

Spatial Transformations for Eye-Hand Coordination

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Introduction

One of the most important ways in which humans interact with our environment is through the use of our hands, regardless of whether we manipulate objects directly or whether we use tools. In order to accurately reach and grasp objects of interest, we require precise egocentric information about where the object is relative to our body. The direction of an object is specified by the location on the retina that it stimulates. The distance of the object is provided through stereoscopic vision arising from the slightly different views of the two eyes. The eyes, however, only provide the spatial locations of objects relative to the retinas, which depends on the orientation of the eyes in space (gaze). In contrast, the arm is attached to the shoulder and, therefore, muscle contractions need to be specified with respect to this fixed point. Therefore, information about an object's location must be transformed from a gaze-centered representation into one that is centered on the insertion points of the arm muscles (shoulder and elbow). For simplicity, we will refer to the latter as a shoulder-centered representation.

We begin the following sections by discussing the gaze-centered encoding of reach space as well as some of the implications of this particular choice of representation. Next, we consider how motor output is specified in shoulder-centered coordinates by the brain. Finally we examine the transformation required to map the gaze-centered representation of space onto a shoulder-centered movement plan.

Visual Representations of Reach Space

Gaze-Centered Encoding of Reach Targets

Because the projection of a visual object on the retinas changes with the direction of the eyes, the spatial information that reaches visual cortex depends on gaze direction. This gaze-centered representation of reach targets is not only present in the early visual pathway (i.e., retina, lateral geniculate nucleus, striate cortex) but also later on in the visual pathway (e.g., extrastriate and parietal cortex). Thus, the spatial location of an object that we want to reach to or point at is initially encoded relative to the fovea (Figure 1(a)). The persistence of gaze-centered

representations at intermediate levels such as parietal cortex might seem surprising considering that alternative representations, such as a head-centered coding, would be independent of intervening eye movements and thus more stable (in theory, a head-centered representation adds eye position to the gaze-centered target position to specify its position relative to the head). However, an advantage of gaze-centered representations is that, unlike head-centered ones, they do not require such an integration of eye position until one actually reaches, and so are computationally less expensive for the brain. It is worth mentioning that the sensorimotor system also encodes auditory and proprioceptive targets in gaze-centered coordinates, even though these senses are not fixed to the eye.

How is this gaze-centered representation encoded in the brain? In order to accurately reach for an object, the brain requires knowledge about the object's direction relative to the fovea (horizontal and vertical angular eccentricity) and how far it is from the eyes (egocentric distance). The visual field is projected onto the retina and is transmitted to the visual cortex in a topographically arranged fashion. Whereas angular eccentricity in this topographical map defines the location of a potential reach target, the distance of the target is specified both by monocular (accommodation, relative object size, shading, perspective, etc.) and binocular (retinal disparity and convergence) information.

Early visual areas (yellow areas in Figure 1(b)) compute angular eccentricity based on the retinal images from both eyes, synthesized to provide target direction as seen by a virtual (cyclopean) eye located between the right and left eye. On the other hand, retinal disparity is calculated from the difference between the two eyes' images. Different areas in the early visual pathway carry out the computations related to target direction and disparity. In early movement planning, these signals appear to be recombined into a single 3-D representation of gaze-centered space in the posterior parietal cortex (orange area in Figure 1(b)); different neurons in the monkey parietal cortex have receptive fields that encode a specific angular eccentricity of a target and their activity is modulated by target distance. To summarize, early visual and visuomotor areas compute different spatial aspects of the 3-D location of reach targets in gaze-centered coordinates.

Updating of Spatial Memory

As mentioned in the previous section, the drawback of a gaze-centered representation of space is that it needs to be constantly adjusted as we move. This is

