Sensorimotor integration

Włodzisław Duch, Harold Bekkering, Bas Neggers
MPPF, ... WWW: http://www.phys.uni.torun.pl

Draft summarizing what the problem is, what has been done and what is still needed.

I. INTRODUCTION

What we want is the model that can explain experimental data collected for the tactile-visual integration experiments. This model should include major brain structures involved in the information flow leading to sensomotoric behavior. We deliberatly avoid the statement “motoric responses” because we are not sure if it makes sense to speak about motoric responses to sensory stimuli. It may happen that the feedback connections between different brain structures are so strong that the coupling of all anatomical subsystems can only be understood as one integrated dynamical system in which the motoric actions provide reafferent prioprioceptive signals that not only complement the sensoric input but help to define it. In view of the recent findings that even the primary V1 visual cortex areas need feedback from higher areas for discovering basic structures in the visual data this should not be surprising.

The overall approach should be based on a careful analysis of approximations describing couplings of different brain structures and conditions, under which these approximations hold. For example, people with various neurological problems exhibit different sensomotoric behavior since some of the couplings between their brain structures are different. An alternative is to look at the information processing and postulate unknown mechnisms that should be capable of doing the job. What information is available and what information is needed to enable the specific functions? This seems to be easier but it may create artificial problems such as the transformation of the coordinate system.

In any system where interactions are strong the only chance to understand it is to find specific experimental situations in which most of thes interactions either have no influence or do not change so that differential effects may be investigated (ex: fMRI studies).

II. OVERALL SKETCH

Which brain structures are involved; visual cortex, which layers, parietal and temporal lobe path, supplementary motor area (SMA), premotor cortex, cerebellum (including dentate nuclei), superior colliculus, globus pallidus, putamen, other nuclei - brain stem: raphe nuclei and locus ceruleus? - corpus callosum (M. Iacoboni), basal ganglia, thalamic structures, substantia nigra.

The touch and arm proprioceptive information comes via dorsal column – medial lemniscal system, through the ventral posterior lateral nucleus of thalamus and from there to the somatosensory cortex (S-I). In the cortex input from various submodalities (touch, temperature, pain) interacts, although integration is done in associative areas of the PPC. Shortes response time is to proprioceptive and auditory stimuli, 120 ms, slightly longer to visual stimuli, 150 ms. Preparation for movement is up to 800 ms, but in simple anticipated reaction tasks it is shorter. Premotor areas receive principal inputs from PPC and are involved in preparation for and planning of movments, PPC (area 5 and 7) connects reciprocally to SMA, which influences the primary motor cortex directly as well as via the premotor area.

Some questions: define primary and secondary pathways; How strong are the feedbacks, can we assume a feedforward information flow? which structures should be included and which are not necessary? Is the model of two interacting self-organized topographical networks useful?

A. Internal model

Several experiments point out to an internal model being used in SI. Edmund Rolls has found in monkey hippocampus cells that seem to preserve the absolute frame of reference for the visual model.

Ghahahramani et al. [12] use Kalman filter to simulated the process of arm movement in the dark and measuring the discrepancy between real movement and estimated movement. The bias of the estimated position grows and peaks at about one second after movement initiation, when most probably the estimation gradually switches from the internal to the reafferent estimation reducing the bias and preventing the variance from growing.

III. MAJOR PATH

Oculomotor control in vertebrates: Types of control

- Saccades (high velocity, ballistic movements)
- Continuous tracking
- Vestibulo-ocular reflex (visual fixation during head movement)
- Optokinetic reflex (visual fixation during body movement)
- Convergence (independent tracking as object approaches/recedes)
- Motor pathway: frontal cortex → oculomotor nuclei → extrinsic eye muscles (n. III,IV,VI)
  sup colliculus → reticular formation → oculomotor nuclei → eye muscles
- Sensory pathway: eye → lat genic → vis cortex → cerebellum → reticular formation
  eye → superior colliculus → reticular formation
  inner ear, joints → vestibular nucleus
- Sensorimotor integration: Saccades: eye → sup collic→ reticular form → oculomotor nuclei → muscles
- Others: eye → LGN → visual cortex → (cerebell, reticular formation, vestibular system) → oculomotor nuclei → muscles

IV. INTEGRATION OF INFORMATION

Ghahramani et al. [12] has tested experimentally three different models of information integration using visual and auditory stimuli.

