Review

Ocular kinematics and eye-hand coordination

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Abstract   Eye-hand coordination is complicated by the fact that the eyes are constantly in motion relative to the head. This poses problems in interpreting the spatial information gathered from the retinas and using this to guide hand motion. In particular, eye-centered visual information must somehow be spatially updated across eye movements to be useful for future actions, and these representations must then be transformed into commands appropriate for arm motion. In this review, we present evidence that early visuomotor representations for arm movement are remapped relative to the gaze direction during each saccade. We find that this mechanism holds for targets in both far and near visual space. We then show how the brain incorporates the three-dimensional, rotary geometry of the eyes when interpreting retinal images and transforming these into commands for arm movement. Next, we explore the possibility that hand-eye alignment is optimized for the eye with the best field of view. Finally, we describe how head orientation influences the linkage between oculocentric visual frames and bodycentric motor frames. These findings are framed in terms of our 'conversion-on-demand' model, in which only those representations selected for action are put through the complex visuomotor transformations required for interaction with objects in personal space, thus providing a virtual on-line map of visuomotor space.

Key words   Eye-hand coordination; eye movements; spatial updating; ocular dominance; reference frames.

Introduction   Eye-hand coordination dominates many aspects of our daily lives. We need good eye-hand coordination to reach out and pick up a coffee cup, press a doorbell, or catch a ball. Although

scientists have studied eye-hand coordination for decades, if not centuries, it seems that only recently has eye-hand coordination emerged as a distinctive, cohesive field of study. This is not surprising, since a complete understanding of eye-head coordination requires a thorough understanding of spatial vision, eye movements, several aspects of cognition and neurophysiology, and of course the muscular control of the arm and hand. Perhaps only now have we learned enough about these individual topics to begin synthesizing them under the rubric of eye-hand coordination.

In order to approach the topic of eye-hand coordination one must begin with a useful definition. Some students of the field focus on the motor act of coordinating the eyes and hand – moving them both toward the same target in unison. The layperson probably has a more general notion of eye-hand coordination, one that encompasses all aspects of the use of vision in guiding the hand to purposeful action. In this review we will focus on the spatial aspects of the transformation between vision and action, with a focus on the intermediate role played by ocular kinematics.

Our particular interest is in the geometric aspects of the forward serial transformations within the brain that use vision to guide movement of the hand. Although many studies of eye-hand coordination look at the input (vision) and the output (hand movement), our focus is on the transformations that account for all of the linkages in between – from eye, to head, to body, to arm, to hand. Most of our studies are on pointing or 'touching', a pared-down version of eye-hand coordination minus the grasp element. Our goal is to build up a rigorous model – the kind that could actually control such a system if one were to build it from scratch. Our belief is that in building up such a model, we will gain a clearer understanding of the neural processes that one should look for in the brain. The following is not a general review of the topic: in the short space allowed here our aim is to summarize our own work in this area, and to show how this work has motivated our thinking about eye-hand coordination.

Description of experiments

GAZE DIRECTION AND POINTING ACCURACY   A number of experiments have demonstrated the intimate coupling between movements of the eyes and hand.[1–4] But why do we need this? What is the advantage of coupling the eye and hand? One way to find out is to de-couple the system and see what happens, i.e., to ask people to reach or point toward objects that they are not looking at. Under these conditions, Roland Johansson and colleagues have shown how reaching / manipulating movements that are normally precise become relatively clumsy.[5]

We wanted to quantify the effects of uncoupling on pointing performance.[6,7] This work followed from earlier observations by Bock[8] and Enright,[9] showing that people point past remembered targets located in their visual periphery, which we confirmed and expanded on. (These and other investigations from our lab that are reviewed in this paper were performed according to the guidelines of the 'Declaration of Helsinki'.)

We found that when forced to point toward a central target in the absence of visual feedback, with the eyes deviated, subjects showed systematic misjudgments of target direction. Individual subjects showed different patterns of error, which varied rather anisotropically depending on the direction of the target relative to gaze. But overall, subjects showed a consistent pattern: a tendency to overestimate the distance of the target relative to gaze. When asked to direct their gaze 30°, 15°, and 5° both to the right and left of the pointing target, subjects' past-pointing increased with the amount of gaze deviation until saturating at about 2–4° error at 15° gaze deviation. When provided with full visual feedback of the hand with gaze deviated from the target, subjects reported anecdotally that they noticed their own pointing errors and attempted to correct for them, although we did not quantify this adaptation. Further controls – in which both the gaze target and pointing target were varied – confirmed Bock's finding that this effect was related to the amount of retinal deviation of the target, not eye position per se.[8] In other words, when the pointing target was shifted left or right from center, this caused the profile of gaze-related pointing errors to shift by the same amount, indpendent of eye position.

Why this degradation in performance? One obvious reason is that foveal vision has a much higher acuity. However this cannot be the full answer, because retinal acuity 5–15° from the fovea is still too good to explain the poor performance in our studies, and systematic pointing performance does not seem to drop off for further retinal eccentricities.

