1999 American Association for the Advancement of Science.

the superior colliculus of rhesus monkeys code the locations of auditory stimuli in an eye-centred reference frame; more recent studies have also shown that neurons in the superior colliculus of cats code auditory stimuli in an eye-centred reference frame[53,54]. In another population of neurons (33%), the peak location of the response profile was not shifted by changes in eye position. It is likely that these neurons code sound-source location in a head-centred reference frame (FIG. 2c) — the reference frame in which sound location is initially coded[38–40]. However, these neurons might also code auditory-target location in a body- or world-centred reference frame; this issue needs to be addressed directly in the future. The remaining neurons (23%) seemed to code the location of a sound in a reference frame that was intermediate between a head-centred and eye-centred frame of reference (FIG. 2d). The last two observations indicate that area LIP might contain a neural circuit that transforms head-centred representations of sound into eye-centred representations; this topic will be discussed further below.

The reference frame of activity in PRR has also been examined. We proposed that PRR activity would be in one of two frames of reference. As PRR neurons are involved in reach planning, they might code target locations in a reference frame that is based on the difference between current hand location and target location (a limb-centred reference frame; FIG. 2b). Alternatively, PRR neurons might code the location of targets in an eye-centred frame (FIG. 2a).

To decide between these two hypotheses, the reference frame of PRR neurons was determined by examining activity while monkeys participated in two interleaved variations of the delayed-reach task[7] (FIG. 3). In the first variation, a monkey made identical reaches to remembered visual stimulus targets from two fixation positions. In this variation, the monkey's initial hand position was on a central button and he maintained fixation at locations to the left or to the right of the central button. If PRR neurons code target locations in an eye-centred reference frame, then the target location that


Different eye positions

Different initial hand positions

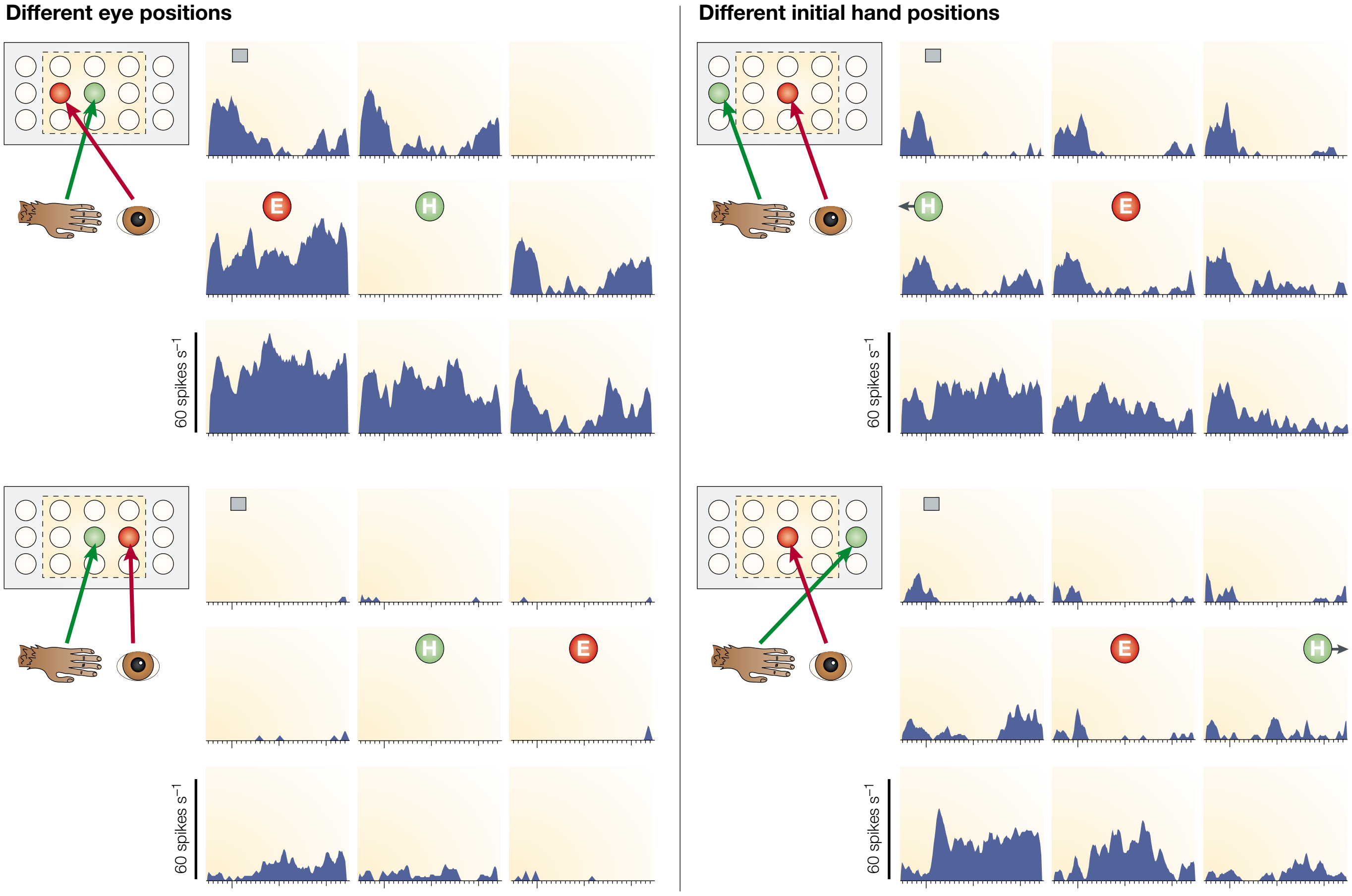
Figure 4 | **A PRR neuron that encodes reaches to auditory targets in an eye-centred reference frame.** The same conventions apply as in FIG. 3, except that auditory rather than visual sensory targets were used. Arrows next to circled 'H' symbols indicate that the initial hand position was outside the target area. When eye position varied, the peak of the response profile shifted. By contrast, when initial hand position varied, the response profiles did not shift. Tic interval, 100 ms. PRR, parietal reach region. Modified, with permission, from REF. 8 © 2000 Elsevier Science.