Conclusions: stochastic model is out, vision (more reliable) acts as the teaching signal for other modalities (audition, tactile). Most probable: minimum variance integration.

In a recent paper Ghahramani and Wolpert [14] support the idea of a modular decomposition in visuomotor learning with rersults of experriment and theoretical model. Motor system adapts itself quickly to different perturbations, for example using distorted vision, inverted prisms or even two different prismatic displacements separated temporally. It is probable that a modular system is responsible for such quick adaptation, i.e. multiple modules that work as expert curcuitry for specific tasks but may replace each other in different context. In the experiments visuomotor map was perturbed by providing visual feedback that was identical for two different hand positions, depending on the starting location of the movement. In the model one assumes that two separated visuomotor mappings may influence the motor output, each gated by a smooth sigmoidal function. Learning two such mappings leads (in experiments with humans) to smooth generalization at intermediate locations, suggesting a mixing of two separate neuronal populations that influence motoric outcomes.

In experiments 7 starting locations on a line were selected, and the target was placed in the middle between the furtherst two locations shifted forwards. There was no perturbation from the first group of subjects, overshooting left/right in the second, overshooting up/down in the third and undershooting left/right in the fourth. Interestingly in 3rd group all responses were shiftted to the right and in 2nd and 4th upwards, with elliptic shapes, but these effects were not discussed in the paper.

Q: How many independent maappings can we learn? Is the mixing done in two separate structures (eg. SC and PPC) or in one? If in two spearate structures than learning 3 locations will already be difficult. If in one structure, than slow gradual increase in the number of errors should be expected. What if after learning the target is shown briefly but no continous visual input is provided?

Same results could probably be obtained with Salinas and Abbott coupled population netowrks [34] in a more neurobiologically plausible way.

V. HOW THE INFORMATION FLOWS

How is the position and speed of movement estimated when arms are moved without visual feedback? By reafference (sensory inflow), integrated motor outflow (dead reckoning) or both?

Contributions of the retinal and extraretinal signals to manual tracking movements were analyzed by Donkelaar et.al. [7]. The conclusion of a series of experiments with using hands to track target velocity in different conditions (full vision, no vision of the hand, fixation on a LED) are: vision of the hand and its initial position relative to target is necessary to catch up with the target, while extraretinal signal – eye velocity – is required to produce an accurate steady state hand velocity. In normal conditions latencies of 250 ms (5 cm/s target speeds) to 190 ms (for 25 cm/s speeds) were observed while in no vision or fixation case latencies increased to 260 to 230 ms. The shorting of latencies with the increased speed of targets is well established now. Conclusion that there are two components of latencies: detection and processing time required too prepare the response, although consistent with results of Donkelaar et.al. [7] seems to be correct in context of these experiments, ad is based on an assumption of separate neural circuitry processing the detection and response. In other experimental situations, for example habituated or learned reflexes (jumping to the side, playing video games) this would be much harder to justify. Although the paper does not discuss the neurophysiological reasons for such findings one may draw several conclusions that are useful for modelling.

Perhaps by providing an attention signal the brain will prepare for action reducing the latencies to a normal level (i.e. the same as with the visible hand). It is also interesting to compare these results with report by Brown et al. [5] that the latencies are actually decreased – in patients with cerebellar damage – if the initial position of the handle is not shown. Perhaps this is really due to the cerebellar damadge or maybe due to different experimental conditions – in Donkelaar experiments subjects could see their hand next to the target and the task was just to start moving, so no saccades between the final target and the initial positions were made.

Without seeing the hand, i.e. in the absence of retinal visual signals accuracy of position estimation decreases and the subjects are not able to catch up with the moving target. This phenomenon is probably due to the coupling of the visual and motoric maps in the superior colliculus. It would be very interesting to analyse the SC maps and see if the accuracy depends on the actual representation of stimuli in SC. To some degree lower accuracy of hand positions in experiments with fixation or eccentric fixation are understandable from this point of view: accuracy of SC representations around the center and close to the eyes is higher than at the peripheries [24]. Unfortunately good drawings of the four types of SC maps are not available.