Another possibility is that a 'gaze-guidance' system can use the line of sight as a special cue to guide the hand toward foveated targets. We tested this in another study where our subjects placed their finger onto a remembered virtual target site in the dark.[10] In this study, subjects spontaneously made errors in retaining fixation on the remembered target location. However, these errors in fixation did not correlate with errors in reaching. For instance, when subjects looked slightly to the left of the target, they were no more likely to mis-reach to the left than to the right. Thus, contrary to what might be predicted by a gaze-guidance hypothesis, small, unconscious deviations in gaze do not drag the hand with them, though they do cause small non-specific degradations in performance. Instead, subjects may mis-reach more when their gaze misses the target site because the target falls outside of foveal vision.
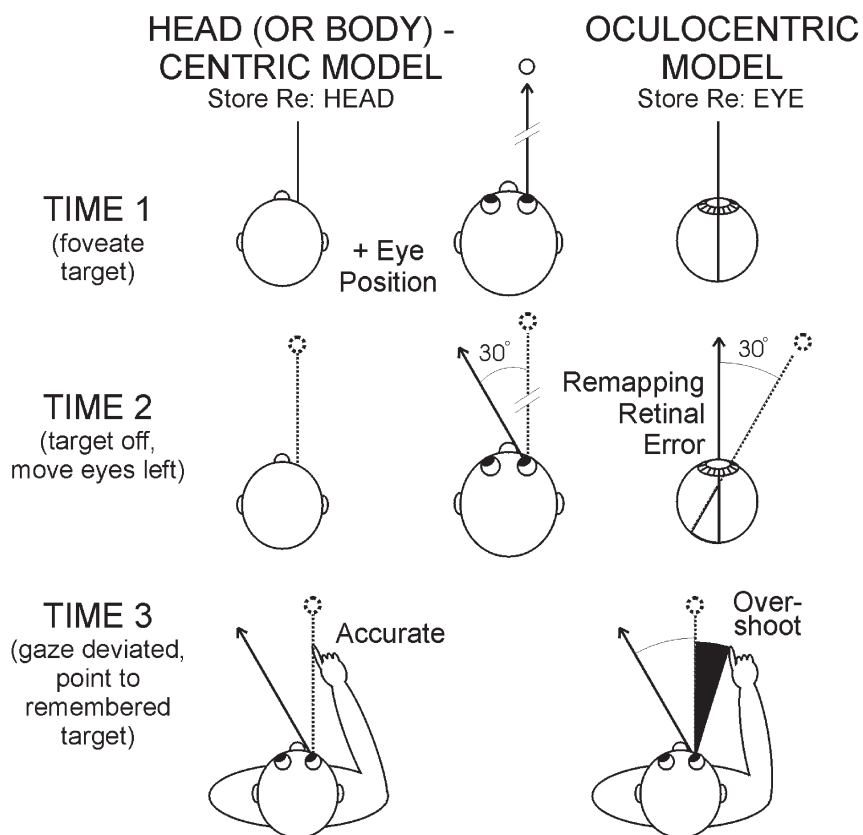
Thus, our favored explanation is that the system is simply better calibrated for foveated targets, and that conversely the neural outputs of other patches of retina are poorly calibrated for eye-hand coordination. This does not explain the specific overshooting pattern that we found, but that is a topic we will take up again in a later section.

UPDATING SPATIAL MEMORY ACROSS EYE MOVEMENTS Numerous studies have considered the question of how we can look at a target, look away from it so that it is out of sight, and still know where it is.[11,12] Clearly, a fixed retinal impression of the target location would be insufficient and downright misleading, so the brain must be doing something more sophisticated.

One idea was that the brain builds up representations of space by comparing vision with eye position, head position, and so on.[13] Unfortunately, the neurophysiological evidence for this mechanism, at least in visuomotor transformations, remains somewhat sketchy, boiling down to some fairly subtle eye position signals[14–18] with no clear maps of head-centered or body-centered space. Perhaps these maps are distributed in some way.[14,17] But a more recent suggestion, consistent with certain signals recorded in the visuomotor structures of the brain,[19,20] suggests that each time the eyes move, an internal copy of this movement is used to remap our internal on-line representations of visual space in a retinal frame.

