

Spatial constancy mechanisms in motor control

W. Pieter Medendorp

Phil. Trans. R. Soc. B 2011 **366**, 476-491

doi: 10.1098/rstb.2010.0089

References

[This article cites 145 articles, 72 of which can be accessed free](#)

<http://rstb.royalsocietypublishing.org/content/366/1564/476.full.html#ref-list-1>

[Article cited in:](#)

<http://rstb.royalsocietypublishing.org/content/366/1564/476.full.html#related-urls>

Subject collections

Articles on similar topics can be found in the following collections

[neuroscience](#) (280 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Review

Spatial constancy mechanisms in motor control

W. Pieter Medendorp*

Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, PO Box 9104, NL-6500 HE Nijmegen, The Netherlands

The success of the human species in interacting with the environment depends on the ability to maintain spatial stability despite the continuous changes in sensory and motor inputs owing to movements of eyes, head and body. In this paper, I will review recent advances in the understanding of how the brain deals with the dynamic flow of sensory and motor information in order to maintain spatial constancy of movement goals. The first part summarizes studies in the saccadic system, showing that spatial constancy is governed by a dynamic feed-forward process, by gaze-centred remapping of target representations in anticipation of and across eye movements. The subsequent sections relate to other oculomotor behaviour, such as eye–head gaze shifts, smooth pursuit and vergence eye movements, and their implications for feed-forward mechanisms for spatial constancy. Work that studied the geometric complexities in spatial constancy and saccadic guidance across head and body movements, distinguishing between self-generated and passively induced motion, indicates that both feed-forward and sensory feedback processing play a role in spatial updating of movement goals. The paper ends with a discussion of the behavioural mechanisms of spatial constancy for arm motor control and their physiological implications for the brain. Taken together, the emerging picture is that the brain computes an evolving representation of three-dimensional action space, whose internal metric is updated in a nonlinear way, by optimally integrating noisy and ambiguous afferent and efferent signals.

Keywords: inflow versus outflow; reference frames; Bayesian; neural; whole-body motion

1. INTRODUCTION

Immanuel Kant argued that spatial representation plays a fundamental role in how we construct our thoughts and intuitions [1]. According to the philosopher, we cannot experience and grasp objects without being able to represent them in a spatial context. While Kant's view has highly influenced the field of philosophy, corollaries of his work are also seen in many other research fields today, such as computer science and psychology. Without taking a philosophical stance, the notion of spatial representation is also a critical assumption in many concepts and theories in neuroscience and offers a tractable approach to understanding information processing in the brain. More specifically, how the brain represents space and uses this information to generate goal-directed actions is a longstanding question that is crucial for a better understanding of movement disorders. While this basic question is still the topic of many research endeavours, by now it is widely accepted that the brain does not construct a single, unitary representation of space, but instead produces multiple representations of space

to subserve stable perception, spatial awareness and motor guidance (see [2,3], for reviews).

A compromising factor in the coding of a spatial representation is keeping it online and up-to-date during self-motion. Are we able to maintain an accurate representation of the world, and the objects within it, even when we move around? Our perception of external space indicates that this is the case. Our perception of the world remains stable when we make a saccade, even though the image of the world shifts on our retinas in the back of our eyes. And when we walk around, we are not disturbed by the even more complex changes in the optic flow on our retinas and we can act rather effortlessly upon our surrounding objects, even though they continuously change location relative to our effectors. Thus, despite our movement, we perceive the world as stable and are able to act upon the objects in it with great accuracy. How do we do this? How does the brain achieve spatial stability with its ever-changing sensory and motor inputs? This ability is also referred to as spatial constancy, or spatial updating, and as we will see later, involves a prodigious control system in the brain. In the past, this problem has attracted the attention of many distinguished scientists, such as Descartes, Von Helmholtz and Gibson. Although the control of spatial constancy was first seen as an important component mediating stable perception, similar mechanisms may

*p.medendorp@donders.ru.nl

One contribution of 11 to a Theme Issue 'Visual stability'.

also be needed to support behaviour in non-perceptual tasks, such as in action control.

In recent years, the neural computations for spatial constancy as well as the role of various inflow and outflow signals have become topics of direct neurophysiological demonstrations. In this review, I will cover recent developments in this field, with the main focus on the mechanisms that play a role in maintaining spatial constancy for ensuring the spatial accuracy of movements. This means that, besides a brief historical overview, I will not address in detail the seminal work that has been performed in relation to pure perceptual processes (but e.g. [4–6]). Also the work in relation to building cognitive maps for spatial navigation will be outside the scope of this paper (but see [7] for review). I will summarize pertinent experimental studies that have been performed in the oculomotor system with visual stimuli, and from that gradually expand by reviewing spatial updating experiments during more complex self-motion conditions and in other effector systems. Mathematical concepts such as computation, optimization and inference will be used to guide this review where possible.

2. HISTORICAL BACKGROUND

In a discussion of spatial constancy mechanisms, it is important to make a distinction between the ability to correct for intervening motion in goal-directed motor control and the ability to keep perceptual stability despite intervening motion, although it is undeniable that these are mutually related. Throughout this review, we will refer to the former as sensorimotor constancy and to the latter as perceptual stability. Classically, the spatial constancy problem was predominantly considered a perceptual problem.

The visual world has the property of being stable
By stability is meant the fact that it does not seem to move when one turns his eyes or himself around
The perceptual experience of the stable, unbounded visual world comes from the information in the ambient array that is sampled by a mobile retina. The reason the world does not seem to move when the eye moves, therefore, is not as complicated as it has seemed to be. Why should it move? The movement of the eye and its retina is registered instead; the retina is proprioceptive.
[8, p. 256]

Gibson argued that the brain relies on the fact that the world is stable ecologically as an inbuilt assumption, so that any motion of the image as a whole must be due to the eye movement rather than the world movement [9]. However, knowing that there is a change in the information in the optic array sampled by the retina does not suffice to indicate what type of signal about the eye movement is used for visual stability. Descartes [10] was the first to point out that the world seems to move when the retina is passively displaced by tapping on the canthus of the eye, which argues against the sole use of retinal cues for visual stability.

In stabilizing the visual world across saccades, therefore, the information about the eye movement must be of extraretinal nature. Two types of extraretinal information about the eye movements are

centrally available: *inflow* and *outflow* signals. Inflow relates to reafferent feedback, which includes somatosensory signals and proprioceptive signals from the eye muscles. Descartes' experiment would also argue against a contribution of proprioceptive information about the extraocular muscles. That is, the stretch receptors in the extraocular muscles by themselves cannot prevent the destabilization of the visual world in response to the tap (but see [11] for a role of proprioceptive inflow to spatial constancy under some conditions).

The outflow signal relates to a copy of the motor command, also termed efference copy (or corollary discharge), and is only present in the context of actively generated motion, such as during saccades. Von Helmholtz [12] was the first to discuss the potential importance of efference copy in perceptual stability. He proposed that visual stability is achieved by using a copy of a movement command (which he called 'effort of will') to simultaneously adjust perception for the corresponding eye movement. In other words, the brain transmits a copy of a movement command, like sending a cc in your email communication, into ostensibly sensory areas, effectively informing itself about the sensory consequences of its own actions [13,14]. Put differently, the efference copy is thought to help differentiating between sensations that arise as a consequence of one's own actions from those that arise from the environment, and hence contributes to maintaining perceptual stability across saccades.

In the next section, I will review neurophysiological evidence for a putative role of efference copy in spatial constancy across saccades. The evidence stems mainly from regions located within the dorsal action stream, which has led some authors to put forward the perspective that efference copy signals support primarily spatial constancy for action, not perception [15].

3. SACCADIC UPDATING

Hallett & Lightstone [16] were the first to systematically investigate sensorimotor constancy for saccadic control, using a so-called double-step saccade task. Subjects were briefly presented with two targets in the visual periphery, one after the other, and subsequently asked to make saccadic eye movements to both locations in quick succession. Because the second target disappeared before the first saccade occurred, the second saccade will not reach the target if its metrics are based on the retinal coordinates of the target only. Instead, for accurate performance, subjects must compute the dimensions of the second saccade by combining the retinal coordinates of the target and the metrics of the first saccade. Their observation that the eye reaches the final target position irrespective of the amplitude of the first saccade suggests that sensorimotor constancy is maintained during oculomotor performance by correcting target representations for intervening eye movements.

Similar findings in totally different experimental settings were made in a monkey neurophysiological experiment by Mays & Sparks [17]. They tested the accuracy of saccades towards brief visual stimuli.

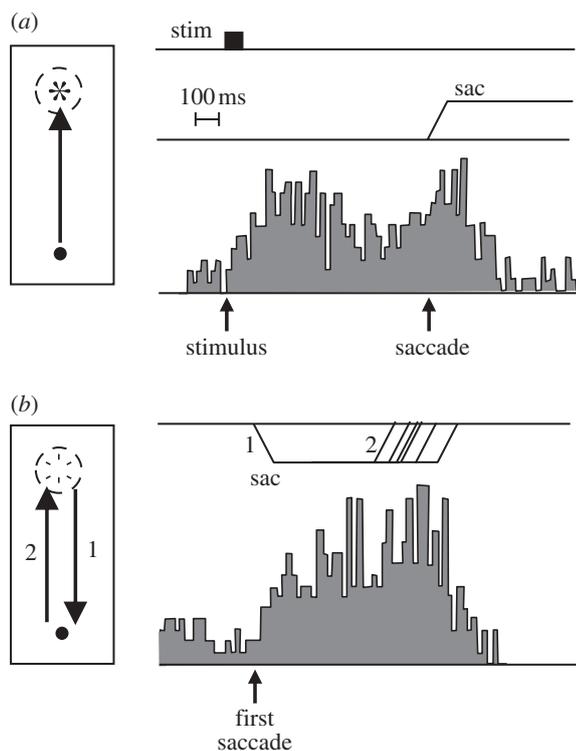


Figure 1. Spatial updating in parietal area LIP. (a) The neuron responded physically to the onset of visual stimulus in its receptive field (RF), sustained its activation during the memory interval and had again a phasic burst during the saccade. Trials have been aligned with the beginning of the saccade. (b) Response of the neuron during double-saccade trials with a movement first down then back up into the cell's RF. The activity of the neuron increased as soon as the first target was achieved and the next saccade was planned into the cell's response field, when its RF covered the previously stimulated location. Trials are aligned to the first movement. Modified from Gnadt & Andersen [19], with permission.

Just before the monkeys moved their eyes, the superior colliculus (SC)—a midbrain area involved in the generation of eye movements—was electrically stimulated. To correct for the stimulation-induced eye movement, the brain generated a corrective saccade to bring the eyes to the target location, even though the target was no longer visible.

Similar corrective saccades for maintaining updating accuracy were obtained while stimulating areas more upstream from the SC, such as the frontal eye fields (FEFs), but remained absent when stimulation was applied downstream of the SC, on the motor neurons or nerves (reviewed in [18]). This would be consistent with the notion that an efference copy, rather than muscular proprioception, plays an important role in maintaining spatial constancy across saccades.