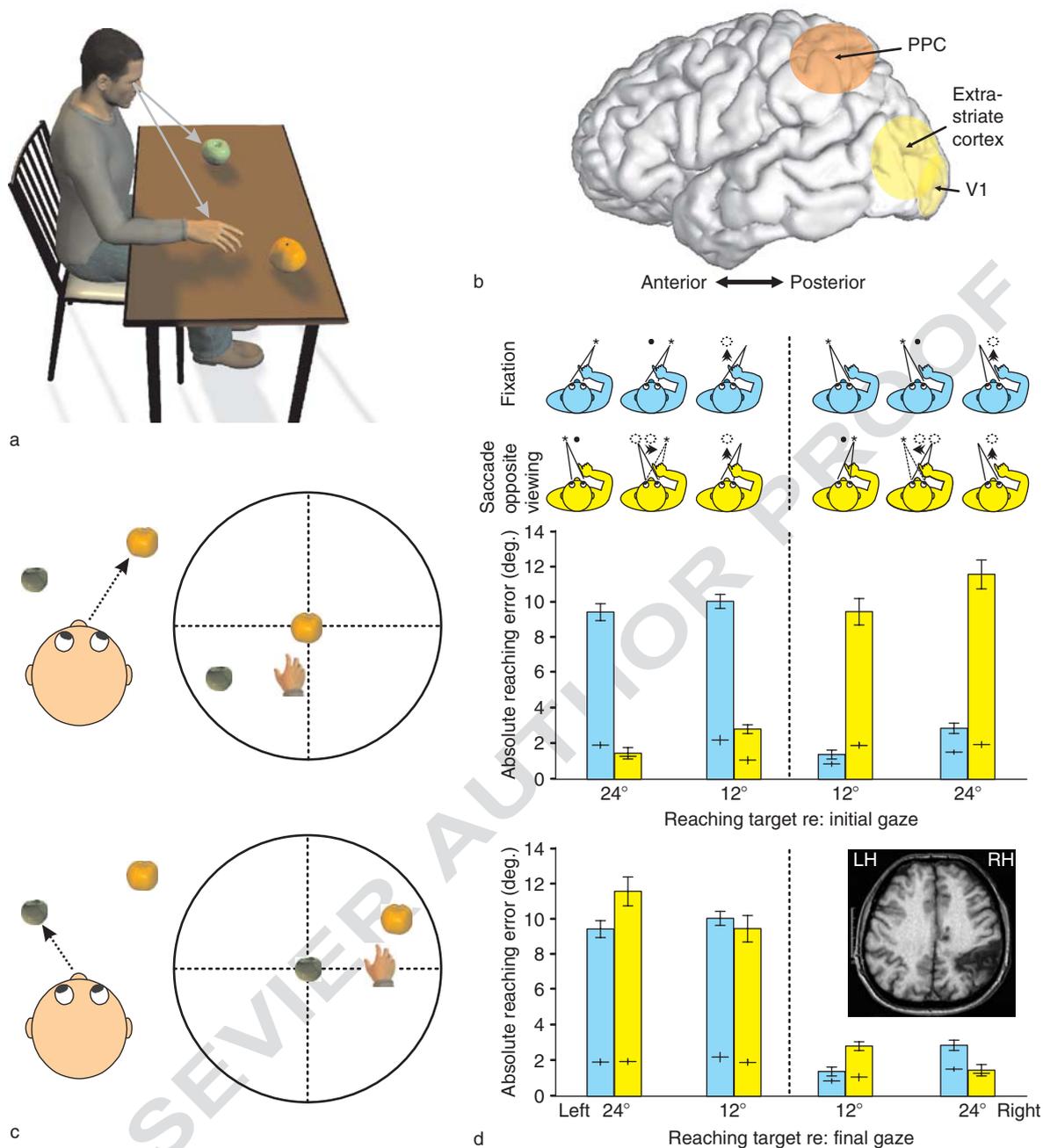


Figure 1 Gaze-centered encoding of reach space. (a) Drawing depicting the egocentric visual directions of the hand, an orange, and an apple, as shown by the gray arrows. (b) Side view of a human brain showing areas (highlighted in yellow and orange) that encode reach space in gaze-centered coordinates: V1, striate cortex; PPC, posterior parietal cortex. (c) The consequence of an eye movement on the gaze-centered representation of the visual field. The head/eye diagrams depict current gaze position; the circles represent the gaze-centered representation of this visual scene (dotted lines represent visual horizontal and vertical axes and intersect at the fovea). If the person in the upper diagram looks at the orange, the hand and apple are represented in the left visual field (upper circle). In contrast, if the person fixates the apple (lower diagram), the orange and hand are now represented in the right visual field (lower circle). If the orange and the hand were no longer visible when the eye movement occurred, the brain would need to remap their position by taking the intervening eye movement into account. (d) Remapping in optic ataxia. The fixation task (first row, blue) shows a typical pattern of reaching errors (identical blue bars in both graphs) for this disorder, where errors are greater when the reach target is in the contralesional (opposite to the lesion) visual field (left half of each graph). The remapping task (second row, yellow) required the person to view the target peripherally in one visual field and then make an eye movement to the opposite side before reaching to the target. If no remapping takes place, then errors (yellow bars) should be greater when plotted as a function of reach target location relative to initial gaze (first graph), whereas if the reach target is remapped with the eye movement, then errors should be greater when plotted against reach target relative to the final gaze position (second graph). The reaching errors in the second graph match very well to the control task errors, suggesting that the location of the reach target in the internal representation was indeed remapped during the eye movement. (d) Adapted from Khan AZ, Pisella L, Vighetto A, et al. (2005) Optic ataxia errors depend on remapped, not viewed, target location. *Nature Neuroscience* 8(4): 418–420, with permission.