The gaze-dependent pointing errors described in the previous section provided the opportunity to test between these mechanisms in the eye-hand coordination system (Figure 1). We reasoned that since subjects make pointing errors as a function of retinal eccentricity (as described above), then they should make these same errors when redirecting their gaze produces a similar 'retinal eccentricity' for the remembered fixated target site – as if their internal representations were remapped to the same retinal location during an eye movement (Figure 1, *right column*), even if they looked at the target with the fovea.[6] For instance, if subjects point past a remembered target seen while they are looking 15° to its left, they should also past-point after they move their eyes to 15° left subsequent to fixating the flashed target. On the other hand, if

Fig. 1. Predictions of a headcentric (or bodycentric) model (left) and oculocentric (right) model of visuospatial memory. The test paradigm (shown in the middle, as well as in Figure 2C), has subjects look at the target (time 1) and then look 30° left after the target disappears (time 2) before pointing to its remembered location (time 3). The key feature of this test is that during the visuomotor transformation for pointing, subjects usually exaggerate the retinal eccentricity of the remembered direction of non-foveal targets. The headcentric model holds that we compute target direction relative to the head (by combining retinal signals with eye position) as soon as we fixate the target (in time 1). Note that retinal eccentricity at time 1 is zero and therefore is not subject to the exaggeration effect. According to the headcentric model, this head-centered memory trace remains stable during the intervening eye movement at time 2, so that accurate pointing is predicted at time 3. The oculocentric model holds that the target is coded relative to current gaze direction and as a result the leftward eye movement at time 2 must be compensated for, by the counter-rotating of the retinotopic memory trace 30° to the right (time 2, right panel). Now the subject must point based on a peripherally shifted retinotopic memory trace, which is susceptible to the exaggeration effect. Therefore, the oculocentric model predicts subject will past-point in the direction opposite to the final gaze direction. Modified from Henriques et al.[6]

HEAD (OR BODY) - CENTRIC MODEL
Store Re: HEAD

OCULOCENTRIC MODEL
Store Re: EYE

TIME 1
(foveate target)

+ Eye Position

TIME 2
(target off, move eyes left)

30°   30°   Remapping Retinal Error

TIME 3
(gaze deviated, point to remembered target)

Accurate   Over-shoot

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subjects formed static, head- or body-centered representations of targets (Figure 1, *left column*), then pointing based on an initially foveated target should not be affected by subsequent eye movements (that, indeed is the point of this model).

In summary, in the paradigm illustrated in Figure 1 a head-centered model would predict accurate open-loop pointing (Figure 1, *bottom left*), whereas an eye-centered remapping model would predict that subjects past-point in the direction opposite to gaze (Figure 1, *bottom right*) like they do when they point to the remembered location of a peripherally viewed target.

In order to test between these models, we first had subjects perform two controls. In the first (Figure 2A) they simply looked and pointed toward a central flashed target, in which case pointing was quite accurate except for a vertical undershoot. In the second 'static paradigm', subjects performed the same task with gaze deviated to the right or left (Figure 2B). This confirmed the pattern of gaze-centered past-pointing discussed in the previous section. Then subjects performed the paradigm illustrated in Figure 1 with these same targets. Since they only viewed the central target while fixating it, the headcentric model predicted that they should be as accurate in pointing as the first control (Figure 2A), whereas the eye-centric model predicts that the pointing target would be peripherally re-mapped (internally) and they would point with the same errors as observed in Figure 2B.
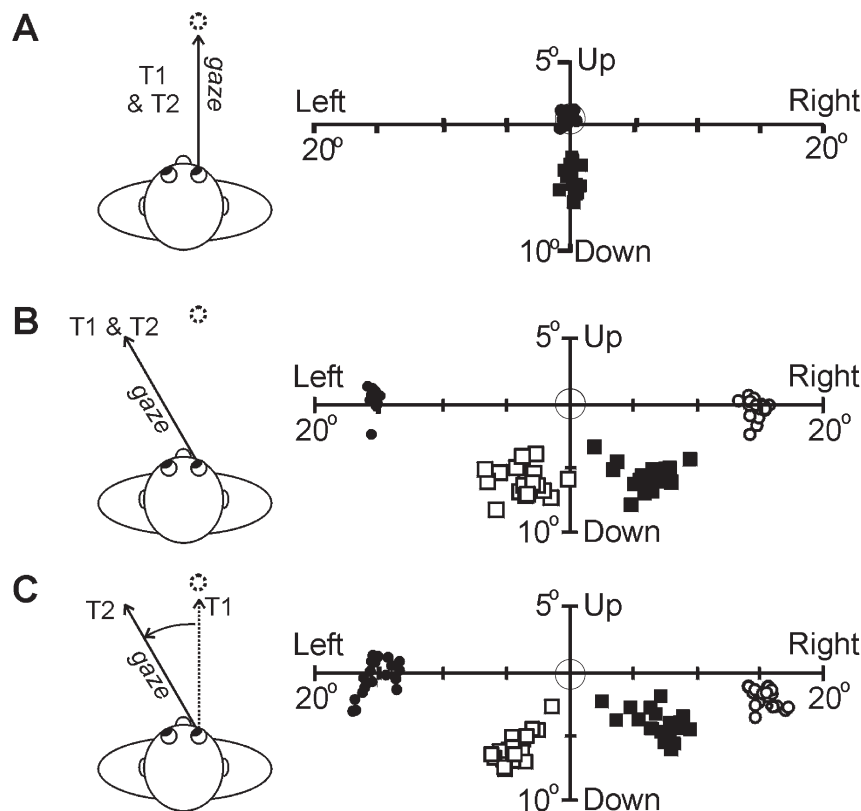