The neural signature of the updating process was first observed by Gnadt & Andersen [19], in the lateral intraparietal area (LIP). They trained monkeys to look from an extinguished fixation spot towards a briefly flashed target and then back towards the remembered fixation position in complete darkness. They identified neurons that increased their firing rate after the monkey achieved the first target and planned the return saccade to the remembered fixation

spot, the location of which was in their response fields. Because these neurons never had the fixation stimulus physically presented in their receptive field (RF), their response must reflect updating (figure 1). This means that the representation of the fixation stimulus is transferred, or remapped, from the group of neurons that was physically stimulated by it, to the group of neurons that have their RFs at the location of the, now extinguished, fixation stimulus after the first saccade.

A few years later, Duhamel *et al.* [20] published a landmark study on spatial constancy mechanisms, showing that most neurons in LIP respond when a saccade brings the location of a previously flashed stimulus into their RF. More importantly, some (not all) LIP neurons responded predictively to the 'new' situation that would arise after the saccade. They shifted their eye-centred RF in anticipation of the saccade that would bring a stationary stimulus into their RF, as if they are transiently craniotopic [21]. This shifting seems to take the form of a jump, rather than a spread, in a direction parallel to the saccade [22]. Predictive updating implies that these neurons have access to the size and direction of the upcoming eye movement, which can be provided by an efference copy signal of the motor command. At the population level, the remapping of activity takes place independent of saccade direction, indicating that LIP neurons have access to spatial information throughout the visual field [23]. Recently, it was demonstrated that extrastriate areas V2, V3 and V3A also remap activity across saccades, but the proportion of neurons in these regions showing this behaviour becomes smaller and smaller when going backward from LIP in the visual pathway and the latency of remapping increases (i.e. the remapping becomes less predictive) relative to saccade onset [24]. Also more motor-related areas such as the FEFs [25] and the SC [26,27] have been shown to remap neural activity across saccades.

Recently, Sommer & Wurtz [22,25,28] and Wurtz [29] have identified a pathway providing an efference copy signal related to the forthcoming eye movement. This pathway runs from the SC via the mediodorsal thalamus to the FEF. Sommer & Wurtz found that inactivation of the mediodorsal nucleus impaired the spatial processing and remapping of RFs in the FEF, which implied and was observed behaviourally as impaired performance in the double-step saccade task. It should be noted, however, that the behavioural updating deficits were only modest, i.e. 19 per cent on average. This suggests that other pathways may be involved in relaying the efferent signal. Indeed, recent work has shown that parietal areas receive eye position and velocity inputs in association with oculomotor functions via an ascending prepositothalamo-cortical pathway [30–32]. Conversely, inactivation of area LIP has been shown to also impair performance in monkey's double saccades [33].

Thus, the remapping mechanism operates such that sensorimotor constancy is maintained dynamically, i.e. by updating spatial information in an eye-based gaze-centred reference frame. Bringing this in relation with perception, following the Helmholtzian view,

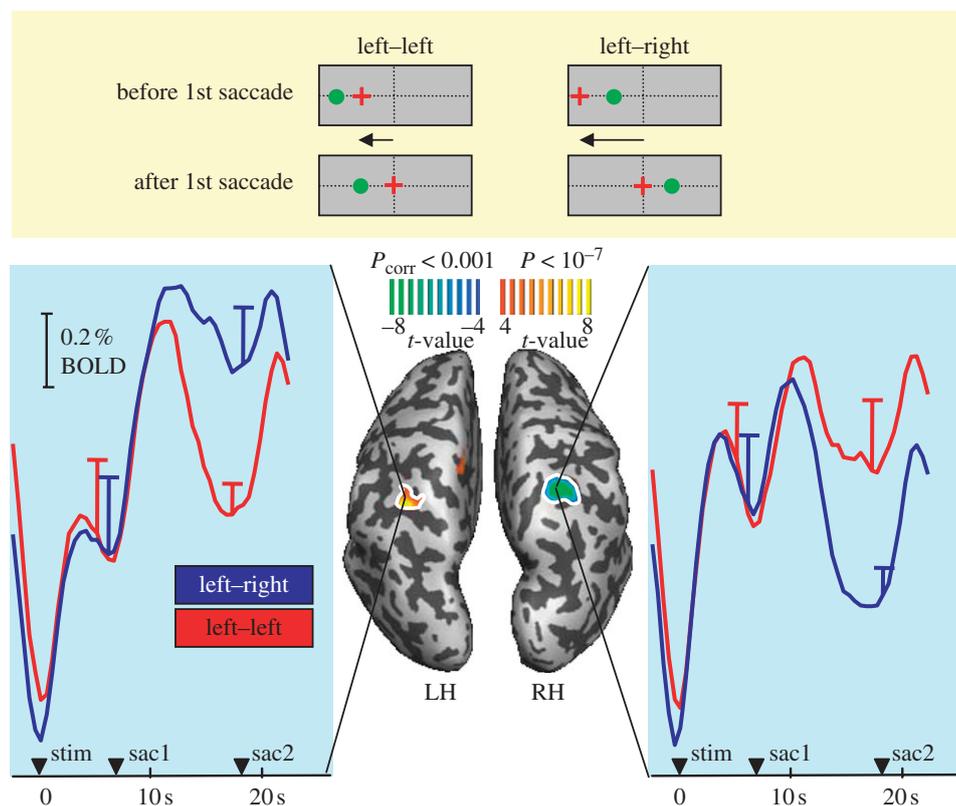


Figure 2. A bilateral region (indicated by white thick lines) in the human posterior parietal cortex is involved in spatial updating during double-step saccades. Two stimuli (stim), flashed in the left hemifield, cause increased activity in the right parietal area. After a 7 s delay, the subject makes the first saccade (sac1) and another 12 s later the second saccade (sac2) is executed. After the first saccade, the remembered target of the second saccade remains in the left hemifield (left–left trial) or switches to the right hemifield (left–right trial). For the latter trials, the region’s sustained activation also shifted: if the target shifted into the right hemifield, a high sustained activation was observed in the left parietal area, prior to the second saccade. Activation related to the execution of the second saccade is not shown. LH, left hemisphere; RH, right hemisphere. Modified from Medendorp *et al.* [36].

comparing the remapped information with re-afferent sensory feedback of the same saccade, if available, would allow for the evaluation of perceptual stability [34] and/or detect changes in the spatial world by external sources (i.e. ex-afference). Whether LIP or FEF is also involved in this comparison (see [35] for a preliminary report), by means of their efference copy inputs and visual inputs from occipital cortex, or whether another neural structure (e.g. the cerebellum) is implicated, is still an open question. Double-step saccade experiments in complete darkness do not assess this comparison—they only address the remapping ability (but see §10).

In the human, gaze-centred remapping observations for saccades have also been made, using the coarse time resolution of functional magnetic resonance imaging (fMRI) [36–39], the millisecond temporal resolution of magneto- and electroencephalography [40,41] and transcranial magnetic stimulation experiments [42,43]. In the fMRI studies by Medendorp *et al.* [36,37,44], remapping was demonstrated in the human posterior parietal cortex during a double-step saccade task, in a region showing contralateral topography of memorized target locations, perhaps the analogue of monkey LIP [45,46]. It was found that when eye movements reversed the side of the remembered target location relative to fixation, the region exchanged activity across the two cortical lobules. As shown in figure 2,

the activity in the right parietal region increases when the two targets are presented to the left of fixation. If, after the first saccade, the location of the second target remains to the left, the activity remains high in the right region, but when its location shifts to the right of fixation, the activity decreases, and in due course the activity increases in the left parietal region. This shows that the location of the second target is remapped from the right to the left hemisphere (figure 2). Similar remapping observations were observed when the two targets were initially presented in the right hemifield (not shown).

As in the monkey, remapping of activity has also been shown in earlier visual areas, with decreasing strength towards areas lower in the hierarchy from V3A down to V2/V1 [39]. It is also important to point out that the gaze-centred remapping observations do not argue against the idea that these regions may also implicitly code their representations into other reference frames, using position signals of the eyes or other body parts, expressed in gain fields [47–49] or muscle proprioception [50,51].

4. SMOOTH MOVEMENTS

Although the double-step saccade task has yielded many insights in the mechanisms resulting in sensorimotor constancy, it is not trivial that these mechanisms also apply to other oculomotor functions.

Saccades are fast and highly stereotyped movements, which make the use of an efference copy signal in sensorimotor constancy (and perceptual stability) a feasible, if not necessary, conception. For a complete picture it is equally important to understand sensorimotor constancy and its neural implementation across other types of eye movements, such as saccadic eye-head gaze shifts, smooth pursuit, vergence and vestibular nystagmus.

Starting with the first, Vliegen *et al.* [52,53] have recently demonstrated that correct double-step eye-head gaze shifts can be made to two remembered target locations, irrespective of whether the second target was presented visually or acoustically. In fact, even when the second target was presented in mid-flight during the first movement, the second movement reached that target accurately. The latter finding would argue against an updating mechanism that operates solely on the basis of a predictive motor command, i.e. using an efference copy of the pre-programmed gaze displacement, and at least suggests that continuous dynamic feedback about the actual movements of eyes and head also plays a role in this updating behaviour (see figure 7).

The quality of spatial constancy during smooth pursuit has been tested in many studies, often in a paradigm requiring subjects to make saccades to briefly flashed targets, after an intervening smooth eye movement. Recent observations based on this paradigm, made by Blohm *et al.* [54], have resolved an apparent discrepancy in this field. These authors found that short-latency (less than 175 ms) saccades were coded based on the initial retinal location of the target (cf. [55,56]), whereas longer latency (greater than 175 ms) saccades were programmed based on the initial retinal target location and extraretinal information about the smooth eye displacement (cf. [57–60]). Blohm *et al.*'s [54] findings suggest that the extra-retinal information about the motion of the eye is not available at a very short latency but takes some time to be integrated before it can mediate spatial constancy in the oculomotor system. Neurophysiological data supporting this idea are lacking, but preliminary reports allude to a role of the posterior parietal cortex (see [61,62]).

Spatial updating across vergence eye movements has been rarely studied. One study was performed by Krommenhoek & Van Gisbergen [63], testing combined version-vergence movements during double-step target jumps in direction and depth. Non-retinal information about the first movement in direction and depth was used in the execution of the second movement, but compensation was clearly better for the directional than depth component of the intervening eye movement. Like for pursuit updating, physiological correlates of these manifestations of spatial updating remain to be revealed. However, it has been shown that neurons in parietal (LIP) and frontal areas (FEF) have three-dimensional RFs [64–67], showing that these neurons are not only sensitive to the direction of a target but also to its depth. Given that these regions are involved in updating across saccades, it would be interesting to test whether the anticipatory shifting can be shown also in

three-dimensional visual RFs. In this context, Genovesio *et al.* [68] recorded neural activity in LIP while monkeys performed saccades between targets at different depths. They showed that in the post-saccadic period, neural activity is influenced jointly by both the eye displacement and the new eye position. It can be argued that these signals play a role in the dynamic retinal representation of visual space and in the further transformation of spatial information into other coordinates systems [47,68].