maximally activates a neuron should shift with the monkey's fixation point (FIG. 2a). In the second version, different reaches were made to visual targets from the same fixation position. In this version, the monkey's initial hand position was on a button that was either to the left or to the right of the central button, and his fixation was focused on the centre button. If PRR neurons encode target locations in a limb-centred reference frame, then the target location that maximally activates a neuron should shift with the monkey's initial hand position (FIG. 2b).

An example of a PRR neuron that was recorded during this task is shown in FIG. 3. Changes in initial hand position did not alter the target location that maximally activated the neuron. By contrast, when the monkey shifted his fixation point from left to right, the target location that maximally activated the neuron shifted accordingly. This neuron is typical of most neurons examined in coding the locations of visual targets in an eye-centred reference frame[7].

As PRR neurons code visual-target locations in an eye-centred frame of reference, we reasoned that they might also code auditory-target locations in an eye-centred reference frame. This hypothesis is not intuitive, however, as the original head-centred sensory representation of a sound can be converted directly into a limb-centred representation that is useful for reaches. To test this prediction, we recorded PRR activity from monkeys while they participated in a version of the reach task that is used to examine the reference frame of visual activity in PRR neurons[8]. However, in this version of the task, we required monkeys to make reaches to remembered locations of auditory targets. FIGURE 4 shows an example of a neuron that was recorded during this task. This neuron codes the locations of auditory targets in an eye-centred reference frame: the location that maximally activates the neuron shifts with eye position but not with initial hand position.

As in the LIP study[9], data were analysed during the delay period of the reach task. A significant proportion (42%) of PRR neurons codes auditory-target location in an eye-centred reference frame[8]. A further population of neurons (45%) did not shift their tuning curves with changes in eye or hand position, indicating that these neurons might code the locations of auditory targets in a head-centred reference frame (FIG. 2c). The remaining neurons coded auditory-target location in a reference


Different eye positions

Different initial hand positions

Figure 5 | **A PRR neuron that encodes reaches to auditory targets in a head-centred reference frame and is substantially gain modulated by eye position.** The same conventions apply as in FIGS 3 and 4. When eye position varied, the magnitude or gain of the response varied substantially. By contrast, when initial hand position varied, the gain of the response was essentially constant. PRR, parietal reach region.

frame that was intermediate between eye- and head-centred representations (FIG. 2d). Again, these intermediate-reference-frame neurons might be indicative of the role of PPR in reference-frame transformations, and will be discussed further below.