Fig. 2. Gaze-Centerd Pointing performance in humans. *Left column*: The three tasks, where subjects either (A) look directly toward the target before pointing (control task), or (B) view the target peripherally before pointing (Static Task) or (C) foveate the target (T1) before looking toward the peripheral target (T2) and then pointing (Dynamic Task). *Right column*: Final 2-D pointing directions (squares) and gaze direction (circles) relative to central target for a head-fixed subject. In the control task (A), subjects pointed accurately with a little vertical undershoot. In the static task (B), the subject past-points in the direction opposite to gaze; this is due to an overestimation of the retinal eccentricity of the target. In the dynamic task (C), the subject also past-points in the direction opposite to their final gaze direction, although they fixated the target first (this paradigm is further illustrated in Figure 2, middle column). Open symbols indicate 15° rightward fixation trials; solid symbols indicate 15° leftward fixation trials. Modified from Henriques et al.[6]

Our results clearly favored the eye-centered re-mapping model (Figure 2C). When subjects foveated a briefly flashed target in complete darkness, and then deviated their eyes, they did not point as accurately as they did when they maintained their gaze on the remembered target site throughout the trial. Instead, they made the same errors in pointing as in the static paradigm (Compare Figure 2C to Figure 2B). In other words, it looks like they were pointing based on a shifted, retinotopic representation.

Based on this result, we concluded that the eye-hand coordination system uses this same mechanism[6] that had previously been proposed and described for the oculomotor system. Shortly afterwards, Richard Andersen and colleagues[21] discovered that single-unit responses are consistent with such a mechanism in the Parietal Reach Region (PRR) – an arm control center with retinally organized receptive fields.

CODING NEAR SPACE VS. FAR SPACE   In the study described above (Henriques et al.[6]), the pointing targets were well beyond reach, in so-called extra-personal space. However, a number of neuropsychological studies have suggested that different neural mechanisms are used for coding near (peripersonal) space (for a review see Colby and Goldberg[22]). This makes some sense for eye-hand coordination. Anything within reach is coded by preparatory activity in primary motor cortex (M1), whose signals are clearly not organized in eye-centered coordinates.[23–26] Why not code for near targets using the stable, muscle-centered, eye-movement independent codes of M1?

To test which spatial mechanism dominates human reaching behavior, across eye movements, in near space, we repeated the paradigm in Henriques et al.[6] but this time using three sets of arm pointing/reaching targets – one beyond reach, one at 42 cm, and one at 15 cm (Figure 3). According to the hypothesis that near and far space are

Fig. 3. Spatial coding of reach locations in depth. *Top Row*: Schematics of the task. *Bottom row*: Final finger-tip position from one subject plotted in the horizontal plane. In the *control* task , the subject simply fixates a central (straight ahead) target at one of three depths, and then reaches toward it's remembered 3-D location in the dark after the target turns off. This results in very accurate reaching. In the *'Static'* Paradigm the subject follows the same procedure, but now gaze is deviated to the left or right. Leftward gaze fixations (not shown) result in rightward mis-reaching (○) whereas rightward fixations result in leftward mis-reaching (●). Note that the effect is constant in terms of visual angle from the origin. In the *dynamic* paradigm, the subject fixates the targets while they are illuminated, before deviating gaze to the left or right. But the final pointing performance resembles that of the static paradigm performance, i.e., in terms of *angular* error, it is gaze-centered independent of target depth. When quantified across subjects, this data follows the predictions of the eye-centered re-mapping model for all target depths. Modified from Medendorp and Crawford.[27]

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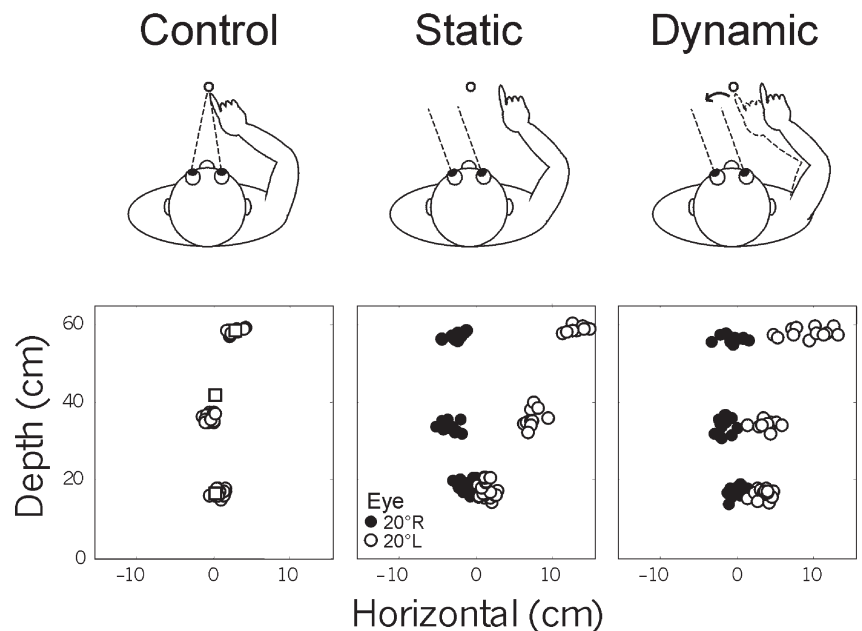
coded differently, subjects should have shown the same result as before for the far target, but should have shown a more stable reaching response for the near targets, unaffected by the intervening eye movement. But this is not what happened.[27] Instead, subjects showed the same effect for all three-target sets; the effect predicted by the eye-centered remapping model.