Spatial constancy in the oculomotor system has also been shown during ongoing nystagmus, as generated by whole-body rotations in complete darkness [69]. Rotating subjects can saccade to flashed visual targets, compensating for the quick-phases that intervene between the presentation of target and the execution of the saccade. Whether these quick-phases can induce a remapping of activity in cortical structures, or whether their effects are accounted for at a subcortical level requires further investigation.

The wealth of studies reviewed so far indicates that significant progress has been made in understanding the computational constraints and the physiological implementation of (visuo)motor constancy in the oculomotor system. Sensorimotor constancy is maintained for both smooth and fast intervening eye movements, and elements of underlying neural correlates have begun to be discovered. But sensorimotor constancy is not only important across eye movements—it should also be maintained across head and body movements to serve accurate motor control. The following sections expand to these conditions.

5. PASSIVE VERSUS ACTIVE SELF-MOTION

A distinction has to be made between passive and active self-motion. These types of movement differ in the presence of efference copies of motor commands, which are only available during active motion. Only efference copies of intended movements can play a role in predictive spatial updating, as argued above for saccade updating. When movements are passive, such as when we ride in a train or drive a car, the amount of self-motion can only be estimated by our internal sensors. Because these sensory signals are caused by the actual motion, they obviously cannot account for predictive properties of spatial updating. In the following section, I discuss the sensory sources available to estimate self-motion during passive movement.

First there is the optokinetic system, a visual subsystem for motion detection based on optic flow [70,71]. Optokinetic cues are mainly important for the detection of low-frequency body translations and rotations. Flight simulations, for example, exploit that the brain interprets sustained large-field optic flow as owing to self motion. Recent evidence by Wolbers *et al.* [72] suggests that the brain can use optic flow to monitor target locations in an egocentric map of space (see figure 7). Also, Warren & Rushton [73] showed a role of optic flow in the estimation of scene-relative object movement during self movement.

Information about head motion in space may also come from the vestibular system. The vestibular

system, located in the inner ear, is comprised of the otoliths and semicircular canals, which detect the head's linear acceleration and angular velocity, respectively (see [74], for a review). The otoliths sense gravito-inertial force and cannot distinguish between tilt and linear accelerations for elementary physics reasons [75]. In essence, this is simply a consequence of Einstein's equivalence principle stating that inertial accelerations and gravitational acceleration are physically indistinguishable. One recent theory suggests that the canal signal is used to disambiguate the otolith signal [74,76,77]. Neural underpinnings for this theory have been found at various levels in the brain, including the cerebellum, thalamus and brainstem [78]. Otolith disambiguation is obviously very important in compensating for linear self-motion (thus not confusing it for tilt) in order not to compromise spatial constancy.

Also the somatosensory system may contribute to spatial constancy by detecting the changing pressures on the skin during motion and possible differences in posture, including proprioceptive signals that provide information about the relative position of body, head and eyes [79,80].

How all these sensory signals affect the neural computations underlying spatial constancy is a difficult question, given the differences in noise properties, internal dynamics and intrinsic reference frames of the various sensors (see [81] for a review of computational approaches). Moreover, signals from vestibular and somatosensory receptors are intermingled and cannot easily be separated even at the level of the vestibular nucleus (see [82] for review). A later section will describe some recent insights on signal combination for spatial constancy in the motor system.

6. ROTATIONAL SELF-MOTION

Many studies have tested spatial constancy mechanisms during both active and passive head and body rotations (reviewed in [18]). The conclusion drawn from these studies is that the quality of spatial constancy depends on the axis of rotation, the presence of gravitational cues, and on the availability of efference copies. The evidence is as follows. Updating is quite accurate for active rotations, in both yaw [83] and roll directions [84]. For passive rotations, updating in yaw is substantially compromised (approx. 70% compensation) [83,85,86], but still nearly perfect in roll [85,87]. This suggests that updating for active yaw rotations, which leave the body fixed relative to gravity, relies on efference copy signals. To further test the contribution of gravitational cues, Klier *et al.* tested rotation updating with supine body orientations. Gravitational cues had differential effects: yaw updating in supine condition does not improve when these cues are available, while roll updating deteriorates significantly when these cues are taken away [85,87].

A number of additional conclusions in relation to the computations for spatial constancy can be made on the basis of these studies. For the transformations considered in the previous sections, it is often thought that updating simply shifts the stored locations of all

targets uniformly, by a common vector, when the eye or head turns. That is, the updating mechanism is modelled as a subtraction of the vector representing the eye or head movement from other vectors representing the target locations relative to the eye. Although such a uniform shift would often approximate the real changes in location of targets in front of the subject during yaw rotations, for roll rotations with the body upright, a simple vector subtraction would be inadequate. The observed accurate roll updating suggests a more geometrically exact remapping, which involves rotating the stored target locations through the inverse of the eye's rotation in space [84,88]. This conclusion holds irrespective of how the spatial constancy is implemented, whether it works with efference copy or vestibular inputs, whether it operates in gaze coordinates or in another reference frame. Recently, it has been shown that spatial updating also handles the non-commutativity of two rotations in a geometrically correct fashion [89,90].

Two studies were recently performed that explicitly asked which reference frame underlies the implementation of sensorimotor constancy during head and body rotations. Baker *et al.* [59] trained monkeys to make saccades to locations of briefly flashed targets that were remembered as either fixed in the world or fixed to gaze, after upright yaw rotations. They found saccade endpoints to be less variable when the targets were memorized in a gaze-fixed frame as opposed to a world-fixed frame. This suggests that a gaze-centred mechanism is involved in coding sensorimotor constancy during these rotations, which is in line with the findings for saccadic updating, reviewed above.

In contrast, for roll updating, Van Pelt *et al.* [91] found evidence for world-centred representations, not gaze-centred coding. In their test, they exploited the fact that subjects, when in a static tilt position in the dark, make systematic errors in indicating world-centred directions [92,93], while the estimation of egocentric directions remain unaffected. Updating accuracy during dynamic tilts, as probed by memory-guided saccades, was in favour of the allocentric model, with the saccade errors more closely related to the amount of subjective allocentric distortion at both the initial and final tilt angle than to the amount of intervening rotation (figure 3). This work suggests that the brain uses an allocentric reference frame, possibly gravity-based, to construct and maintain a spatial representation during rotation in roll. It remains an open question of how such an allocentric representation is encoded in the brain.

This difference in ego- versus allocentric coding of spatial constancy depending on rotation direction is consistent with the earlier suggestions that the brain can implement spatial constancy in multiple frames of reference, depending on sensory inputs and task demands (see [94] for review). Most probably, the brain interchanges information between allocentric maps and egocentric representations in the organization of spatially guided motor behaviour in complex environments [95]. Of course, ultimately, for movement generation, all spatial representations must be transformed in effector-related, muscle-based reference frames, depending on the motor system under control.

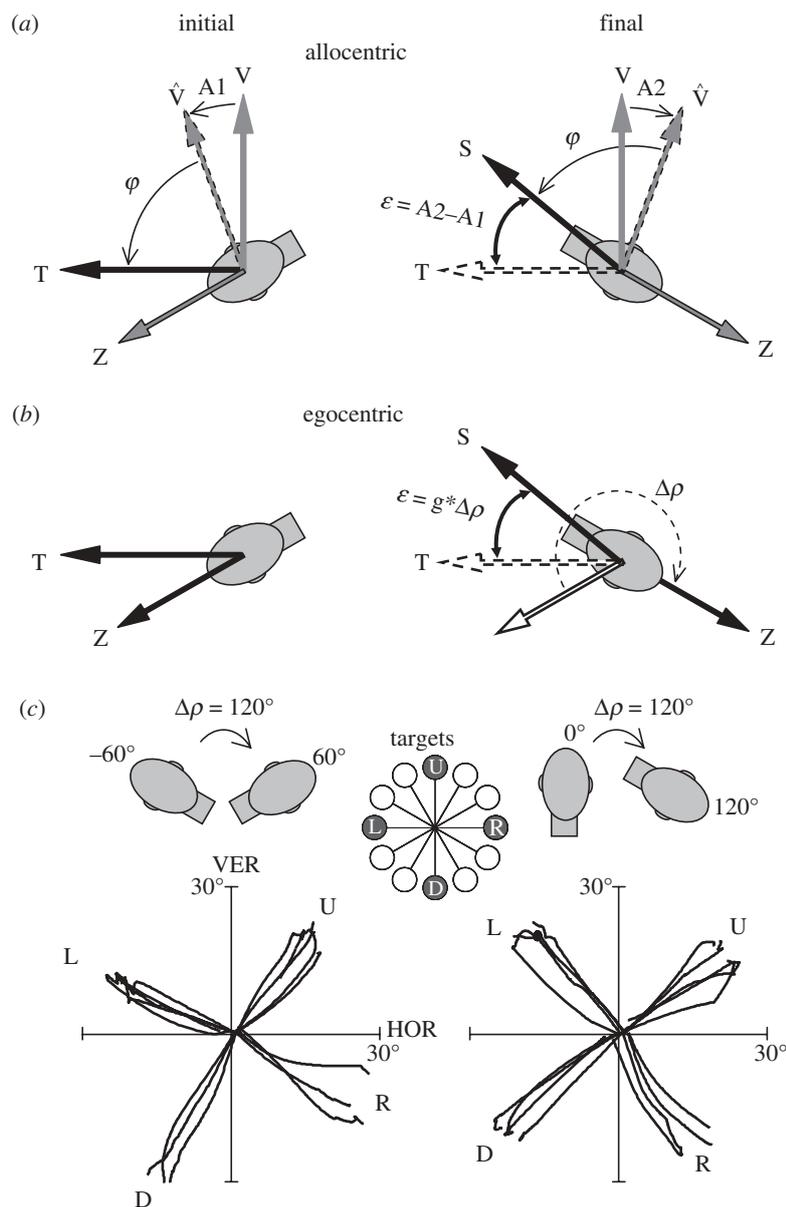


Figure 3. The involvement of allocentric coordinates in spatial constancy during body roll. (a) Tilted subjects make systematic errors (here A1 and A2 at the initial and final position) when indicating the direction of the gravitational vertical (V). If a target (T) is stored in such distorted allocentric frame (i.e. relative to \hat{V}), then the directional error of a saccade S towards this target, briefly presented before the roll rotation, should be equal to the difference in frame distortion when storing and probing the target ($\epsilon = A2 - A1$). (b) If the saccade target is stored in egocentric coordinates, the saccade is only affected by errors, if any, related to the amount of intervening rotation ($\epsilon = g * \Delta\rho$). (c) Updating for two testing conditions that had identical intervening body rotation ($+120^\circ$), but different combinations of initial and final body positions, for one subject. Traces show multiple saccade trajectories towards memorized targets that were presented, prior to rotation, on one of the four world-fixed cardinal axes (up, down, left and right). Saccades in the two conditions show different directional errors, despite the equal amount of intervening rotation. Updating matched the predictions of the allocentric model (a) very closely. Modified from Van Pelt *et al.* [91].