necessary to maintain a stable representation of our environment despite shifts and rotations of the eyes. This adjustment of the gaze-centered representation through different types of movements is called updating or remapping. Remapping has been demonstrated to be a general phenomenon that occurs during different types of eye movements – that is, slow eye tracking movements (smooth pursuit) and fast orientation movements (saccades). Updating also occurs for both the rotation and the translational components during head and body movements. Consider the example in **Figure 1(c)**; if the viewer initially looks at the orange (upper left panel), the apple is located to the left and down of it. In the internal representation of this visual scene (represented by the schematic in the upper right panel), the orange is represented at the center of the representation – that is, the fovea – and the apple is mapped onto the lower left quadrant of the visual field. After a saccade to the apple (lower left panel), both the apple and the orange are remapped by the same amount of rotation as the saccade, but in the opposite direction. As a result, the apple is now represented at the fovea and the orange is mapped onto the upper right quadrant. In everyday life, incoming visual information usually contributes to specify the new target location for these internal representations, but many experiments have shown that the brain can accomplish this remapping internally, even if vision is removed, by using eye movement signals from the oculomotor system. Also, it has recently been shown that remapping and vision give better performance compared to vision alone. Psychophysical evidence suggests that about four targets can be represented and remapped in this way.

Intuitively, it would make sense to simply shift the locations of the internal representation by the same magnitude as the eye movement, but in the opposite direction. However, recent studies have shown that because of the kinematics of eye movements (i.e., there is a nonzero torsional component about the line of gaze in noncentral eye positions), shifting the locations by the eye movement vector does not produce correct remapping. Moreover, during pointing to remembered targets, subjects perform in a manner that suggests that they do remap correctly after eye movements, which reveals that the brain does take the rotational component of the eye movement into account during remapping.

It is generally accepted that the areas in and around the medial bank of the intraparietal sulcus of the parietal cortex play a major role in representing and remapping reach targets in gaze-centered coordinates. The receptive fields (a receptive field corresponds to the visual locations in space that activate the neuron) of individual parietal neurons have been

shown to shift during an eye movement to correspond to the remapped location of the target. At the population level, the remapping of individual receptive fields results in an updated memorized target position. Remapping of target location across saccades has also been shown in the posterior parietal cortex through human functional magnetic resonance imaging studies. Moreover, recent neural recordings in the monkey show evidence of updating in a number of extrastriate visual areas such as areas V3A, V3, and V2. This leads to the question of the specific roles these different areas could play in the remapping process for reach movements.

One way to demonstrate the role that parietal and occipital cortex play in remapping is to test unilateral optic ataxia patients with damage to the (right) superior parietal cortex. Optic ataxia generally manifests itself as a deficit in performing accurate visually guided movements to peripherally viewed objects in the contralesional (opposite side to the lesion) visual field. **Figure 1(d)** depicts reach errors in such a patient. After an intervening saccade, errors to previously memorized targets were better explained by the remapped gaze-centered representation than by the initial retinal encoding pattern. The fact that this patient was able to remap despite damage to the right superior parietal cortex is consistent with a distributed remapping process that involves both extrastriate visual and parietal areas. Occipital cortex probably plays a more general role for remapping in perception and action, whereas remapping signals in parietal cortex might be specific for actions like reaching and saccades. In summary, the complete 3-D locations of reach goals are represented in gaze-centered coordinates and these representations are updated during various movements of the body.

Motor Coding of Reach Movements

Shoulder-Centered Encoding of Reach Plans

In order to understand eye-hand coordination, we must also consider the physiology of limb control. A gaze-centered representation of a reach target is inappropriate for reaching because muscle activations which move the arm are determined with respect to the shoulder. Consequently, the brain needs to specify the desired movement vector in a coordinate system relative to the shoulder, which is defined as the difference between the current and desired hand position (**Figure 2(a)**). In this section, we illustrate how and where such shoulder-centered motor plans are encoded. The subsequent section briefly describes how these motor plans are transformed into the appropriate muscle activations.