It would be a mistake to conclude that this means that the muscle/body centered representations are never used to code near space in M1 and other structures, but this result does suggest structures like PRR that apparently show remapping override those responses, updating them after each eye movement. Perhaps, the near-far distinction may be more relevant for perception than for action. If so, our results support the notion that target locations are remembered by shifting retinotopic representations as a function of each eye movement, and suggest that this is a general spatial mechanism for near and far space.

COORDINATING ONE HAND WITH TWO EYES   When one speaks of eye-hand coordination, one implicitly propagates an error. Most of us have to coordinate *two* eyes with *two* hands. However, one generally chooses one hand in reaching, often the dominant hand. But which eye is chosen? Or is it some synthesis of the two?

This gets us into the sticky territory of ocular dominance and the cyclopean eye.[28,29] Ocular dominance has many meanings. Here we consider just alignment of the hand with the eye. For example, in our monocular pointing studies, we have found that subjects tend to align the fingertip between the eye and the target, as if they were reaching out to touch it (as opposed to aligning the line of the arm to the target). So, which eye do they choose? In neurophysiological terms, which eye dominates the eye-centered representations in the brain described above?

One appealing idea, put forward in the 19th century by Wells[30] and more recently championed by Ono and colleagues,[29] is that the inputs from the two eyes are synthesized into and referenced to a virtual 'cyclopean eye'. However, even this theory would require that the fingertip to be positioned along the line of sight of one eye for the image of the finger to be perceived (from that eye) as aligning with the cyclopean eye (this may sound contradictory, but makes sense in terms of Wells' original experiments. He had subjects look down a pair of lines on the horizontal plane drawn between the eyes and the fixation point; subjects perceived these as one line projecting out from the bridge of the nose). Thus, the question arises again, which eye does the hand coordinate with?

A number of classical studies suggest that the hand prefers to align with a dominant eye.[28,31–33] However, we noted that all of these studies were done with targets located straight ahead. But what about more peripheral targets? Wouldn't it make sense for the system to be more flexible, and choose either eye, depending on which one had the better field of view?

To test this idea, we used a variation of an old paradigm[32] where we had subjects reach out and grasp a ring while visually fixating a target

through that ring, and then bring the ring back to 'the eye' without allowing it to cross the line of sight. Subjects are expected to choose the 'dominant' line of sight, and indicate this by bringing the ring back to the corresponding eye. Their performance on this task proceeded as we had expected:[34] subjects tended to choose the right eye for rightward (but still binocular) targets, and the left eye for leftward targets (Figure 4). The switch in choice generally occurred surprisingly close to, but just off, center, so that if subjects had been tested only at the center target they would have appeared to be either left eye or right eye dominant.

In a similar, more recent test of this hypothesis, we asked subjects to point toward targets at various horizontal eccentricities, and then examined the kinematics of their arm position to determine if the hand had been aligned with the left or right eye.[35] Again, we found a clear tendency for subjects to choose the left eye for leftward targets and vice versa, although curiously this tendency was reduced by visual feedback. This may be a motor strategy that allows the hand to coordinate with either one eye or the other in way that optimizes vision, perhaps relying on eye position signals or some other cue.

THE GEOMETRY OF RETINAL PROJECTION AND EYE ORIENTATION
When one considers eye-hand coordination as a control system, it is important to ask how this system transforms eye-centered visual signals into useable commands for arm movement. At first glance, the eye-centered remapping mechanism described in the previous sections would seem to obviate the need to continuously take eye position into account. But that is only true with regards to the mechanism for coding and storing spatial memory described in those sections. Once one has to actually act on those representations, the eye positions signals become vital.

Why is this so? Supposing that one always started off by looking and pointing in the same direction, one might think it a simple matter to drive the arm along the arc in parallel with the displacement of the target as coded on the retina, or the target's retinal displacement. To code the arm movement, the brain would map the retinal vector