We choose to examine delay-period activity, because activity during this period can be disambiguated from activity due to the sensory stimulus itself and from activity due to a motor action. But it is worth noting that our observations are not dependent on examinations of delay-period activity. Indeed, an analysis of PRR activity during the presentation of the auditory stimulus and during the reach itself indicated that a significant number of neurons coded locations in a format that was more consistent with an eye-centred representation than a limb-centred representation (Y.E.C. and R.A.A., unpublished observations).

Together, these results indicate that a significant proportion of LIP and PRR neurons encodes target location in a common eye-centred reference frame. We consider this reference frame to be an abstract representation of sensory-target location for two reasons. First, it is not a motor-based reference frame, because it seems to be the same regardless of whether the planned action is an eye movement or a reach. Second, this representation is not stimulus-based, because it seems to be the same regardless of whether the sensory target is auditory or visual.

However, besides the coordinate frame of the response field, there is a further feature to consider of these representations in areas LIP and PRR: for many cells, the magnitude of responses in LIP and PRR neurons is also 'gain' modulated by such factors as eye, head, body or initial hand position[47,48,55–58] (FIG. 2e). An example of a neuron with substantial gain modulation by eye position is shown in FIG. 5. Although this neuron codes the location of auditory targets in a head-centred reference frame (the auditory-target location to which the neuron responds maximally does not shift with initial hand or eye position), its level of responsiveness is clearly modulated by eye position. When the monkey's eye position was to the left, the neuron responded robustly, but when the eye position was to the right, the neuron barely responded. By contrast, the level of response was not affected by changes in initial hand position.

Gain fields in conjunction with eye-centred representations produce a distributed representation of target locations in different reference frames and provide a mechanism for coordinate transformations[9,47,48,59–62] (see below; FIG. 6). The representation is distributed because the gain fields in conjunction with eye-centred representations of target location enable neurons in the PPC or other cortical areas to 'read out' stimulus-target location in different frames of reference. For example, a population of neurons that code the eye-centred location of a stimulus target with different eye-position gains can represent a stimulus in head-centred coordinates. This type of integration might occur in the ventral intraparietal cortex: this region contains cells that encode visual targets in a head-centred reference frame[56]. Or eye- and head-position information might be combined to code locations with respect to the body. But the locations of the stimuli in eye coordinates can also be read out from the same population of gain-modulated neurons by another area. Simultaneous readout of many reference frames is possible through this unique representation of information.

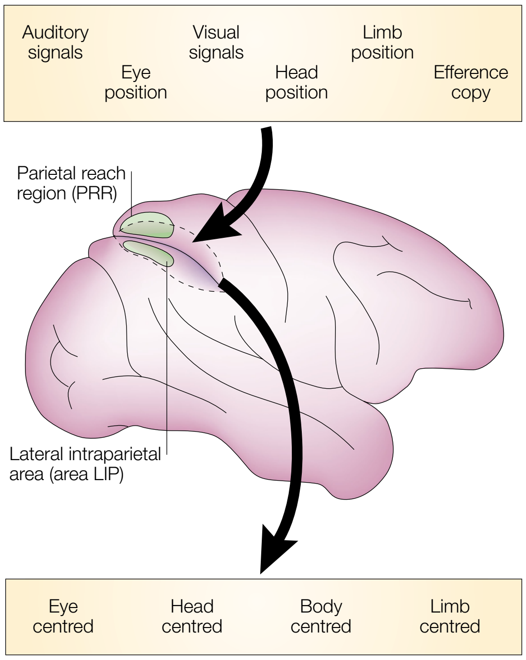


Figure 6 | **Gain modulation of eye-centred representations.** The eye-centred representations that are found in lateral intraparietal area (LIP) and parietal reach region (PRR) neurons are modulated by eye-, hand-, head- and body-position signals, as well as by other signals. In both parietal areas, these gain-modulated signals form a distributed representation of sensory-target locations that can be read out in different frames of reference (for example, head- and body-centred reference frames), depending on how LIP and PRR neurons are sampled.

Where does the transformation occur?