7. TRANSLATIONAL SELF-MOTION

In natural situations, our head and body not only rotate but also translate through the environment; for example, when we walk or drive a car, and even when the head rotates about the vertebral column, eye translations are being induced. To compensate for the effects of translations, the brain must perform more sophisticated computations than for rotational motion. First, distances of objects relative to the observer change during translations, not during rotations. Second, during translations, stationary objects show

motion parallax: their directions relative to the observer change at different rates, depending on their distance relative to the observer. In the absence of allocentric cues, translational updating in an egocentric, gaze-centred frame requires each target to be handled differently, depending on its distance. Does the brain incorporate the geometry of parallax in the computations for spatial constancy? Medendorp *et al.* [96] were the first to address this question. In their test, subjects fixated a distant target, while targets were flashed, at different distances, onto the retinal

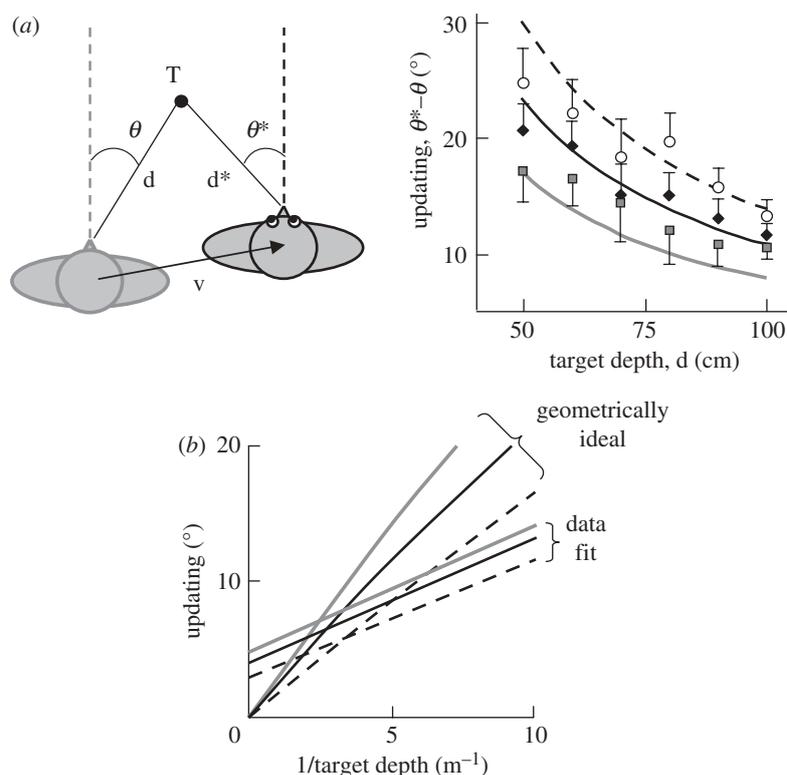


Figure 4. Saccadic updating after translational body motion in (a) humans and (b) monkeys. (a) Left-panel, geometry of translational updating. Target angle (θ^*) after translation depends on the initial distance of the target from the eyes (d), its direction relative to the eyes (θ), and the eyes' translation (\vec{T}), constituting a distance (T) and directional component (τ). Updating equations are described by the following two functions: $d^* = \sqrt{(d^2 + T^2 - 2dT\sin(\theta - \tau))}$ and $\theta^* = \arcsin((T \cos \tau - d \sin \theta)/d^*)$. Right panel, the average amount (\pm s.e.) of updating ($\theta^* - \theta$) of six subjects (data binned) for updating targets at initial direction (θ) of 30° , and different translational displacements. They show the same nonlinear patterns as perfect updating (lines). Modified from Medendorp *et al.* [96]. (b) Updating saccades of monkeys after passively imposed translations scale less with inverse distance than expected according to the geometry. Relationships quantified using linear regression lines. Adapted from Li *et al.* [99] with permission. (a) Circles, $v = 25$ cm; diamonds, $v = 20$ cm; squares, $v = 15$ cm. (b) Dashed lines, $v = 5$ cm; black lines, $v = 4$ cm; grey lines, $v = 3$ cm.

periphery. Subjects then actively translated sideways while keeping gaze on the distant target and subsequently had to make a combined saccade–vergence movement to the remembered target location. The eye movements corrected almost perfectly for parallax: the changes in both version (direction) and vergence (depth) angles of the eyes followed the required nonlinear patterns (figure 4a).

Recently, it was shown that human subjects can, to a large degree, also update the locations of visual targets in space following passively induced translations [97]. Similar experiments in monkeys have also suggested a clear compensation for translational motion in their updating of visual space, although the amount of updating was typically less than geometrically required (figure 4b, [98,99]).

In labyrinthectomized monkeys, however, updating for translations was found to be severely compromised [98,100]. This clearly suggests that in the intact brain vestibular information (from the otoliths) interacts with visual information to update the goal of memory-guided eye movements. Whether this process works via temporal integration of velocity and/or acceleration information from the vestibular system, via efference copies of the vestibulo-ocular reflex (VOR), or internal signals that suppress the VOR, is unknown. Also the anatomical and functional

pathways transmitting such signals to cortical areas that mediate spatial constancy remain to be delineated in future studies.

8. SENSORIMOTOR CONSTANCY FOR ARM MOVEMENTS

Spatial constancy is not only important in relation to eye movement planning, but also in the spatial guidance of other effectors, such as the arm and the hand. It has been suggested that the posterior parietal cortex, which is seen as a key structure in maintaining spatial constancy, contains specialized subunits for the processing of spatial goals of saccades and reaching movements. The LIP is involved in representing targets locations of saccades; the medial intraparietal area (MIP) and extrastriate visual area V6A, together called the parietal reach region (PRR), code targets of reaching movements (see [2,3,101,102] for reviews). Similar distinctions have been proposed in the frontal cortex, with the FEF and the dorsal premotor area (PMd) coding for eye and reaching movements, respectively (see [103] for review).

If there are separate spatial representations for saccades and reaching movements, then maintaining and updating them might involve different mechanisms that perhaps rely on different sources of

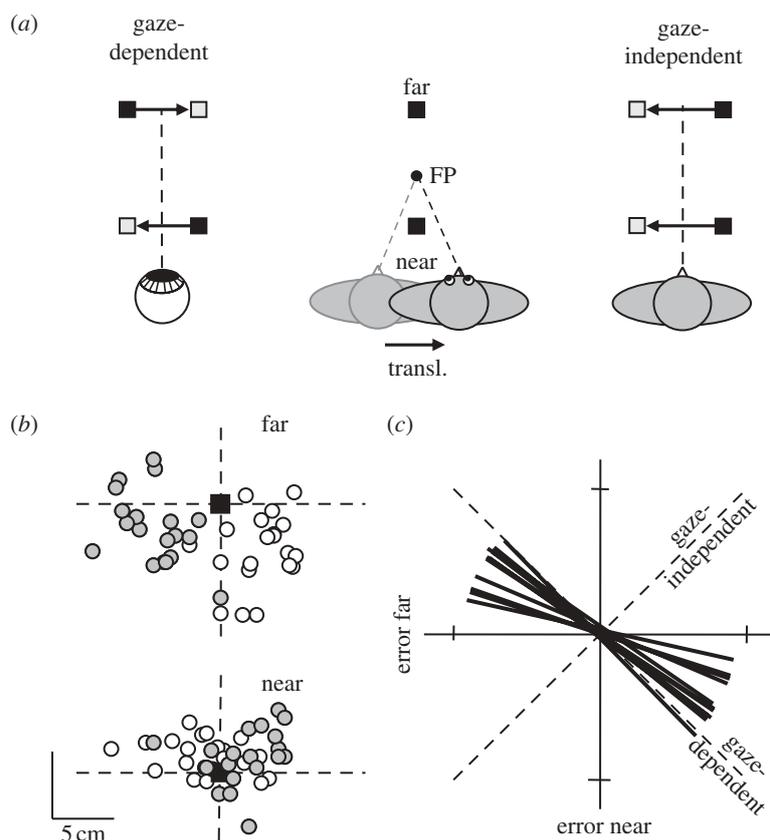


Figure 6. Gaze-dependent updating during translational body motion. (a) If targets, presented in front of or behind the eyes' fixation point, are stored in gaze-centred coordinates, they must be updated in opposite directions when the eyes and body translate. If the same targets are stored in gaze-independent coordinates, sensorimotor constancy necessitates the same updating directions. (b) Reaching after translational motion. Reach errors depend on the direction of the intervened translation (leftward or rightward translation) and on the depth of the target from fixation, consistent with the predictions of the gaze-dependent updating model. (c) Reach errors to targets at opposite, but same distances from fixation, plotted versus each other. All subjects support the gaze-dependent model. Modified from Van Pelt & Medendorp [126]. (b) White circles, leftward translation; grey circles, rightward translation.

target relative to gaze when programming repeated movements. These findings are consistent with recent neurophysiological observations that the parietal cortex, particularly the gaze-centred PRR, represents immediate and subsequent movement goals in a sequential movement task [44,118,119].

In the remainder of this section, we will discuss the effects of head and body motion on the updating of reach targets. Bresciani *et al.* [120,121] compared the performance of human subjects while reaching to a remembered target under continuous passively induced body rotation about an Earth-vertical yaw axis and when the rotation occurred before the reach. It was found that subjects are more accurate when the vestibular signals are processed for online control of the reach than when they are used to update the internal representation of reaching space.

In contrast to rotations, however, target updating seems fairly veridical for reaching after super-threshold translational motion [107,122–125]. Recently, Van Pelt & Medendorp [126] examined the dominant reference frame in the updating of reach targets during active translation of the whole body. Targets were presented at opposite positions (near versus far) from the subjects' fixation plane (figure 6a, middle panel). They argued that if spatial constancy is implemented in gaze-centred coordinates, then

representations of the far and near targets should shift in opposite directions in spatial memory during the translation (figure 6a, left panel). Hence, if the amount of translation is misestimated in the updating process, the updated target representations will have opposite biases relative to their actual locations in space. In contrast, if the brain implements spatial constancy across translation motion in a gaze-independent reference frame (e.g. a body-centred frame), misjudging translations would lead to biases in the updated representations in the same direction, irrespective of their initial location relative to gaze (figure 6a, right panel). The observed error patterns clearly favoured the gaze-centred scheme (figure 6b,c), indicating that translational updating is organized similarly as head-fixed saccadic updating. In other words, the brain encodes a geometrically complete, dynamic map of remembered space, whose spatial accuracy is maintained in gaze-centred coordinates by internally simulating the geometry of motion parallax during translations of the body. Taken together, the results of saccade and reaching studies on moving subjects suggest that vestibular signals interact with retinal disparity and eccentricity information to retain three-dimensional spatial constancy during body motion in space—a proposal that now awaits testing at the physiological level.