Fig. 4. Gaze-position-dependence of ocular dominance, as measured by grasping a ring and bringing it back toward the head without allowing it to cross the line of gaze. A: The percentage of trials where the right eye was dominant (0% indicates that the left eye was always dominant) is plotted for each gaze/target direction. For example, if subjects brought the ring to the left eye 60% of the time and to the right eye 40% of the time for a given target direction, this would give score of 40% for that gaze direction. Each line joins the data one subject across the different target directions tested, for a total of ten subjects. Note that all subjects reversed 'ocular dominance' within the range tested, but most did this to one side of center so that they would seem right or left eye dominant at central gaze. Solid lines: right eye dominance at center. Dashed lines: left eye dominance at center. Modified from Khan & Crawford.[34]
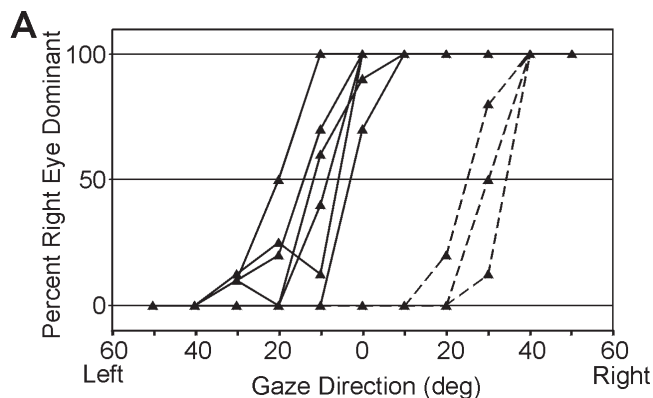
directly onto a motor vector. One obvious flaw with coding arm motor commands this way is that most of the time the arm does not start aligned with gaze. When we go from a resting position to reach for a target, we are generally accurate, even when we do not have visual feedback of the arm and target.[7,36] The only way to do this is by combining the visual signal with an internal sense of eye position.[37,38]

The recognition that the brain needs to take eye position into account when computing target direction has led some theories to suggest that the brain might approximate the required arm/eye rotation by a simple vector addition – merely adding all retinal vectors onto a vector coding initial eye direction.[11–13] But this vector-addition strategy would lead to marked errors in some situations because displacements in retinal coordinates are not the same as displacements in head or shoulder coordinates.[36]

The reason why this is so has been described in detail[36] elsewhere, but essentially one cannot treat the geometry of the retina and eye position like a flat slide screen which translates up, down, left, and right. The retina is a curved surface that rotates with respect to the world. As a result, spatial displacements that might be visually horizontal (i.e., on the retina) at one eye position become oblique at other eye positions, whereas in head/ shoulder coordinates they stay the same. If the brain tried to compute these objects' locations relative to the head or the shoulder simply by using vector addition, it would misestimate the elevations of at least some objects, and would misaim resultant arm movements (Figure 5A).

To test the way that the eye-hand coordination system handles this problem, we had subjects point between various horizontally displaced targets, in the absence of visual feedback.[36] What we found was that (1) the projections of these target displacements onto the retina varied strongly with eye position in a complex, non-linear fashion (Figure 5A), and (2), despite this, pointing movements were essentially accurate
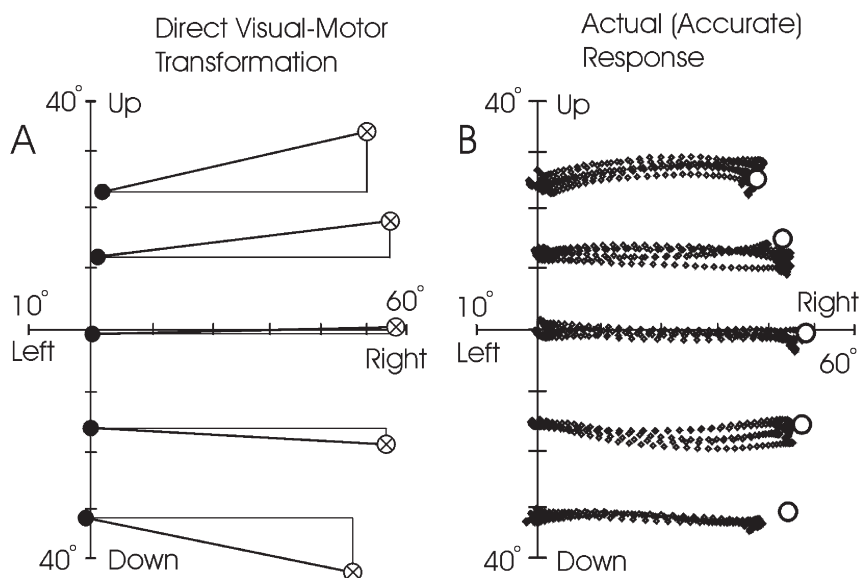
Fig. 5. Comparing the predictions of a model that provides a direct vectorial visuomotor transformation to the actual performance of a subject in a pointing task. In this task, subjects begin by looking at pointing toward visual targets at various vertical levels along the central axis, in an otherwise dark room. Another light is then flashed directly to the right of the fixation target in body coordinates. The subject is then required to continue fixating, but then rotate the arm toward the remembered location of the rightward target. It can be shown (and measured experimentally) that these rightward targets stimulate non-horizontal points on the retina, depending on initial eye position. If the brain mapped these retinal stimuli directly onto a motor command for the arm in a fixed fashion (or added eye position signal to the visual signal in a vectorial fashion), this would result in the splaying out pattern of errors (gray wedges) shown in A. However, actual subjects are able to produce relatively accurate arm trajectories (B), demonstrating that the visuomotor transformation accounts for eye orientation and its non-linear influence on the geometry of retinal projection. Modified from Crawford et al.[36]

(Figure 5B). In other words, the visuomotor transformation for pointing didn't just take the 'first-order' aspects of eye position into account (i.e., adding the visual vector to an eye position vector), it in effect accounted for 3-D eye rotation and performed the correct non-linear reference frame transformation.