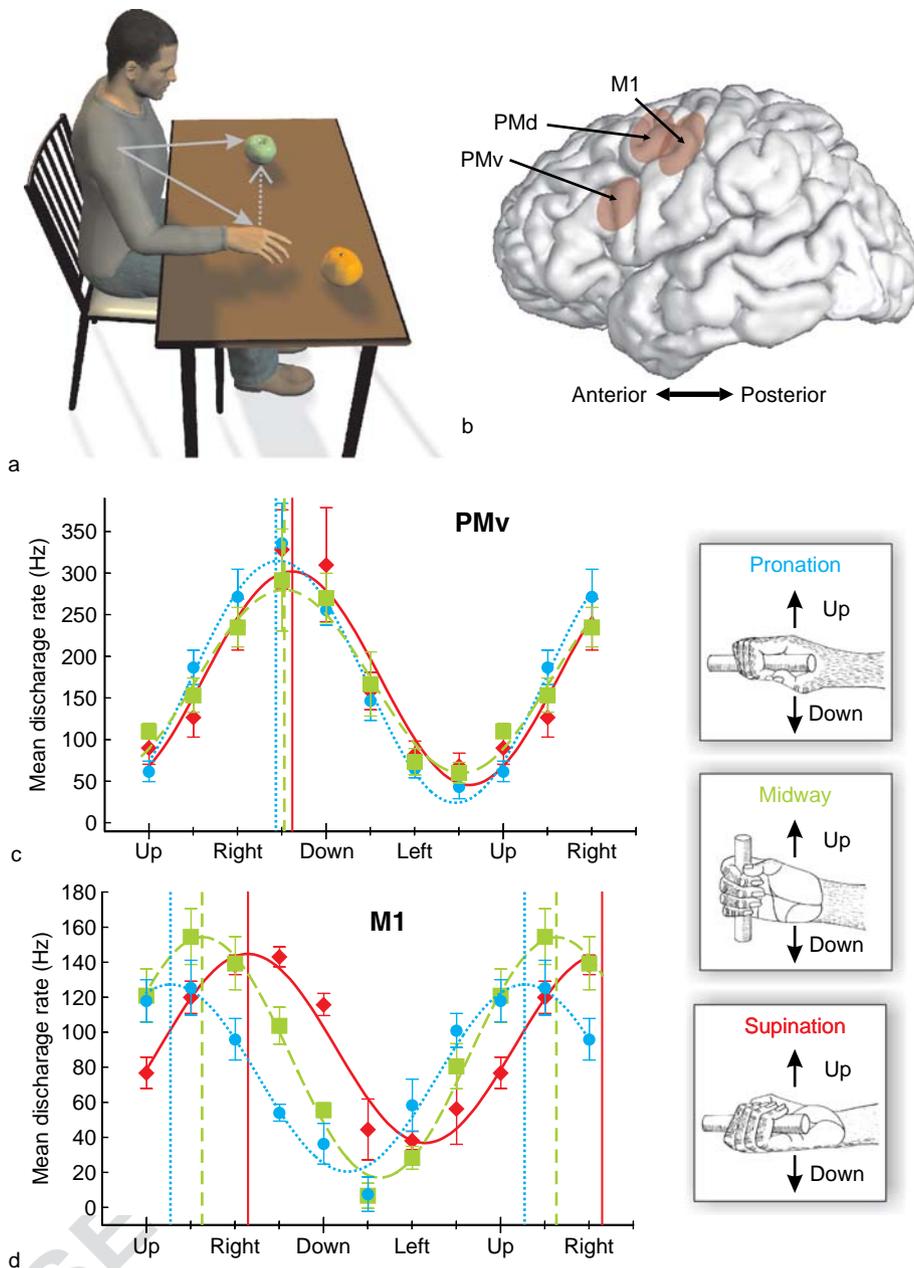


Figure 2 Motor representation of reaches. (a) The diagram depicts the position of the hand and apple encoded relative to the shoulder (gray solid arrows) as well as the desired movement vector (gray dotted arrow). (b) Schematic of the human brain (side view) showing areas (highlighted in red) that encode the desired movement vector in shoulder-centered or musclelike joint-centered coordinates: PMd, dorsal premotor cortex; PMv, ventral premotor cortex; M1, primary motor cortex. (c) Tuning curve of an example neuron in PMv. In this experiment, nonhuman primates were trained to perform wrist movements to visual targets in different spatial directions (x-axis) and the posture of the wrist was modified systematically. The three panels on the right show the three different postures used – pronation, midway (between pronation and supination), and supination. Each curve in the graph corresponds to the tuning curve of the same neuron recorded under those three different postural conditions. Clearly, this PMv neuron does not modulate its discharge rate with posture, which is consistent with a shoulder-centered representation of the desired reach. (d) Example neuron in M1 showing musclelike tuning curves. Here, the neuron’s discharge was modified by the three different postural conditions. The directional shift of the tuning curve is in phase with the muscle activations required for a specific movement direction. Therefore, this M1 neuron shows a musclelike joint-centered encoding of the desired reach. (c and d) Modified from Kakei S, Hoffman DS, and Strick PL (2003) Sensorimotor transformations in cortical motor areas. *Neuroscience Research* 46(1): 1–10, with permission. Copyright 2003 by Elsevier.