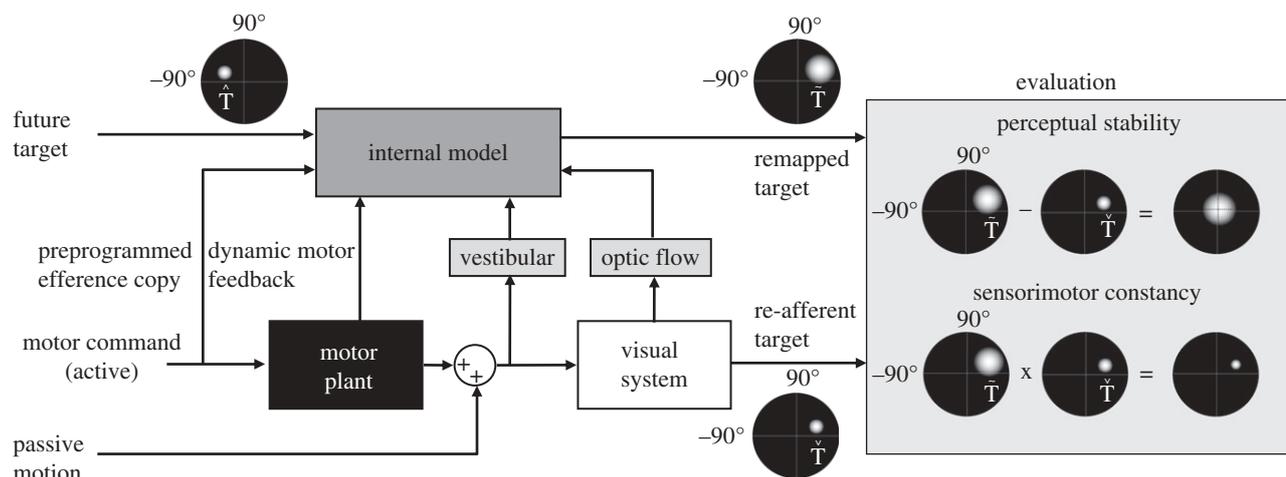


Figure 7. Schematic of multisensory processing for spatial constancy. The visually derived internal representation of a future target (\hat{T}) is assumed accurate but contaminated by noise. Movements (of parts) of the body affect this internal representation. Both passive and active (self-initiated) movements are registered by multiple sensory organs, including the visual, and vestibular/somatosensory systems. These signals are used by an internal model, which updates the representation of the location of the future target. When the movement is self-initiated, the internal model can use continuous dynamic feedback about the actual movements (dynamic motor feedback) to update the future target location, or even predict the new location of the target, by remapping based on a copy of the preprogrammed movement command (preprogrammed efference copy). The operations of the internal model add noise to the internally remapped representation of the future target, as indicated by \hat{T} . This signal drives the motor action in the absence of vision. In the presence of vision, the brain could evaluate the belief of perceptual stability in statistical terms by comparing the actual, refferent sensory input of the target, indicated by \check{T} , to the remapped target location \hat{T} . For sensorimotor constancy, the brain could combine the remapped target representation and the new refferent information about the target in order to drive the motor action by a more precise estimate of target location than could be obtained from either source alone. The circular panels show the probability densities of the respective internal signals.

9. SENSORY VERSUS MOTOR REPRESENTATIONS

In a review of the spatial constancy mechanisms for motor control, an important question to address is whether the updating mechanisms pertain merely to the coordinates of the sensory stimulus or more so to the coordinates of the movement plan. The answer to this question is difficult to pin down. Because sensory and motor coordinates require essentially the same updating during self-motion, the updating results described so far are consistent with both interpretations. One way to obtain further insights is by examining the activation of the neural structures involved in spatial constancy during tasks that explicitly dissociate the sensory from the motor goal representations. Antimovements, which dissociate stimulus and movement direction, are thought to serve this purpose [127]. Zhang & Barash [128] have shown that in a memory-delayed version of the antisaccade task, population activity in LIP turns very rapidly, within 50 ms, from the visual direction to the motor direction during the memory interval. Recent observations in the human posterior parietal cortex on fMRI and magnetoencephalography have also shown reversal of activity during antisaccade tasks [37,129]. Gail & Andersen [130] provided evidence that, during the delay period of a memory reach task, monkey PRR represents motor goals, not sensory memories. Relating these results to the spatial constancy findings, it may be suggested that the updating relates to the goal of a movement, not to a pure sensory representation of the physical stimulus

location. Collins *et al.* [131] used saccadic adaptation with pro- and antisaccades to visual stimuli to further address the nature of the updated goal representation. They found rightward saccade adaptation to transfer to rightward antisaccades but not to leftward antisaccades, suggesting that the sensory coordinates of the movement goal are updated. Recent results of Fernandez-Ruiz *et al.* [132] are consistent with this notion. Using fMRI, they showed that the movement-related topography in the human PRR reverses when subjects are adapted to left/right reversing prisms. Together, the results of these studies indicate that the mechanisms for spatial constancy in the motor system operate at an abstract level, i.e. they update locations of movement goals in sensory, gaze-centred coordinates, not the sensory stimuli or the upcoming motor commands.

10. OPTIMAL INTEGRATION FOR SENSORIMOTOR CONSTANCY

Finally, the question remains how the reviewed experimental evidence using remembered target stimuli relates to everyday life experience. In many daily actions, targets do not disappear from the sensory environment during the self-motion. For example, one can view a cup of coffee in central vision, but can pick it up after an intervening eye movement, which has brought the cup into peripheral vision. In such cases, re-afferent sensory feedback of the same stimuli will become available after the self-motion, e.g. after the saccade. Von Helmholtz suggested that the sensory feedback and the internally updated

information could be compared ('subtracted') to detect a change of the sensory world, but 'addition' of the two sources of information might serve a useful motor purpose [133]. More specifically, since both bits of information are to some extent unreliable, using them in combination could assist in obtaining a better estimate of the state of the world. Within this perspective, recent reports have suggested that Bayesian statistics may be a fundamental element in such signal combination (see figure 7). This idea entails that the brain processes the noisy neuronal signals in a statistically optimal fashion, implementing the rules of Bayesian inference [92,134–137]. In other words, Bayesian models combine various sources of information, taking into account their uncertainty, to optimize performance in the context of optimal observer theory. At the neural level, Ma *et al.* [138] proposed recently a scheme for the implementation of optimal statistical inference, suggesting that neurons could accomplish Bayesian integration via linear summation of unimodal inputs.

Vaziri *et al.* [133] tested reaches to visual targets that were initially on the fovea, but saccadically brought to the periphery, before the reach. The authors manipulated the uncertainty of the post-saccadic peripheral target information by varying the length of target exposure. They reported evidence that the motor system optimally integrates the updated spatial information and the actual visual feedback: there was a more precise estimate of the target location than could be obtained from either source alone. Likewise, Munuera *et al.* [139] showed that, in double-step saccades, visual cues and efference copies of the first saccade are combined. They asked subjects to perform two eye movements in quick succession, and introduced an artificial motor error by randomly moving the target of the first saccade during the movement. The extent to which the second saccade was corrected for this visual feedback obeyed the Bayesian rules of inference. It is noteworthy that Bayesian computations have also been implicated in relation to perceptual stability of items in a visual world, and their integration and decay across saccadic eye movements ([140–142]. Whether these optimal integration principles also apply to spatial constancy across more complex conditions of self-motion, where visual, vestibular and somatosensory signals as well as efference copies and other forms of instantaneous motor feedback are concurrently available, is still an open question [135,143]. A complicating factor in these computations is that the feed-forward and feedback signals are encoded in different reference frames, which necessitate coordinate transformations before they can be integrated [74].

While the Bayesian concept may provide a valuable scaffolding to model signal combination for spatial constancy, it is also worth stressing that other modelling approaches have been shown useful in dealing with other aspects of spatial constancy. For example, neural network studies have successfully modelled the dynamic remapping of RFs [126,144–147], have dealt with non-commutativity issues [96,148], and have revealed a role of gain fields for coordinate transformations [108,149,150].

11. CONCLUSION

In this paper, we have reviewed recent advances in the understanding of the spatial constancy mechanisms for motor control. The picture that emerges is drawn in figure 7, which regards sensorimotor constancy as a multisensory process, integrating efference copies, motor feedback and other sensory signals to update target locations, in an optimal fashion. The anticipatory shifts of RFs in the LIP and FEF during saccadic eye movements implicate these regions as components of a forward internal model for updating spatial movement goals in sensory (gaze-centred) coordinates. Such feed-forward processes do not play a role during passive body motion when updating is entirely dependent on sensory feedback signals, including visual, vestibular and other proprioceptive signals. During active body translations, however, both efference copies, in combination with a forward model of body dynamics, and sensory feedback can assist in the spatial updating of movement goals. Despite all these new insights in mechanisms of spatial updating, throughout this review we have listed numerous questions that require further study. These studies should not only address the neural correlates and pathways of spatial updating, but should also come up with new paradigms to reverse-engineer the key computational processes that enable spatial constancy for motor control.

I thank my colleagues Jan Van Gisbergen, Luc Selen, Maaïke De Vrijer and Frank Leoné for many fruitful discussions and critical comments on previous versions of this manuscript. This work was supported by grants from The Netherlands Organization for Scientific Research (VIDI: 452-03-307) and the Human Frontier Science Programme Organization.

REFERENCES

- 1 Kant, I. 1781/1787 *Critique of pure reason*. A24/B38–9. London, UK: Macmillan.
- 2 Andersen, R. A. & Buneo, C. A. 2002 Intentional maps in posterior parietal cortex. *Annu. Rev. Neurosci.* **25**, 189–220. (doi:10.1146/annurev.neuro.25.112701.142922)
- 3 Colby, C. L. & Goldberg, M. E. 1999 Space and attention in parietal cortex. *Annu. Rev. Neurosci.* **22**, 319–349. (doi:10.1146/annurev.neuro.22.1.319)
- 4 Melcher, D. & Colby, C. L. 2008 Trans-saccadic perception. *Trends Cogn. Sci.* **12**, 466–473. (doi:10.1016/j.tics.2008.09.003)
- 5 Prime, S. L., Niemeier, M. & Crawford, J. D. 2006 Transsaccadic integration of visual features in a line intersection task. *Exp. Brain Res.* **169**, 532–548. (doi:10.1007/s00221-005-0164-1)
- 6 Vingerhoets, R. A., Medendorp, W. P. & Van Gisbergen, J. A. M. 2008 Body-tilt and visual verticality perception during multiple cycles of roll rotation. *J. Neurophysiol.* **99**, 2264–2280. (doi:10.1152/jn.00704.2007)
- 7 Moser, E. I., Kropff, E. & Moser, M. B. 2008 Place cells, grid cells, and the brain's spatial representation system. *Annu. Rev. Neurosci.* **31**, 69–89. (doi:10.1146/annurev.neuro.31.061307.090723)
- 8 Gibson, J. J. 1996 *The senses considered as perceptual systems*. Boston, MA: Houghton Mifflin.
- 9 Bridgeman, B., Van der Heijden, A. H. C. & Velichkovsky, B. M. 1994 A theory of visual stability across saccadic eye movements. *Behav. Brain Sci.* **17**, 247–292. (doi:10.1017/S0140525X00034361)