HEAD ORIENTATION AND ITS EFFECTS ON EYE-SHOULDER GEOMETRY

When the head is allowed to move, as it normally is, one must also take head orientation into account in order to interpret visual direction, following similar principles to those discussed in the previous section on the eye. However, head movement has other, special implications for eye-hand coordination. This is because the centers of rotation of the eye, head and shoulder do not coincide. As a result, each time the head rotates, it causes the eyes to translate through space relative to the shoulder, which changes the angular direction of targets relative to the eye, but not the shoulder (Figure 6). One could rely on visual feedback of the hand – during pointing or reaching – to make up for any differences this might make, but we were interested to see if the system took this into account without such feedback.

To do this, we had subjects point toward distant targets with the head in different horizontal positions.[39] We did this with the left eye patched to avoid complications from the binocular dominance effects described above. Head rotations caused significant changes in the line from the eye to the target (recall that this is the line that subjects use for aligning pointing when looking straight ahead). Nevertheless, subjects were able to re-calculate this line, and accurately place the fingertip at the right location for any head position.

In a related experiment[10] we found that subjects were similarly able to account for head orientation and the resulting translation of eye location when computing the visual angle of near targets for reaching movements. These results not only show that head orientation is taken into account, but also that the eye-hand coordination system possesses a sophisticated *representation* of body geometry that takes into account the differences in the centers of rotation of the eyes, head, and

Fig. 6. Effect (schematic) of head rotation and eye-shoulder linkage geometry on eye-hand alignment in pointing. In our experiment, subjects were required to point toward a distant target. With the head centered (*center column*) the aligned the fingertip along the line (—) between the target and the right (non-occluded) eye, rather than aligning it with the shoulder-target line. When the head was rotated to the left or right, this caused the eye-target line to similarly shift leftward or rightward (←, →). (This happens because of the linkage geometry of the eye, head, and shoulder, as illustrated by the dotted lines). However, subjects continued to align the fingertip with the eye-target line, even when pointing toward remembered targets without visual feedback of either the target or hand. Modified from Henriques and Crawford.[39]

Head 40° Left   Head Center   Head 40° Right

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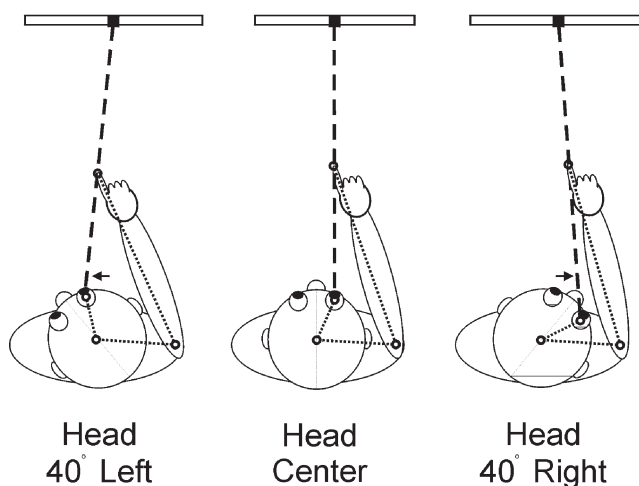
shoulder in the absence of on-line visual feedback. Such a representation is likely constructed or at least fine-tuned by learning.

Discussion and conclusions   As stated in the Introduction, the aim of this work is to create a model of eye-hand coordination that can help us to understand visually directed arm movements, and help guide our neurophysiological investigations. The working model that we have been using for the past few years is illustrated in Figure 7. Admittedly it is cartoonish in several respects: in its reliance on forward serial transformations (we all know the brain is really heavily parallel and recurrent in organization), in its representation of signals (no one should expect such discrete, explicit representations in the brain), and in its simplicity (even many aspects of the work described here have been left out). And yet in outline, it agrees with much of the known physiology.