Early neural recordings in the primary motor cortex (M1; **Figure 2(b)**) of the monkey during reach movements showed that individual neurons respond best to a certain movement direction, which is known as the neuron's preferred direction. The activity of such neurons decreases as the angular distance between the movement vector and the preferred direction increases. This pattern of activation forms what is known as a cosine tuning of neural activity. The preferred directions of populations of neurons encoding movement seem to be uniformly distributed, thus all possible movements are represented. In summary, neurons with preferred directions and cosine-tuning properties provide the essential neurophysiology for movement encoding in the premotor and motor cortices.

To specify a complete 3-D reach plan one also needs to know the amplitude of the desired movement. Most psychophysical studies seem to indicate that direction and amplitude might be encoded independently, a conclusion drawn from the observation that errors in movement direction are generally smaller than errors in movement amplitude. On the other hand, neurophysiological recordings of neural activity in the dorsal premotor cortex (PMd; **Figure 2(b)**) during reach planning have shown that amplitude and direction are always coded together within the same neuron, where the activity related to a fixed movement direction simply increases or decreases depending on movement amplitude. One unifying solution for these seemingly contradictory findings might be that, at the neuronal level, direction and amplitude are coded together, but are read out by different mechanisms to generate muscle activation.

A large portion of neurons in the monkey ventral premotor cortex (PMv; **Figure 2(b)**) encodes extrinsic movement direction (i.e., the movement vector in an explicit shoulder-centered representation). **Figure 2(c)** shows this pattern for wrist movements where the tuning curve of a neuron in PMv reflects movement direction independent of hand posture (e.g., the palm turned up or down). Apart from the PMv, smaller portions of neurons in the dorsal premotor cortex (PMd) and the primary motor cortex (M1) also show such extrinsic spatial behavior. This shoulder-centered code coexists (in PMd and M1) with other, more muscle-related representations, which may reflect the gradual transformation of those codes into muscle activations. An abstract shoulder-centered programming of a motor plan is a fundamental stepping-stone for the brain to generate the appropriate muscle activations for the actual reach movement.

Planned Movement Vectors and Kinematics

As mentioned earlier, the shoulder-centered motor plan needs to be converted into the appropriate pattern of muscle activations to move the arm. The conversion has to correctly determine not only which muscles to activate (to specify direction) but also the correct force for each set of muscles (to specify amplitude). In addition, the brain has to overcome a series of dynamic constraints, such as the limb inertia and different arm loads due to the load of various hand-held objects. To generate accurate muscle activations, the brain must account for the current posture of the arm. **Figure 2(d)** shows a neuron in M1 with an activity that reflects the influence of posture on its cosine-tuning curve. This particular neuron does not code movement in shoulder-centered coordinates, but instead seems to represent a motor plan with respect to the muscles required for a particular movement. The shoulder-centered motor coding and the muscle-centered movement planning represent the two ends of a continuum, demonstrating the gradual conversion of extrinsic movement information into muscle activation patterns. This conversion involves large portions of neurons in PMd and M1 as well as the cerebellum.

To summarize, the brain represents motor plans in shoulder-centered coordinates in the premotor and motor cortices and then converts those representations of the desired reach into muscle activations. However, since the visual input to the brain specifies the location of a reach target in gaze-centered coordinates, the brain first must transform the early visual signals into appropriate motor commands for the arm in shoulder-centered coordinates. As we will see, simply using a gaze-centered movement vector to move the arm directly would produce large reach errors as a function of eye and head orientation. This visuomotor transformation is the topic of the following section.

The Visuomotor Transformation

Comparison between Hand and Target Positions

To reach out for a visual object, the brain needs to specify the required movement vector by computing the difference between the current hand location and the position of the object in space. This comparison between hand and target positions must satisfy two requirements. First, the areas in the brain that carry out this computation must contain signals providing the complete spatial information of both hand and target locations. Second, this comparison requires

that hand and target locations are represented in the same reference frame in order for both to be combined in a spatially consistent manner. However, it is not yet clear which areas in the brain are involved in this comparison and in which reference frame the comparison is made.

There are three possibilities by which the brain could fulfill these requirements. One way could be to compare the hand and target positions as early as possible in the visuomotor pathway, (i.e., compare the hand position to the target position in gaze-centered coordinates). As mentioned earlier, in the second section, target position has been shown to be encoded in gaze-centered coordinates at the level of the posterior parietal cortex (PPC). Areas in the monkey PPC that code visual objects in gaze-centered coordinates have also been found to code hand position, even when the hand was not seen. This is particularly interesting because it means that the brain can derive the current hand position in gaze-centered coordinates from muscle-related proprioceptive signals. A neural substrate for a comparison between hand and target positions in gaze-centered coordinates has recently been identified in areas closer to the cortical surface of the intraparietal sulcus in the PPC. The activity of neurons in this area depends on both hand and target positions, which is consistent with the formation of a desired movement vector in gaze-centered coordinates.