- 10 Descartes, R. 1644 *Traité de l'homme*. Paris, France.
- 11 Gauthier, G. M., Nommay, D. & Vercher, J.-L. 1990 Ocular muscle proprioception and visual localization of targets in man. *Brain* **113**, 1857–1871. (doi:10.1093/brain/113.6.1857)
- 12 Von Helmholtz, H. 1867 *Handbuch der Physiologischen Optik*. Leipzig, Germany: Voss.
- 13 Sperry, R. W. 1950 Neural basis of the spontaneous optokinetic response produced by visual inversion. *J. Comp. Physiol. Psychol.* **43**, 482–489. (doi:10.1037/h0055479)
- 14 Von Holst, E. & Mittelstaedt, H. 1950 The reafferent principle: reciprocal effects between central nervous system and periphery. *Naturwissenschaften* **37**, 464–476.
- 15 Bays, P. M. & Husain, M. 2007 Spatial remapping of the visual world across saccades. *Neuroreport* **18**, 1207–1213. (doi:10.1097/WNR.0b013e328244e6c3)
- 16 Hallett, P. E. & Lightstone, A. D. 1976 Saccadic eye movements towards stimuli triggered by prior saccades. *Vis. Res.* **16**, 99–106. (doi:10.1016/0042-6989(76)90083-3)
- 17 Mays, L. E. & Sparks, D. L. 1980 Saccades are spatially, not retinocentrically, coded. *Science* **208**, 1163–1165. (doi:10.1126/science.6769161)
- 18 Klier, E. M. & Angelaki, D. E. 2008 Spatial updating and the maintenance of visual constancy. *Neuroscience* **156**, 801–818. (doi:10.1016/j.neuroscience.2008.07.079)
- 19 Gnadt, J. W. & Andersen, R. A. 1988 Memory related motor planning activity in posterior parietal cortex of macaque. *Exp. Brain Res.* **70**, 216–220.
- 20 Duhamel, J. R., Colby, C. L. & Goldberg, M. E. 1992 The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* **255**, 90–92. (doi:10.1126/science.1553535)
- 21 Burr, D. C. & Morrone, M. C. 2005 Eye movements: building a stable world from glance to glance. *Curr. Biol.* **15**, R839–R840. (doi:10.1016/j.cub.2005.10.003)
- 22 Sommer, M. A. & Wurtz, R. H. 2006 Influence of the thalamus on spatial visual processing in frontal cortex. *Nature* **444**, 374–377. (doi:10.1038/nature05279)
- 23 Heiser, L. M. & Colby, C. L. 2006 Spatial updating in area LIP is independent of saccade direction. *J. Neurophysiol.* **95**, 2751–2767. (doi:10.1152/jn.00054.2005)
- 24 Nakamura, K. & Colby, C. L. 2002 Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proc. Natl Acad. Sci. USA* **99**, 4026–4031. (doi:10.1073/pnas.052379899)
- 25 Sommer, M. A. & Wurtz, R. H. 2008 Brain circuits for the internal monitoring of movements. *Annu. Rev. Neurosci.* **31**, 317–338. (doi:10.1146/annurev.neuro.31.060407.125627)
- 26 Sparks, D. L. 1989 The neural encoding of the location of targets for saccadic eye movements. *J. Exp. Biol.* **146**, 195–207.
- 27 Walker, M. F., Fitzgibbon, J. & Goldberg, M. E. 1995 Neurons of the monkey superior colliculus predict the visual result of impending saccadic eye movements. *J. Neurophysiol.* **73**, 1988–2003.
- 28 Sommer, M. A. & Wurtz, R. H. 2002 A pathway in primate brain for internal monitoring of movements. *Science* **296**, 1480–1482. (doi:10.1126/science.1069590)
- 29 Wurtz, R. H. 2008 Neuronal mechanisms of visual stability. *Vis. Res.* **48**, 2070–2089. (doi:10.1016/j.visres.2008.03.021)
- 30 Berman, R. A. & Wurtz, R. H. 2008 Exploring the pulvinar path to visual cortex. *Prog. Brain Res.* **171**, 467–473. (doi:10.1016/S0079-6123(08)00668-7)
- 31 Prevosto, V., Graf, W. & Ugolini, G. 2009 Posterior parietal cortex areas MIP and LIPv receive eye position and velocity inputs via ascending preposito-thalamo-cortical pathways. *Eur. J. Neurosci.* **30**, 1151–1161. (doi:10.1111/j.1460-9568.2009.06885.x)
- 32 Asanuma, C., Andersen, R. A. & Cowan, W. M. 1985 The thalamic relations of the caudal inferior parietal lobule and the lateral prefrontal cortex in monkeys: divergent cortical projections from cell clusters in the medial pulvinar nucleus. *J. Comp. Neurol.* **241**, 357–381. (doi:10.1002/cne.902410309)
- 33 Li, C. S. & Andersen, R. A. 2001 Inactivation of macaque lateral intraparietal area delays initiation of the second saccade predominantly from contralesional eye positions in a double-saccade task. *Exp. Brain Res.* **137**, 45–57. (doi:10.1007/s002210000546)
- 34 MacKay, D. M. 1972 Visual stability. *Invest. Ophthalmol.* **11**, 518–524.
- 35 Crapse, T. B. & Sommer, M. A. 2010 Translation of a visual stimulus during a saccade is more detectable if it moves perpendicular, rather than parallel, to the saccade. *J. Vis.* **10**, 521. (doi:10.1167/10.7.521)
- 36 Medendorp, W. P., Goltz, H. C., Vilis, T. & Crawford, J. D. 2003 Gaze-centered updating of visual space in human parietal cortex. *J. Neurosci.* **23**, 6209–6214.
- 37 Medendorp, W. P., Goltz, H. C. & Vilis, T. 2005 Remapping the remembered target location for anti-saccades in human posterior parietal cortex. *J. Neurophysiol.* **94**, 734–740. (doi:10.1152/jn.01331.2004)
- 38 Merriam, E. P., Genovesi, C. R. & Colby, C. L. 2003 Spatial updating in human parietal cortex. *Neuron* **39**, 361–373. (doi:10.1016/S0896-6273(03)00393-3)
- 39 Merriam, E. P., Genovesi, C. R. & Colby, C. L. 2007 Remapping in human visual cortex. *J. Neurophysiol.* **97**, 1738–1755. (doi:10.1152/jn.00189.2006)
- 40 Bellebaum, C., Hoffmann, K. P. & Daum, I. 2005 Post-saccadic updating of visual space in the posterior parietal cortex in humans. *Behav. Brain Res.* **163**, 194–203. (doi:10.1016/j.bbr.2005.05.007)
- 41 Bellebaum, C. & Daum, I. 2006 Time course of cross-hemispheric spatial updating in the human parietal cortex. *Behav. Brain Res.* **169**, 150–161. (doi:10.1016/j.bbr.2006.01.001)
- 42 Chang, E. & Ro, T. 2007 Maintenance of visual stability in the human posterior parietal cortex. *J. Cogn. Neurosci.* **19**, 266–274. (doi:10.1162/jocn.2007.19.2.266)
- 43 Rushworth, M. F. & Taylor, P. C. 2006 TMS in the parietal cortex: updating representations for attention and action. *Neuropsychologia* **44**, 2700–2716. (doi:10.1016/j.neuropsychologia.2005.12.007)
- 44 Medendorp, W. P., Goltz, H. C. & Vilis, T. 2006 Directional selectivity of BOLD activity in human posterior parietal cortex for memory-guided double-step saccades. *J. Neurophysiol.* **94**, 1432–1442.
- 45 Schluppeck, D., Glimcher, P. & Heeger, J. 2005 Topographic organization for delayed saccades in human posterior parietal cortex. *J. Neurophysiol.* **94**, 1372–1384. (doi:10.1152/jn.01290.2004)
- 46 Sereno, M. I., Pitzalis, S. & Martinez, A. 2001 Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science* **294**, 1350–1354. (doi:10.1126/science.1063695)
- 47 Andersen, R. A., Bracewell, R. M., Barash, S., Gnadt, J. W. & Fogassi, L. 1990 Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *J. Neurosci.* **10**, 1176–1196.
- 48 DeSouza, J. F., Dukelow, S. P., Gati, J. S., Menon, R. S., Andersen, R. A. & Vilis, T. 2000 Eye position signal modulates a human parietal pointing region during memory-guided movements. *J. Neurosci.* **20**, 5835–5840.