Are head-centred representations of a sound transformed into eye-centred representations in the PPC? Or does this reference-frame transformation occur before the information reaches the PPC? Answering these questions is made more difficult by the fact that auditory spatial information is encoded in parallel pathways in the midbrain and cortex[40]. These parallel pathways raise the possibility that spatial information might be transformed independently in both pathways or in a brain area that projects to both the midbrain and cortical pathways.

However, two pieces of evidence point to the PPC as a locus for this reference-frame transformation. First, midbrain and cortical auditory centres that project directly or indirectly to the PPC[30–32,63–65], such as the inferior colliculus[66], the auditory cortex[67] and area Tpt in the temporoparietal association cortex[68], encode the locations of sounds in a head-centred reference frame that is modulated by eye-position gain. The observation that neurons in area Tpt code auditory-target location in a head-centred reference frame is particularly illuminating, because it is probably one of the PPC's main sources of auditory input[30–32,63–65]. The fact that these auditory areas represent target locations in a head-centred reference frame suggests that the PPC is a locus for transforming head-centred representations of auditory targets into eye-centred representations.

The second piece of evidence for the PPC being a site for coordinate transformations is the finding that many LIP and PRR neurons have gain fields and code targets in intermediate frames of reference[8,9]. Different computational models have shown that gain fields and intermediate frames of reference are found in the layers of neural networks that are responsible for the reference-frame transformations and the combining of different sensory signals that are intrinsically represented in dissimilar reference frames[69–71].

In one neural-network model[69,70], a three-layer neural network was trained to perform coordinate transformations. The input layer contained a map of visual-target location in an eye-centred reference frame, a map of sound location in a head-centred reference frame, and units that linearly encoded head and eye position. The second, 'hidden' layer received input from the input layer and projected to the third, output layer. Neurons in the output layer were trained to represent target location in a variety of different reference frames, such as eye centred, head centred and body centred. The networks were often trained to output to more than one reference frame at a time. The three layers abstractly correspond to: layer 1 — the cortical areas that project to the PPC; layer 2 — the PPC; and layer 3 — the cortical areas that receive projections from the PPC.

Two key findings were apparent from an analysis of the hidden layer of the network. First, the neurons in the hidden layer often encoded target location and were gain modulated. For instance, when the output layer of the network was trained to encode target locations in a body-centred representation, the neurons in the hidden layer had gain effects for both eye and head position. Second, a number of neurons coded in an intermediate reference frame. There were at least two factors that contributed to these intermediate frames of reference. A sigmoidal integration of strong eye-position signals and target-location signals caused a nonlinear modulation that distorted the response fields. Furthermore, the response fields of the hidden-layer neurons were large and asymmetrical, which is typical of the response fields of LIP neurons[9].

The nonlinear modulation, interacting with the asymmetrical response field, resulted in a response field that was partially shifted (an intermediate frame of reference).

A second modelling study[71] also used a three-layer neural network. In this model, there was a layer that encoded the eye-centred location of a target and eye position, a second hidden layer, and a third layer that represented the head-centred location of a target. Unlike the model discussed above[69,70], there were both feedforward and feedback connections between adjacent layers of the network, and different functions were used to compute the activity of hidden-layer units. Regardless of the differences between the models, an analysis of the functional properties of the hidden-layer neurons was similar. That is, the hidden units showed both gain fields and intermediate reference frames.

The results of these two independent modelling studies show that, in the layer of a neural-network model that is responsible for coordinate transformations, neurons show gain-field modulation and intermediate frames of reference. As these features are seen in PPC neurons[8,9,47,48,59,61], the data support the idea that the PPC is part of a network for the transformation of head-centred representations of auditory-target location into eye-centred representations[71]. Further experimental and theoretical work is needed to determine whether the mechanisms described in these two modelling studies[69–71], or further, unknown mechanisms, can account for the intermediate response fields that are seen in LIP and PRR neurons[8,9].

Advantages of a common reference frame

The common reference frame might be a prerequisite stage[71] in the transformation of a sensory-based representation into a motor-based representation that can be used to guide an action[72–77]. Another possibility is that it might have its own special purpose, and exist in parallel with other reference-frame transformations and other elements of the sensorimotor transformation[12,77]. For instance, a common reference frame for coding sensory-target locations might provide an efficient way of representing spatial information for the coordinated movement of multiple effectors[7,78]. This common reference scheme might facilitate coordination and communication between movement-planning regions of the PPC, such as areas LIP and PRR, during tasks that require different motor effectors, such as those requiring hand–eye coordination. Consistent with this possibility are observations that humans code reaches to auditory, visual and proprioceptive stimuli in eye-centred coordinates[79–82].