Q: Why is it more diffcult to respond without seeing the hand? This is especially visible at higher target speeds. If I see my hand with an intention to move it, just waiting for the signal, the latency time is short possibly because the threshold for generating the movements by the motor cortex is lowered by the intentional state that I have created. Perhaps such intentional states – they should be rather called anticipation states – lead to an increased availability of neurotransmitters in the regions concerned, lowering the threshold for excitation and thus increasing sesnsitivity and contributing to the increased spiking rates. This may be done using the attentional mechanisms via brain stem nuclei. These neurotransmitters are transported directly to the selected brain circuits; visual inputs help to determine which circuits, via the coordinated superior colliculus visual and motoric maps. Without visual input I forget after a few minutes where my hand is, especially if it is completly at rest and there is little proprioception.

VI. ROLE OF DIFFERENT BRAIN STRUCTURES

The role of the most important brain structures in sensorimotor behavior is described here. Structures contributing to saccades, vision and tactile perceptions are listed. Short executive summary:

Visual system structures:
V1=striate cortex, primary visual cortex; other V2-V5 = extrastriate cortex, divided already in the LGN into magnocellural system specializing in motion and spatial relationships, and the second path called the parvocellular system. The first path ends at V5, which is also called MT (middle temporal) and deals mostly with motion detection and 3D organization of objects (seeng where). The parvocellular system specializes in form and color (seeing what) and leads to the IT (inferotemporal) areas.
MST (medial superior temporal area), known also as V5a, smooth pursuit, optokinetic reflex

Parietal structures:
PPC (posterior parietal cortex)
PPC 7a - integration of somatic and visual sensations;
PCv (Ventral PC)
PCd (dorsal PC)
PEF (parietal eye field) - not mentioned by Kandel; involved in reflexive visual exploration.

Frontal cortex structures:
SEF (supplementary eye field) - involved in preparation of motor programs (sequences of saccades), signal the type of task that should be performed.
FEF (frontal eye field) - control of the voluntary saccades.

Cerebellum:
Posterior vermis.
Dentate nuclei: fastigal nucleus.

Thalamic structures:
Superior colliculus: generation of saccades
substantia nigra
caudate nucleus
basal ganglia
putamen
corpus callosum (M. Iacoboni)

Brain stem structures:
Occulomotor nuclei
Pontine reticular formation
Inferior olive
NPH (nucleus prepositus hypoglossi) – integration of velocity-related inputs that influence eye positions, neural integration used to hold eye positions of fixation following saccades.
NRTP
Red nucleus
raphe nuclei and locus ceruleus?

Other:
MVN (medial portion of the vestibular nuclei) – integration of velocity-related inputs that influence eye positions.

A. The Ocular Motor System

Eyes make 5 types of movements and are controlled by 6 muscles. Fovea covers only 1 deg, although the whole viewing angle is 200 deg. Vestibulo-ocular and optokinetic subsystems should not be important in our case, also vergence can be omitted. Two important movements are saccades and smooth persuit. Smooth persuit movements follow the moving visual targets after an initial saccade that takes about 200-300 ms, with slower moving targets eliciting slower responses.

Three pairs of extraocular muscles control eye movements. Is there any information about the relative speed of movement in different directions? This probably contributes very little to the overall movement time. The extraocular muscles are controlled by three groups of motor neurons extending from the brain stem nuclei called oculomotorr, trochlear and abducens nucleus. Saccades are created by bursts or pulses of activity in neurons connecting the muscles with these nuclei. All motor neurons participate in all types of eye movements. After the pulse the average discharge frequency change, allowing the eye to maintain the new possition - this is called the step.

The velocity and the step signals for saccades and the smooth persuit are provided by the interneurons in the brain stem reticular formation. The horizontal components (controlling lateral rectus) are controled by paramedian pontine reticular formation (PPRF) or more precisely by abducens nuclei neurons laying deeper in the brain stem. Abducence nuclei control the vestibular-ocular reflexes. Vertical and rotation components are controlled by the mesencephalic reticular centers, or more precisley by oculmotor nuclei neurons control medial, superior and inferior rectus (eye muscles), and trochlear nuclei (TN) controling superior oblique rectus. These oculomotor and TN nuclei are in the brain stem close to the superior colliculus. Pulses are generated by burst cells. Integration of signals determining the step takes place in the nucleus prepositus (where in the brain stem is it?). The network that generates saccade seems to be relatively well known and is composed from burst, burst-tonic, tonic and pause cells.