Alternatively, hand and target positions could be compared at a much later stage (e.g., in shoulder-centered rather than in gaze-centered coordinates). This would require target position to be first transformed from gaze- to shoulder-centered coordinates. The hand position signal used for this comparison could be derived either from visual signals, which go through the same transformation process as target position, or from proprioceptive inputs. The latter joint- or muscle-related signals would require an intermediate transformation into shoulder-centered coordinates through an inverse model of the arm, and then a further transformation into gaze-centered coordinates would be unnecessary. Evidence for a late comparison of hand and target positions in shoulder-centered coordinates comes from several psychophysical experiments. If the hand is unseen, error of reaching toward memorized target locations are compatible with a shoulder-centered hand and target comparison. In contrast, simply providing visual hand position feedback shifted the errors toward a pattern compatible with the comparison of hand and target locations in gaze-centered coordinates.

Finally, the comparison between hand and target could be a distributed process involving multiple

stages of representations taking place across several brain areas. This might seem redundant or contradictory, but it is well known that the brain can derive information from multiple sources (e.g., in sensory integration) and combine these inputs using Bayesian-like algorithms to compute the most reliable estimate. This scheme potentially enables the brain to access the same information encoded in different frames of reference, which would allow it to use the different representations, depending on task requirements. This is supported by behavioral findings which show that task context can alter the reference frame in which the comparison between hand and target locations is carried out. Regardless of where this comparison is done, a reference frame transformation between the gaze- and shoulder-centered representations is necessary. This visuomotor transformation could either be carried out for hand and target locations independently or for the combined signal (i.e., the desired movement vector).

Reference Frame Transformations

To transform gaze-centered into shoulder-centered signals, the brain has to perform a cascade of conversions which require knowledge about the three-dimensional orientation of body parts. Theoretically, the transformation involves a set of serial steps which gradually combine eye-in-head, then the head-on-neck, orientation, and subsequently the shoulder rotation with the visual representation, to produce a head-centered, body-centered, and ultimately shoulder-centered representation. But how do we know that these reference frame transformations are even necessary?

To answer this question, consider the example depicted in **Figure 3(a)**, where a study participant is asked to reach out to a target toward the left. When the head is upright and the eyes are fixating straight ahead, the gaze-centered coordinate system has the same orientation as the shoulder-centered coordinate system and is only translated with respect to the latter. Therefore, the desired movement vector is the same in both reference frames and no explicit reference frame transformation would be required. But what would happen if the head was tilted, say, toward the left shoulder, and the person maintained straight-ahead gaze? Since the eyes remain more or less in the same position relative to the head, the retinas are now tilted in space. Therefore, the projection of hand and target onto the retina would be rotated (in gaze-centered coordinates) in the opposite direction as the head – that is, toward the right. If this vector was directly used to guide the reach, the arm movement would be inaccurate and the move would be up and to the left instead of simply horizontally. Everyday experience

and experimental evidence suggests that people generally do not make such errors, which demonstrates that the brain performs a reference frame transformation of the desired movement vector.

The preceding example illustrates a simplified portrayal of a reference frame transformation. However, this visuomotor transformation is actually much more complex. A large part of this complexity arises