Why are eye-centred response fields used for this common reference frame? *A priori*, movement plans could be represented in any of several different reference frames. However, it seems likely that an eye-centred representation is used because vision in primates is the sensory modality with the highest spatial acuity. Indeed, many aspects of auditory perception are modulated by eye position or the location of a visual stimulus[82–86]. Moreover, vision has a key role in calibrating the auditory system's ability to localize a sound source[87–89].

Organization and mechanisms in human PPC

Several lines of evidence indicate that the functional organization and computational mechanisms that are found at the level of single neurons in the PPC of nonhuman primates are present in humans. For example, the human PPC seems to contain functional regions that are specialized for planning eye movements, reaches and grasps[90–93]. Imaging studies also indicate that neurons in the human PPC are polysensory, and contribute to tasks that use auditory and visual stimuli[94–96]. Finally, the human PPC is involved in coordinate transformations[97–100] and might also code target locations in an eye-centred reference frame[101] that is gain modulated further by factors such as eye position[91,102].

Future directions

The finding of a common reference frame for movement planning for a significant number of neurons, at least in parts of the PPC, opens several new lines of research. One obvious question is whether this common frame is specific to PRR and LIP, perhaps reflecting a specialization for hand–eye coordination, or is found in other areas within the parietal and frontal lobes.

Is the commonality of reference frames in PRR and LIP seen at the single-cell level? In both areas, there is a mix of reference frames for the auditory responses, whereas the visual responses tend to be eye centred, so it is possible that the commonality of the reference frames is realized in the readout from populations of cells, rather than from single cells.

Another question relates to the biological mechanisms by which reference-frame transformations are mediated. Computational studies[60,69–71] indicate that gain fields are important computational mechanisms for reference-frame transformations. However, there is no direct neurophysiological evidence to support this proposal. It would be most informative to establish a direct causal neurophysiological link between the gain modulation and coordinate transformations.

Can the common coordinate-frame concept be extended to somatosensory stimuli? We have recently found that PRR neurons, which code the goals of reaches in eye coordinates, are gain modulated by the initial position of the hand before reaches. This initial hand position effect is also coded in eye coordinates[103]. As each monkey was pressing a lighted button in the dark, he could see his hand. If the hand is out of sight of the animal, and his only awareness of hand position is derived from limb proprioceptive and somatosensory cues, would this gain effect still be seen in eye coordinates?

Are the representations in PPC task dependent? For instance, would the same neurons show a dynamic change in reference frames, depending on behaviour? It is possible that tasks that require hand–eye coordination might be more likely to use a common coordinate frame.

The finding of intentional maps within the parietal cortex, and the understanding of the reference frames used by these representations, might be useful for neural prosthetic applications. As PPC codes the plans for actions, reading out these action plans in paralysed patients using recordings from arrays of implanted electrodes could enable them to control external devices. Experiments using real-time decoding from cell activity in the motor cortex[104–107] in a closed-loop condition, and from motor, premotor and parietal cortex in an open-loop condition[106], indicate that such a prosthetic is feasible. One possible advantage of using the PPC for such prosthetic control is the fact that intended movement activity can be sustained in these areas by just thinking about a movement, without actually initiating one[108,109]. Moreover, the abstract nature of the representation might simplify the readout of the thoughts for action. The fact that PRR codes reaches in visual coordinates[7] indicates that it codes the goal of an action (for example, reach for the cup) rather than the details of how to achieve the action (which can be performed by computers outside the body that interprets the subject's intentions). That PRR is a visual area might mean that it is less likely to degenerate with paralysis, as a main input to the area is vision, which is not generally effected by paralysis. Also, cortical feedback signals for learning would still be directly available to PRR, being closely associated with the visual cortex[6,29], whereas the motor cortex would lose its main sources of sensory feedback: somatosensory and proprioceptive feedback. Finally, the PRR representation seems to be highly plastic and modifiable with feedback (D. Meeker, S. Cao, J. W. Burdick and R.A.A., unpublished observations) — a useful feature if patients are to learn to use their recorded thoughts to operate different devices.

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