In particular, the recently discovered 'parietal reach region' (PRR), located within the intraparietal sulcus, appears to encode and update reaching targets in an eye-centered frame,[21] as predicted in the initial representational stages of our model (Figure 7A). This provides a neural substrate for our behavioral findings that reach targets are
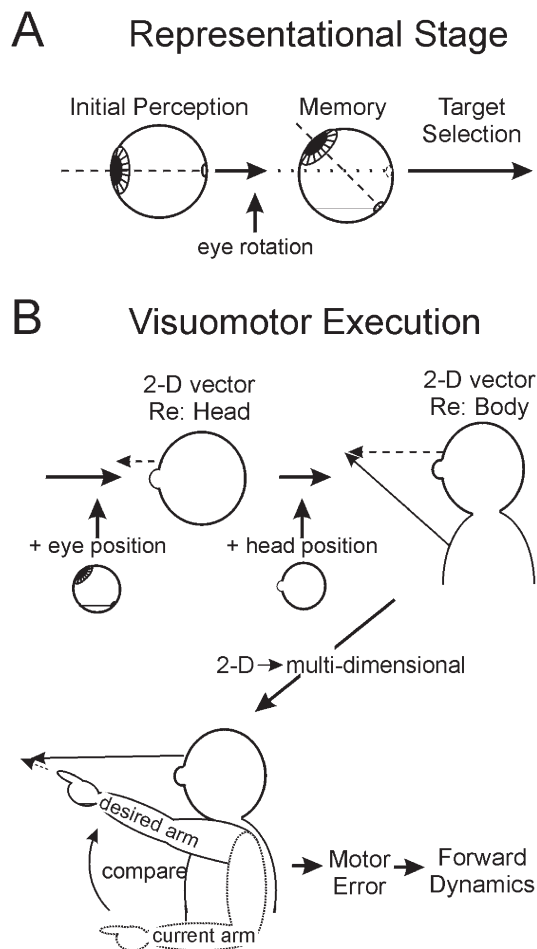

A   Representational Stage

Initial Perception   Memory   Target Selection

eye rotation

B   Visuomotor Execution

2-D vector Re: Head   2-D vector Re: Body

+ eye position   + head position

2-D → multi-dimensional

desired arm

compare

current arm

Motor Error → Forward Dynamics

Fig. 7. Conversion-on-demand hypothesis of visuomotor representation and visuomotor control. Target representations are initially held in an eye-centered frame, and can be shifted in this frame to compensate for intervening eye movements through dynamic remapping (A). Once a target has been selected for action, its final retinal representation is put through a reference frame transformation (by comparing it with 3-D orientation of eyes and head) to generate an accurate 3-D motor signal in motor reference frame (B). Modified from Henriques et al.[6]

coded in a gaze-centered frame.[6,27] Further eye and head position-dependencies in the parietal and frontal cortex[25,40,41] could provide the substrate for many of the remaining transformations in our model (Figure 7B), providing a progression of eye-to-shoulder reference frame transformations between the PRR, premotor cortex, and primary motor cortex.[42] This would provide the neural substrate for our findings that eye-hand coordination accounts for the complexities of eye and head geometry.[36,39] The tendency of subjects to align the hand with one eye or the other is something that could be attributed to filtering of visual information in the early stages of the the model (Figure 7A), or in the geometry of eye hand coordination (Figure 7B),[34,35] but we have not yet formally incorporated this into our model.

Another possible area where the model may need to be updated is in the comparison between target direction and hand position: a recent study[43] suggests that this comparison is done at a more early stage, in retinal coordinates (necessitating of course that hand information derived from proprioceptive information also be transformed into retinal coordinates, using eye position and other information). One can argue over the functional advantages of this, but one empirical consideration is that by placing this comparison at an early stage one derives vector-like representations of movement displacement commands that are consistent with the known neurophysiology of this system.[42]

It has been suggested that by making such comparisons between target direction and hand position in eye coordinates, one can perform a more direct sensorimotor transformation,[43] perhaps getting rid of the need for comparisons with eye and head position. However, the work reviewed above shows that this is not possible when one considers the real geometry of the system. For example, we showed above that a desired displacement of the hand in eye coordinates does not map trivially onto a hand displacement in shoulder coordinates (Figure 5). Such a mapping can only be achieved through a successive comparison with eye and head positions signals. However, such reference frame transformations could be accomplished through fairly subtle eye/head position modulations on motor displacement codes,[44,45] again consistent with the known physiology of this system.

A central feature that emerges from this discussion is that we can speculatively divide the control system for eye-hand coordination into two stages. The first is an early *representational* stage where multiple visual targets are represented and mapped in a retinal frame[6,27] (Figure 7A). Thus, one might speculate that only the target that is selected for action is put through the subsequent transformations of the second *visuomotor execution* stage (Figure 7B). The latter stage would involve the computations required to compute motor commands in multiple head- and body-centric reference frames, i.e., comparisons with eye and head orientations,[36,39] computation of inverse kinematics and dynamics of the arm and so on. From a biological perspective, this is a space and energy saving feature: there would be an enormous cost to try to perform these operations on every point in space.[6]

If correct, this scheme has a surprising implication. Whereas introspection may suggest that we have a complete map of visuomotor

space, our model suggests that this is an illusion – only the overall transformation provides such a map, and only on those representations we choose to act on. The catch is that every time we test our intuition by choosing to act on a representation, it confirms our intuition of a complete map. In this sense, this is a sparse 'virtual' map of space, similar to ideas that have been proposed for visual perception.[46]

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