Modulation of the sacaddic system is done by cerebellum; at least damage to the dorsal cerebellar vermis, fastigal nuclei, and in flocculus, have strong influence on the pulse and the step sizes. For the smooth pursuit velocity signals are carried by the paramedian pontine reticular formation. The smooth pursuit pathway involves the following:

Striate cortex (VI visual area) → Prestriate motion areas MT, MST → directly to Dorsolateral pons in the brain stem, and indirectly through the Frontal eye field in the lateral frontal cortex to the Dorsolateral pons → Cerebellar flocculus → directly to pontine gaze center and indirectly through the neural integrator (nucleus prepositus ?) to the pontine gaze center → ocular motor neurons.

Is SC not involved in this at all?

Saccadic eye movements (3/sec on average in humans, no more than 40 ms spend on saccade movement) are created by the brain stem saccade generator (BSSG) which receives inputs from the SC and frontal eye field (FEF) cortex area directly. FEF receives information from the posterior parietal cortex which in turn gets it from the lower levels of the visual system. About a quater of the neurons in FEF area respond to visual stimuli that become targets for the saccades; half of the FEF neurons respond to visual stimuli (and the other half?). Neurons in the posterior parietal cortex have enhanced responses to stimuli that are attended to (peripherial vision stimuli?) but not necessarily saccade to. Parietal corrtex also projects visual attentional excitations directly to SC. FEF neurons that project to SC are not the visual input neurons but "neurons that discharge before saccades that are relevant to animal's behavior" (?). FEF sends motor commands to the intermideate SC layers and indireclty neurons from the same FEF layer project to caudate nucleus and excite neurons that inhibit substantia nigra, and thus releasing SC from inhibition by substantia nigra pars reticulata). Substantia nigra may inhibit generation of saccades. FEF projects also to the pontine and mesoencephalic reticular formations, but not directly to the bursting regions. FEF receives also projections from the supplementary eye field (rostral part of the SMA), which projects also to subcortical areas (which?), and dorsolateral prefrontal cortex.

B. Superior colliculus

The most important brain structure in which integration of multimodal sensory and motoric information takes place is the superior colliculus (SC), or in non-mammals the optic tectum. It is the 'roof' of the midbrain. Inferior colliculus is concerned predominantly with the auditory signals, while SC with visual and many other modalities.

Structure: SC is a layered midbrain structure, with 3 superficial, 2 intermediate and 2 deep layers.

Inputs: superficial layers receive visual inputs directly from the retina (directly?), (frontal eye field ?) and visual striate cortex, while deep layers receive visual, somatosensory (from S-I or directly through VPL thalamus?), auditory (from inferior colliculus presumably) and motor-related inputs. Other inputs: parietal cortex, premotor cortex (PMC), primary motor cortex (M-I).

Most (over 50%) of deep layer inputs are multisensory, with visuo-auditory neurons being about 30%. An important input source for SC is the inferior colliculus, involved in changes in the adaptation of auditory maps in blind-reared owls.

The outputs project to brain stem and peripherial organs influencing orientation of eyes, head, limbs and other parts of the body. Outputs are not influenced by the initial eye position (probably cerebellum decides on the dynamics of muscle contraction, since lesions lead to dysmetrias).

Superficial layer: half of the neurons respond to a visual stimuls when a saccade will be made (are they simply directing saccade movements?), but not other actions like hand movements in response to visual stimuli. Neurons do not project directly to intermediate layer, but to pulvinar and lateral posterior nuclei of thalamus and via cortical connections (feedback to visual areas?) back to intermediate layers. A topographics representation of the contralateral visual hemifield based on the retinal input and visuotopically organized striate and extrastriate inputs is located there.

Intermediate layer: receive visual inputs from prestriate, middle temporal, parietal cortices, motor input from FEF. In addition somatosensory and auditory location maps are found there, including bimodal neurons. A large population of cells fires before each saccade (population-response coding). Motoric outputs of the intermediate layers seem to be independend from the superficial layer activity and vv.

Deep layers: inputs primarily from the somatic sensory and auditory systems plus some visual inputs from the upper layers. Motor map is located here. This layer projects to cerebellum, brainstem, substantia nigra and various cortical regions. The deep and intermediate layers are sometimes combined together in SC models [23]. Motor areas receive inputs from the intraparietal sulcus (LIP area) processing visual and oculomotor informaiton.