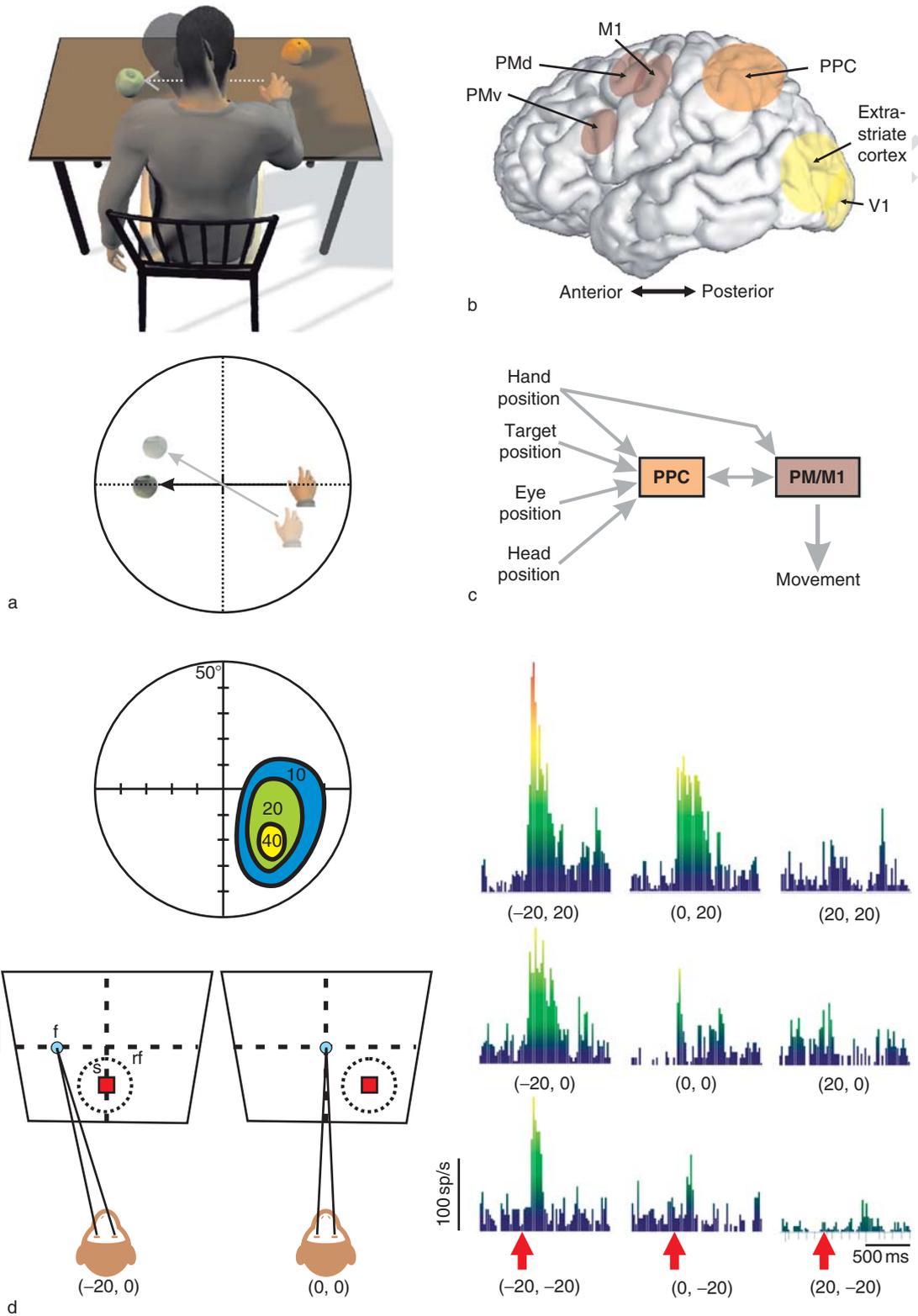


Figure 3 Continued

because body parts rotate around their anchor points; for example, the eye rotates in the ocular cavity and the head rotates around the base of the skull. Since rotations are nonlinear and noncommutative (sequence matters) operations, the relationship between gaze-centered and shoulder-centered coordinates can become quite complicated. In addition, the anchor points for different body parts are offset one from another. For example, if the head rotates, the eyes shift their position in space. Not taking translations into account could result in a mislocalization of target position during the reach. In sum, an accurate visuomotor transformation has to take into account the rotational and translational aspects of body geometry.

Brain areas involved in this transformation would necessarily require extraretinal signals about the rotation of the eyes and head in addition to representing the three-dimensional hand and/or target locations. The translational components are also implemented, probably acquired through experience. How would the brain purposefully combine these different signals in a population of neurons? A potential window into the distributed processing in neural populations is provided by the analysis of artificial neural networks trained to perform reference frame transformations. Artificial neural networks are highly simplified mathematical analogies of real networks of neurons and are believed to reflect fundamental mechanisms underlying brain function. Probably the most important finding is the discovery of neurons (both real and simulated) which alter their response magnitude based on extraretinal eye and/or head position signals, without changing the gaze-centered location of their visual receptive fields. This modulation of response magnitude is known as a gain field and is illustrated in Figure 3(d).

Mathematically speaking, gain fields operate through a nonlinear combination of different sources of information (e.g., visual input, eye position, head position) within the same neuron. If many different neurons incorporate multiple combinations of these signals, then the neural population has a complete distributed representation of space relative to different body parts. The individual multimodal neurons inside this population act like basis functions in that they provide a unique representational set and can be combined (by linear summation) in different ways to produce the desired reference frame output. Thus, using the same population of basis functions, it is possible to extract target position in multiple frames of reference.

The shortcoming of the concept of basis function neurons is that every possible combination of signals must be represented, which could lead to a large number of units in the population, a dilemma called the curse of dimensionality. Therefore, it is believed by some that the brain compromises between basis function neurons – implying the presence of gain fields – and explicit representations (e.g., shoulder-centered encoding of the desired movement vector) in various reference frames. Evidence for this comes from brain areas such as the posterior parietal cortex, which contains many neurons encoding reach space in gaze-centered coordinates. A significant proportion of posterior parietal cortex neurons with gaze-centered receptive fields also show eye-position-dependent gain fields. Neurons in the premotor and motor cortices show movement coding in shoulder-centered coordinates, which constitute another form of explicit representation of reach space. Gain fields are thought to be the implicit code that implements the visuomotor transformation between an explicit gaze-centered code and an explicit shoulder-centered reach plan.