- 49 Snyder, L. H., Grieve, K. L., Brotchie, P. & Andersen, R. A. 1998 Separate body- and world-referenced representations of visual space in parietal cortex. *Nature* **394**, 887–891. (doi:10.1038/29777)
- 50 Balslev, D. & Miall, R. C. 2008 Eye position representation in human anterior parietal cortex. *J. Neurosci.* **28**, 8968–8972. (doi:10.1523/JNEUROSCI.1513-08.2008)
- 51 Wang, X., Zhang, M., Cohen, I. S. & Goldberg, M. E. 2007 The proprioceptive representation of eye position in monkey primary somatosensory cortex. *Nat. Neurosci.* **10**, 640–646. (doi:10.1038/nn1878)
- 52 Vliegen, J., Van Grootel, T. J. & Van Opstal, A. J. 2004 Dynamic sound localization during rapid eye-head gaze shifts. *J. Neurosci.* **24**, 9291–9302. (doi:10.1523/JNEUROSCI.2671-04.2004)
- 53 Vliegen, J., Van Grootel, T. J. & Van Opstal, A. J. 2005 Gaze orienting in dynamic visual double steps. *J. Neurophysiol.* **94**, 4300–4313. (doi:10.1152/jn.00027.2005)
- 54 Blohm, G., Missal, M. & Lefèvre, P. 2005 Processing of retinal and extraretinal signals for memory-guided saccades during smooth pursuit. *J. Neurophysiol.* **93**, 1510–1522. (doi:10.1152/jn.00543.2004)
- 55 Gellman, R. S. & Fletcher, W. A. 1992 Eye position signals in human saccadic processing. *Exp. Brain Res.* **89**, 425–434. (doi:10.1007/BF00228258)
- 56 McKenzie, A. & Lisberger, S. G. 1986 Properties of signals that determine the amplitude and direction of saccadic eye movements in monkeys. *J. Neurophysiol.* **56**, 196–207.
- 57 Herter, T. M. & Guitton, D. 1998 Human head-free gaze saccades to targets flashed before gaze-pursuit are spatially accurate. *J. Neurophysiol.* **80**, 2785–2789.
- 58 Schlag, J., Schlag-Rey, M. & Dassonville, P. 1990 Saccades can be aimed at the spatial location of targets flashed during pursuit. *J. Neurophysiol.* **64**, 575–581.
- 59 Baker, J. T., Harper, T. M. & Snyder, L. H. 2003 Spatial memory following shifts of gaze. I. Saccades to memorized world-fixed and gaze-fixed targets. *J. Neurophysiol.* **89**, 2564–2576. (doi:10.1152/jn.00610.2002)
- 60 Zivotofsky, A. Z., Rottach, K. G., Averbuch-Heller, L., Kori, A. A., Thomas, C. W., Dell’Osso, L. F. & Leigh, R. J. 1996 Saccades to remembered targets: the effects of smooth pursuit and illusory stimulus motion. *J. Neurophysiol.* **76**, 3617–3632.
- 61 Baker, J. T., White, R. L. & Snyder, L. H. 2002 Reference frames and spatial memory operations: area LIP and saccade behavior. *Soc. Neurosci. Abstr.* **57**, 16.
- 62 Powell, K. D. & Goldberg, M. E. 1997 Remapping of visual responses in primate parietal cortex during smooth changes in gaze. *Soc. Neurosci. Abstr.* **1**, 14.11.
- 63 Krommenhoek, K. P. & Van Gisbergen, J. A. 1994 Evidence for nonretinal feedback in combined version-vergence eye movements. *Exp. Brain Res.* **102**, 95–109.
- 64 Ferraina, S., Paré, M. & Wurtz, R. H. 2000 Disparity sensitivity of frontal eye field neurons. *J. Neurophysiol.* **83**, 625–629.
- 65 Fukushima, K., Yamanobe, T., Shinmei, Y., Fukushima, J., Kurkin, S. & Peterson, B. W. 2002 Coding of smooth eye movements in three-dimensional space by frontal cortex. *Nature* **419**, 157–162. (doi:10.1038/nature00953)
- 66 Genovesio, A. & Ferraina, S. 2004 Integration of retinal disparity and fixation-distance related signals toward an egocentric coding of distance in the posterior parietal cortex of primates. *J. Neurophysiol.* **91**, 2670–2684. (doi:10.1152/jn.00712.2003)
- 67 Gnadt, J. W. & Mays, L. E. 1995 Neurons in monkey parietal area LIP are tuned for eye-movement parameters in three-dimensional space. *J. Neurophysiol.* **73**, 280–297.
- 68 Genovesio, A., Brunamonti, E., Giusti, M. A. & Ferraina, S. 2007 Postsaccadic activities in the posterior parietal cortex of primates are influenced by both eye movement vectors and eye position. *J. Neurosci.* **27**, 3268–3273. (doi:10.1523/JNEUROSCI.5415-06.2007)
- 69 Van Beuzekom, A. D. & Van Gisbergen, J. A. M. 2000 Properties of the internal representation of gravity inferred from spatial-direction and body-tilt estimates. *J. Neurophysiol.* **84**, 11–27.
- 70 Angelaki, D. E. & Hess, B. J. 2005 Self-motion-induced eye movements: effects on visual acuity and navigation. *Nat. Rev. Neurosci.* **6**, 966–976. (doi:10.1038/nrn1804)
- 71 Dichgans, J., Held, R., Young, L. R. & Brandt, T. 1972 Moving visual scenes influence the apparent direction of gravity. *Science* **178**, 1217–1219. (doi:10.1126/science.178.4066.1217)
- 72 Wolbers, T., Hegarty, M., Büchel, C. & Loomis, J. M. 2008 Spatial updating: how the brain keeps track of changing object locations during observer motion. *Nat. Neurosci.* **11**, 1223–1230. (doi:10.1038/nn.2189)
- 73 Warren, P. A. & Rushton, S. K. 2009 Optic flow processing for the assessment of object movement during ego movement. *Curr. Biol.* **19**, 1555–1560. (doi:10.1016/j.cub.2009.07.057)
- 74 Angelaki, D. E. & Cullen, K. E. 2008 Vestibular system: the many facets of a multimodal sense. *Annu. Rev. Neurosci.* **31**, 125–150. (doi:10.1146/annurev.neuro.31.060407.125555)
- 75 Young, L. R., Oman, C. M., Watt, D. G., Money, K. E. & Lichtenberg, B. K. 1984 Spatial orientation in weightlessness and readaptation to earth’s gravity. *Science* **225**, 205–208. (doi:10.1126/science.6610215)
- 76 Merfeld, D. M. 1995 Modeling the vestibulo-ocular reflex of the squirrel monkey during eccentric rotation and roll tilt. *Exp. Brain Res.* **106**, 123–134.
- 77 Vingerhoets, R. A., Van Gisbergen, J. A. M. & Medendorp, W. P. 2007 Verticality perception during off-vertical axis rotation. *J. Neurophysiol.* **97**, 3256–3268. (doi:10.1152/jn.01333.2006)
- 78 Angelaki, D. E. & Yakusheva, T. A. 2009 How vestibular neurons solve the tilt/translation ambiguity. Comparison of brainstem, cerebellum, and thalamus. *Ann. N. Y. Acad. Sci.* **1164**, 19–28. (doi:10.1111/j.1749-6632.2009.03939.x)
- 79 Jürgens, R. & Becker, W. 2006 Perception of angular displacement without landmarks: evidence for Bayesian fusion of vestibular, optokinetic, podokinesthetic, and cognitive information. *Exp. Brain Res.* **174**, 528–543. (doi:10.1007/s00221-006-0486-7)
- 80 Mergner, T., Nasios, G., Maurer, C. & Becker, W. 2001 Visual object localisation in space. Interaction of retinal, eye position, vestibular and neck proprioceptive information. *Exp. Brain Res.* **141**, 33–51. (doi:10.1007/s002210100826)
- 81 MacNeilage, P. R., Ganesan, N. & Angelaki, D. E. 2008 Computational approaches to spatial orientation: from transfer functions to dynamic Bayesian inference. *J. Neurophysiol.* **100**, 2981–2996. (doi:10.1152/jn.90677.2008)
- 82 Cullen, K. E. 2004 Sensory signals during active versus passive movement. *Curr. Opin. Neurobiol.* **14**, 698–706. (doi:10.1016/j.conb.2004.10.002)
- 83 Blouin, J., Labrousse, L., Simoneau, M., Vercher, J. L. & Gauthier, G. M. 1998 Updating visual space during passive and voluntary head-in-space movements. *Exp. Brain Res.* **122**, 93–100. (doi:10.1007/s002210050495)
- 84 Medendorp, W. P., Smith, M. A., Tweed, D. B. & Crawford, J. D. 2002 Rotational remapping in human

- spatial memory during eye and head motion. *J. Neurosci.* **22**, 196RC.
- 85 Klier, E. M., Hess, B. J. M. & Angelaki, D. E. 2006 Differences in the accuracy of human visuospatial memory after yaw and roll rotations. *J. Neurophysiol.* **95**, 2692–2697. (doi:10.1152/jn.01017.2005)
- 86 Israel, I., Ventre-Dominey, J. & Denise, P. 1999 Vestibular information contributes to update retinotopic maps. *Neuroreport*, **10**, 3479–3483.
- 87 Klier, E. M., Angelaki, D. E. & Hess, B. J. 2005 Roles of gravitational cues and efference copy signals in the rotational updating of memory saccades. *J. Neurophysiol.* **94**, 468–478. (doi:10.1152/jn.00700.2004)
- 88 Smith, M. A. & Crawford, J. D. 2001 Implications of ocular kinematics for the internal updating of visual space. *J. Neurophysiol.* **86**, 2112–2117.
- 89 Glasauer, S. & Brandt, T. 2007 Noncommutative updating of perceived self-orientation in three dimensions. *J. Neurophysiol.* **97**, 2958–2964. (doi:10.1152/jn.00655.2006)
- 90 Klier, E. M., Angelaki, D. E. & Hess, B. J. 2007 Human visuospatial updating after noncommutative rotations. *J. Neurophysiol.* **98**, 537–544. (doi:10.1152/jn.01229.2006)
- 91 Van Pelt, S., Van Gisbergen, J. A. M. & Medendorp, W. P. 2005 Visuospatial memory computations during whole-body rotations in roll. *J. Neurophysiol.* **94**, 1432–1442. (doi:10.1152/jn.00018.2005)
- 92 De Vrijer, M., Medendorp, W. P. & Van Gisbergen, J. A. M. 2008 Shared computational mechanism for tilt compensation accounts for biased verticality percepts in motion and pattern vision. *J. Neurophysiol.* **99**, 915–930. (doi:10.1152/jn.00921.2007)
- 93 Mittelstaedt, H. 1983 A new solution to the problem of the subjective vertical. *Naturwissenschaften* **70**, 272–281. (doi:10.1007/BF00404833)
- 94 Battaglia-Mayer, A., Caminiti, R., Lacquaniti, F. & Zago, M. 2003 Multiple levels of representation of reaching in the parieto-frontal network. *Cereb. Cortex* **13**, 1009–1022. (doi:10.1093/cercor/13.10.1009)
- 95 Crawford, J. D., Medendorp, W. P. & Marotta, J. J. 2004 Spatial transformations for eye–hand coordination. *J. Neurophysiol.* **92**, 10–19. (doi:10.1152/jn.00117.2004)
- 96 Medendorp, W. P., Tweed, D. B. & Crawford, J. D. 2003 Motion parallax is computed in the updating of human spatial memory. *J. Neurosci.* **23**, 8135–8142.
- 97 Klier, E. M., Hess, B. J. & Angelaki, D. E. 2008 Human visuospatial updating after passive translations in three-dimensional space. *J. Neurophysiol.* **99**, 1799–1809. (doi:10.1152/jn.01091.2007)
- 98 Li, N. & Angelaki, D. E. 2005 Updating visual space during motion in depth. *Neuron* **48**, 149–158. (doi:10.1016/j.neuron.2005.08.021)
- 99 Li, N., Wei, M. & Angelaki, D. E. 2005 Primate memory saccade amplitude after intervened motion depends on target distance. *J. Neurophysiol.* **94**, 722–733. (doi:10.1152/jn.01339.2004)
- 100 Wei, M., Li, N., Newlands, D., Dickman, J. D. & Angelaki, D. E. 2006 Deficits and recovery in visuospatial memory during head motion after bilateral labyrinthine lesion. *J. Neurophysiol.* **96**, 1676–1682. (doi:10.1152/jn.00012.2006)
- 101 Culham, J. C. & Valyear, K. F. 2006 Human parietal cortex in action. *Curr. Opin. Neurobiol.* **16**, 205–212. (doi:10.1016/j.conb.2006.03.005)
- 102 Jackson, S. R. & Husain, M. 2006 Visuomotor functions of the posterior parietal cortex. *Neuropsychologia* **44**, 2589–2593. (doi:10.1016/j.neuropsychologia.2006.08.002)
- 103 Wise, S. P., Boussaoud, D., Johnson, P. B. & Caminiti, R. 1997 Premotor and parietal cortex: corticocortical connectivity and combinatorial computations. *Annu. Rev. Neurosci.* **20**, 25–42. (doi:10.1146/annurev.neuro.20.1.25)
- 104 McGuire, L. M. & Sabes, P. N. 2009 Sensory transformations and the use of multiple reference frames for reach planning. *Nat. Neurosci.* **12**, 1056–1061. (doi:10.1038/nn.2357)
- 105 Henriques, D. Y., Klier, E. M., Smith, M. A., Lowy, D. & Crawford, J. D. 1998 Gaze-centered remapping of remembered visual space in an open-loop pointing task. *J. Neurosci.* **18**, 1583–1594.
- 106 Khan, A. Z., Pisella, L., Rossetti, Y., Vighetto, A. & Crawford, J. D. 2005 Impairment of gaze-centered updating of reach targets in bilateral parietal–occipital damaged patients. *Cereb. Cortex* **15**, 1547–1560. (doi:10.1093/cercor/bhi033)
- 107 Van Pelt, S. & Medendorp, W. P. 2008 Updating target distance across eye movements in depth. *J. Neurophysiol.* **99**, 2281–2290. (doi:10.1152/jn.01281.2007)
- 108 Pouget, A., Deneve, S. & Duhamel, J. R. 2002 A computational perspective on the neural basis of multi-sensory spatial representations. *Nat. Rev. Neurosci.* **3**, 741–747. (doi:10.1038/nrn914)
- 109 Medendorp, W. P. & Crawford, J. D. 2002 Visuospatial updating of reaching targets in near and far space. *Neuroreport* **13**, 633–636. (doi:10.1097/00001756-200204160-00019)
- 110 Poljac, E. & van den Berg, A. V. 2003 Representation of heading direction in far and near head space. *Exp. Brain Res.* **151**, 501–513. (doi:10.1007/s00221-003-1498-1)
- 111 Thompson, A. A. & Henriques, D. Y. 2008 Updating visual memory across eye movements for ocular and arm motor control. *J. Neurophysiol.* **100**, 2507–2514. (doi:10.1152/jn.90599.2008)
- 112 Batista, A. P., Buneo, C. A., Snyder, L. H. & Andersen, R. A. 1999 Reach plans in eye-centered coordinates. *Science* **285**, 257–260. (doi:10.1126/science.285.5425.257)
- 113 Dijkerman, H. C., McIntosh, R. D., Anema, H. A., De Haan, E. H., Kappelle, L. J. & Milner, A. D. 2006 Reaching errors in optic ataxia are linked to eye position rather than head or body position. *Neuropsychologia* **44**, 2766–2773. (doi:10.1016/j.neuropsychologia.2005.10.018)
- 114 Vindras, P., Desmurget, M. & Viviani, P. 2005 Error parsing in visuomotor pointing reveals independent processing of amplitude and direction. *J. Neurophysiol.* **94**, 1212–1224. (doi:10.1152/jn.01295.2004)
- 115 Bhattacharyya, R., Musallam, S. & Andersen, R. A. 2009 Parietal reach region encodes reach depth using retinal disparity and vergence angle signals. *J. Neurophysiol.* **102**, 805–816. (doi:10.1152/jn.90359.2008)
- 116 Ferraina, S., Brunamonti, E., Giusti, M. A., Costa, S., Genovesio, A. & Caminiti, R. 2009 Reaching in depth: hand position dominates over binocular eye position in the rostral superior parietal lobule. *J. Neurosci.* **29**, 11461–11470. (doi:10.1523/JNEUROSCI.1305-09.2009)
- 117 Sorrento, G. U. & Henriques, D. Y. 2008 Reference frame conversions for repeated arm movements. *J. Neurophysiol.* **99**, 2968–2984. (doi:10.1152/jn.90225.2008)
- 118 Baldauf, D., Cui, H. & Andersen, R. A. 2008 The posterior parietal cortex encodes in parallel both goals for double-reach sequences. *J. Neurosci.* **28**, 10081–10089. (doi:10.1523/JNEUROSCI.3423-08.2008)