Opstal et al. [32] also mention inputs from nucleus prepositus hypoglossi (NPH) and the medial portion of the vestibular nuclei (MVN), both nuclei involved in the integration of velocity-related inputs that influence eye positions. More recently Delgado-García writes that the neural integration used to hold eye positions of fixation following saccades takes place at the NPH.

The somatosensory SC map represent points in visual space, larger areas for parts close to the eyes, smaller for distant parts such as fingers. Visual map in the superficial layer is aligned vertically with auditory map in the deeper layer and with the somatosensory map (where), i.e. the same regions of space excite both. The 3 maps are aligned with the motor map in the deep layer (precisely how is it done?). The representation of motoric maps is done by population coding, i.e. each cell has it prefered movement field. The size of these fields for neurons corresponds to the size of saccades [36].

Lesions of the whole SC only temporarily disturb the saccadic movements making it slower and less accurate but ultimately animals recover almost completly. Is SC role so crucial then in the genreation of proper saccades? What is known about these lesions? For example, do they impair hand-eye coordination?

It is probable that SC inputs are weighted by their reliability [12]. Signals with different information content and levels of processing seem to be arriving in one structure. SC receives information about the motion in the visual field, about broad outtlines of objects and about visual attentiveness. FEF receive more subtle information about complex visual stimuli.

Animals orient often to a locus betwen the auditory and visual stimuli presented simulataneously. It is possible that interaction of two stimuli in SC itself leads to a maximum activation corresponding to one intermediate activity site; it is also possible that this integration occures at the motor stage which has large receptive fields on SC. It may also be an effect of neural architecture - larger receptive fields at the perifery where adaptation is greater.

Although the main information provided by SC is the amplitude and direction of saccade correlation of neural activity with saccaded velocities have also been found. Opstal et al. [32] in a study on monkeys provide evidence that SC activity (deep layers) may also be influenced by eye position. Very high burst rates of up to 900 Hz have been measured. The burst neurons in the motor SC map fire about 20 ms before the saccade [8]. The movement fields are modeled either as gaussians in 2D, multiplied by the maximal frequency, or as gaussians multiplied by a linear combination of the eye position relatively to the center of the oculomotor range plus the maximum frequency – this was called a gain field and was found significant in about half of the cells. About 50% of the gain fields had a gradient vector colinear with the optimal saccade displacement vector, while 41% were orthogonal and 9% anticollinear. Opstal et al. [32] suggest that the motor map cells in SC code both oculocentric motor error and a desired position of eyes in a craniocentric code. Neural network model using population of gain field neurons with randomly distributed eye position sensistivity vectors has been constructed and encodes both desired motor errors and eye positions in the head-centerred coordinates. Direction of gaze modulates also the activity of the premotor cortex [30].

Lefèvre [26] argues for retinotopic coding in SC, and a relative position feedback loop in the control of gaze saccades. He reviews various arguments for placing the SC in such a feedback loop, dynamically controling the saccades. Examination of experiments with head/eye movements towards the targets leads to conclusion that head movements are made in retinocentric frame. Some subjects may move the head more then the others (interpretation of some data is not clear in the second experiment). A simulation model has been constructed to account for the data. The model includes sacadic movements (brainstem burst cells active) and the compensatory slow-phase mode. If the gaze error is larger than 3.5 degrees saccade is triggered, and if the error is smaller than 3deg saccade is ended. 10 other parameters are included in the model. A 2-D neural model is also mentioned but not described in details.

Computational model of SC and the auditory pathways projecting to it has been presented recently by Jabri et al. [23]. It is a fairly detailed model discussing interaction of burst, build-up and fixation type of neurons in the deep SC layers. One sheet of fixation cells receiving inputs from the PPC, FEF, SEF and from the multisensory maps on the caudal side and one sheet of the burst neurons receiving similar inputs and connected via feedback loop to the brain stem structure has been introduced. The two sheets of neurons interact using inhibitory and excitatory connections. A strong agreement between outputs of this model and recordings from the neurophysiological experiments was obtained.

C. Cerebellum

Source of information: mostly patients with cerebellar disfunctions [5].

Conclusion: During coordinated visuomotor tracking initiation of both eye and arm movements is prolonged; cerebellum may play a coordinative role.