Figure 3 Visuomotor transformation. (a) Diagram depicting two different possible head roll postures (head upright and rolled toward the left shoulder) while a person viewing an apple and an orange is planning to reach out for the apple (gray dotted arrow). The corresponding gaze-centered representation is shown schematically in the circle. Note that the same shoulder-centered movement plan (diagram of person, dotted arrow) leads to different gaze-centered desired movement vectors in the circle, depending on head posture (head upright, black arrow; head roll, faded gray arrow). (b) Schematic of the human brain (side view) showing the visuomotor transformation pathway from early visual to motor structures: PMd, dorsal premotor cortex; PMv, ventral premotor cortex; M1, primary motor cortex. (c) Model of the visuomotor transformation. Visual (target and hand position), nonvisual (proprioceptive hand position), and extraretinal (eye and head position) information is combined in the posterior parietal cortex (PPC) and also in the premotor and motor cortices (PM/M1) to produce an accurate movement. (d) Gain field modulations in area 7a of the posterior parietal cortex. The top circles depict the gaze-centered receptive field of one example neuron. The overlapping circular shapes show different levels of activation for this cell as a function of horizontal and vertical gaze-centered target location. Based on this information, a stimulus (red squares in the lower diagrams) was placed at the location of the highest activity in the neuron's receptive field. The animal fixated at one of nine locations and the activity in response to the stimulus was measured in the neuron's receptive field. The stimulus was always presented at the same location relative to gaze (i.e., in the receptive field, which moved with fixation), as can be seen in the two lower diagrams for two example fixation locations (center left and straight ahead). The graphs on the right show the cell's activity over time (red arrows signify stimulus onset) for the nine fixation locations. The figure shows that the cell's activity for the same stimulus location (relative to gaze) was modulated by eye position, as predicted by the gain field theory. (d) Data modified from Andersen RA, Essick GK, and Siegel RM (1985) Encoding of spatial location by posterior parietal neurons. *Science* 230(4724): 456–458, with permission. Copyright 1985 by AAAS.

Conclusions

Visually guided reaching involves the transformation of sensory information from the eyes and hand into movement commands for the arm. The early representation of sensory input is gaze-centered and appears to be remapped during body movements in order to ensure a stable internal representation of the visual environment. The arm motor plan is calculated by comparing the desired target position to the current hand location. This motor plan is spatially accurate because the brain accounts for eye and head posture through a distributed internal model of body geometry. As a result, the motor plan is specified in shoulder-centered coordinates and then further transformed into muscle activation patterns. This cascade of different representations and mechanisms (e.g., gaze centered, shoulder centered, updating) may seem complex and perhaps redundant at first glance. However, this appears to be the most cost-efficient way to deal with the large amounts of information in the system – that is, by solving distinct computational problems at different stages of the visuomotor transformation, such as making cognitive comparisons between multiple targets at early visual stages and specifying detailed limb dynamics at later stages.

One of the remaining challenges for neuroscientists is to understand the theoretical requirements and mathematical algorithms the brain employs to carry out these transformations. Without such a theoretical framework, it is difficult to interpret the observed properties of individual neurons in the parietal to frontal network. This framework in turn is necessary to explain what goes wrong in patients with neurological disorders affecting visually guided reaching. Further, the field of visuomotor neuroscience is now at a point where we can begin to tackle more complex problems, such as the influence of other sensory modalities, mechanisms engaged when reaching to targets in movement, decision making, target selection, and the role of attention.

See also: Aging and the Eye (00146); Vestibular system (00273); Assessing spatial memory and processing in animals (00288); Magnetic resonance spectroscopy (00300); Computational neuroscience (00330); Memory Representation (00750); Neural representations (00767); Computational models (00768); Cerebral cortex (00771); Anatomical pathways for oculomotor control (01086); Attention and eye movements (01087); Cortical control of eye movements (01091); Eye and head movements

(01092); Saccadic eye movements (01101); Multisensory convergence and integration (01112); Neural coding of spatial representations (01113); Neural prostheses for reaching (01114); Parietal cortex and spatial attention (01117); Spatial cognitive maps (01121); Theoretical approaches to sensorimotor integration (01123); Vision for action and perception (01124); Motor Function (01292); Physiological Circuits (01298); Coding (01322); Kinematics & Dynamics (01324); Bayesian cortical models (01399); Population codes (01401); Gain modulation (01407); Models of sensorimotor integration (01426); Bayesian models of motor control (01429).

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