- 119 Batista, A. P. & Andersen, R. A. 2001 The parietal reach region codes the next planned movement in a sequential reach task. *J. Neurophysiol.* **85**, 539–544.
- 120 Bresciani, J. P., Blouin, J., Sarlegna, F., Bourdin, C., Vercher, J. L. & Gauthier, G. M. 2002 On-line versus off-line vestibular-evoked control of goal-directed arm movements. *Neuroreport* **13**, 1563–1566. (doi:10.1097/00001756-200208270-00015)
- 121 Bresciani, J. P., Gauthier, G. M., Vercher, J. L. & Blouin, J. 2005 On the nature of the vestibular control of arm-reaching movements during whole-body rotations. *Exp. Brain Res.* **164**, 431–441. (doi:10.1007/s00221-005-2263-4)
- 122 Admiraal, M. A., Keijsers, N. L. & Gielen, C. C. 2004 Gaze affects pointing toward remembered visual targets after a self-initiated step. *J. Neurophysiol.* **92**, 2380–2393. (doi:10.1152/jn.01046.2003)
- 123 Flanders, M., Daghestani, L. & Berthoz, A. 1999 Reaching beyond reach. *Exp. Brain Res.* **126**, 19–30. (doi:10.1007/s002210050713)
- 124 Hondzinski, J. M. & Cui, Y. 2006 Allocentric cues do not always improve whole body reaching performance. *Exp. Brain Res.* **174**, 60–73. (doi:10.1007/s00221-006-0421-y)
- 125 Medendorp, W. P., Van Asselt, S. & Gielen, C. C. 1999 Pointing to remembered visual targets after active one-step self-displacements within reaching space. *Exp. Brain Res.* **125**, 50–60. (doi:10.1007/s002210050657)
- 126 Van Pelt, S. & Medendorp, W. P. 2007 Gaze-centered updating of remembered visual space during active whole-body translations. *J. Neurophysiol.* **97**, 1209–1220. (doi:10.1152/jn.00882.2006)
- 127 Munoz, D. P. & Everling, S. 2004 Look away: the anti-saccade task and the voluntary control of eye movement. *Nat. Rev. Neurosci.* **5**, 218–228. (doi:10.1038/nrn1345)
- 128 Zhang, M. S. & Barash, S. 2004 Persistent LIP activity in memory antisaccades: working memory for a sensorimotor transformation. *J. Neurophysiol.* **91**, 1424–1441. (doi:10.1152/jn.00504.2003)
- 129 Van Der Werf, J., Jensen, O., Fries, P. & Medendorp, W. P. 2008 Gamma-band activity in human posterior parietal cortex encodes the motor goal during delayed prosaccades and antisaccades. *J. Neurosci.* **28**, 8397–8405. (doi:10.1523/JNEUROSCI.0630-08.2008)
- 130 Gail, A. & Andersen, R. A. 2006 Neural dynamics in monkey parietal reach region reflect context-specific sensorimotor transformations. *J. Neurosci.* **26**, 9376–9384. (doi:10.1523/JNEUROSCI.1570-06.2006)
- 131 Collins, T., Vergilino-Perez, D., Delisle, L. & Doré-Mazars, K. 2008 Visual versus motor vector inversions in the antisaccade task: a behavioral investigation with saccadic adaptation. *J. Neurophysiol.* **99**, 2708–2718. (doi:10.1152/jn.01082.2007)
- 132 Fernandez-Ruiz, J., Goltz, H. C., DeSouza, J. F., Vilis, T. & Crawford, J. D. 2007 Human parietal ‘reach region’ primarily encodes intrinsic visual direction, not extrinsic movement direction, in a visual motor dissociation task. *Cereb. Cortex* **17**, 2283–2292. (doi:10.1093/cercor/bhl137)
- 133 Vaziri, S., Diedrichsen, J. & Shadmehr, R. 2006 Why does the brain predict sensory consequences of oculomotor commands? Optimal integration of the predicted and the actual sensory feedback. *J. Neurosci.* **26**, 4188–4197. (doi:10.1523/JNEUROSCI.4747-05.2006)
- 134 Körding, K. P. & Wolpert, D. M. 2006 Bayesian decision theory in sensorimotor control. *Trends Cogn. Sci.* **10**, 319–326. (doi:10.1016/j.tics.2006.05.003)
- 135 Laurens, J. & Droulez, J. 2007 Bayesian processing of vestibular information. *Biol. Cybern.* **96**, 389–404. (doi:10.1007/s00422-006-0133-1)
- 136 MacNeilage, P. R., Banks, M. S., Berger, D. R. & Bühlhoff, H. H. 2007 A Bayesian model of the disambiguation of gravito-inertial force by visual cues. *Exp. Brain Res.* **179**, 263–290. (doi:10.1007/s00221-006-0792-0)
- 137 Vingerhoets, R. A., De Vrijer, M., Van Gisbergen, J. A. M. & Medendorp, W. P. 2009 Fusion of visual and vestibular tilt cues in the perception of visual vertical. *J. Neurophysiol.* **101**, 1321–1333. (doi:10.1152/jn.90725.2008)
- 138 Ma, W. J., Beck, J. M., Latham, P. E. & Pouget, A. 2006 Bayesian inference with probabilistic population codes. *Nat. Neurosci.* **9**, 1432–1438. (doi:10.1038/nrn1790)
- 139 Munuera, J., Morel, P., Duhamel, J. R. & Deneve, S. 2009 Optimal sensorimotor control in eye movement sequences. *J. Neurosci.* **29**, 3026–3035. (doi:10.1523/JNEUROSCI.1169-08.2009)
- 140 Brockmole, J. R. & Irwin, D. E. 2005 Eye movements and the integration of visual memory and visual perception. *Percept. Psychophys.* **67**, 495–512.
- 141 Niemeier, M., Crawford, J. D. & Tweed, D. B. 2003 Optimal transsaccadic integration explains distorted spatial perception. *Nature* **422**, 76–80. (doi:10.1038/nature01439)
- 142 Bays, P. M. & Husain, M. 2008 Dynamic shifts of limited working memory resources in human vision. *Science* **321**, 851–854. (doi:10.1126/science.1158023)
- 143 De Vrijer, M., Medendorp, W. P. & Van Gisbergen, J. A. M. 2009 Accuracy-precision trade-off in visual orientation constancy. *J. Vis.* **9**, 9.1–15. (doi:10.1167/9.2.9)
- 144 Quaia, C., Optican, L. M. & Goldberg, M. E. 1998 The maintenance of spatial accuracy by the perisaccadic remapping of visual receptive fields. *Neural. Netw.* **11**, 1229–1240. (doi:10.1016/S0893-6080(98)00069-0)
- 145 Hamker, F. H., Zirnsak, M., Calow, D. & Lappe, M. 2008 The peri-saccadic perception of objects and space. *PLoS Comput. Biol.* **4**, e31. (doi:10.1371/journal.pcbi.0040031)
- 146 Keith, G. P., Blohm, G. & Crawford, J. D. 2010 Influence of saccade efference copy on the spatiotemporal properties of remapping: a neural network study. *J. Neurophysiol.* **103**, 117–139. (doi:10.1152/jn.91191.2008)
- 147 White, R. L. & Snyder, L. H. 2004 A neural network model of flexible spatial updating. *J. Neurophysiol.* **91**, 1608–1619. (doi:10.1152/jn.00277.2003)
- 148 Keith, G. P. & Crawford, J. D. 2008 Saccade-related remapping of target representations between topographic maps: a neural network study. *J. Comput. Neurosci.* **24**, 157–178. (doi:10.1007/s10827-007-0046-6)
- 149 Salinas, E. & Abbott, L. F. 2001 Coordinate transformations in the visual system: how to generate gain fields and what to compute with them. *Prog. Brain Res.* **130**, 175–190. (doi:10.1016/S0079-6123(01)30012-2)
- 150 Zipser, D. & Andersen, R. A. 1988 A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature* **331**, 679–684. (doi:10.1038/331679a0)