Organization of cerebellar architectonics:

- Purkinje cells are the only output from cerebellum, inhibitory on descending motor nuclei. Inhibitory output from Purkinje cells ‘sculpts’ motor output to achieve anticipated result (i.e. to eliminate deviations from expected result).
- Climbing fiber – sensory input from inferior olive (medulla), powerfully excitatory influence
- Granule cells – axons for parallel fibers, perpendicular to Purkinje dendritic arbor, weakly excitatory
- Mossy fibers – sensory input from various medullary nuclei, excite Granules
- Golgi cells – excited by parallel fibers, inhibit adjacent Granules (→ lateral inhibition)
- Basket and Stellate cells - excited by parallel fibers, inhibit Purkinje cells (→ feed-forward inhib)

Somatotopic representation of body surface across 2-D cerebellar surface. Climbing and mossy fibers are collaterals of direct sensory and motor pathways → cerebellum receives ‘copy’ of intended motor output and expected sensory consequences.

Cerebellum uses the limb afferent information. In primates kinaesthetic information of the arm movement is used at higher control level to coordinate eye-hand motion, most probably in cerebellum (but: see dentate nucleus). Inactivation of posterior vermis or fastigal nucleus of the cerebellum decreases saccadic accuracy. Stimulation of posterior vermis produces saccades and influences ongoing saccades while recordings in this area show saccade related firings. There seem to be 3 major inputs to the cerebellum posterior vermis area: SC sends projections to the NRTP (nucleus reticularis tegmenti pontis), sending mossy fibers to posterior vermis; SC to inferior olive (a part of medial accessory nucleus) and via climbing fibers to posterior vermis. This path seems to be used to send the error signals necessary for learning to make accurate saccades. Third input comes from NPH (nucleus prepositus hypoglossi, where is it ???) which seems to have information about the current eye position. Amplitude of saccades generated by vermal stimulation depends on the initial eye positions. The sole inhibitory output from the oculomotor vermis goes via axons of Purkinje cells to the fastigal nucleus, one of the dentate nuclei. From there projection to the brain stem structures is made: pontine reticular formation, which receives signals also from SC. Pontine RF connects to the oculomotor nuclei controlling eye muscles. The cerebellum input to these structures seems to adjust the local feedback loop for different eye position mechnics.

Dentate nuclei (DN), deep nuclei of the cerebellum, may serve as a coordination center for combining the eye and the limb movements using kinaesthetic information. DN and other deep nuclei (fastigal, globose, emboliform) tranmit all cerebellar output to the motor cortex region and to the brain stem (via a tract called cerebellar peduncle). DN is connected to the lateral part of the posterior lobe.

Initiation of purposive limb movements is slower in patients with cerebellar damages (and primates) and less accurate. Such demadges do not influence initiation of saccadic eye movements, but create saccadic dismetria (?, does it influence the timings?). Cerebellum plays direct role in ”determinig the metrics of independently generated eye and limb movements” [5]. A change in target position elicits saccades after 230-240 ms. During eye-arm tracking initiation of both the saccadic and limb motor systems is delayed in patients with cerebellar damadges. During eye tracking only this is a small effect, more pronounced in extension movement (about 25 ms longer) than in flexion movements, where it seems to be within the error bars. In coordinated eye-arm tracking it is quite large, for extension movements about 70 ms and for flexion movements about 40 ms longer. Thus the need to make arm movement seems to slow down the eye movements. Blanking the target increases the saccadic onset times on about 60 ms in people with cerebellar dysfunction [why could that be? without sepcific point to saccade to perhaps larger popoulation of neurons in SC fires more weakly contributing to a saccade and the integration time is longer?]. Removal of the initial arm (or handle used for manipulation) position decreases. Brown et al. write that using proprioceptive information in place of retinal information the processing time for initiating coordinate movements is reduced. It is also possible that visual representation of the starting point increases the probability of small saccades around it (this is similar to inertia of the eyes, which is smaller if there is nothing to look at at a given spot).

Gauthier et al. proposed that cerebellum is a complementary system to the normal control of eyes and limb movements. Some neurons in the lateral cerebellum respond both to eye and arm movements. It is unclear whether the cerebellar damge does not influence the movements by actually sending confusing information to the brain stem nuclei through which the final outputs for the muscle flow; in such a case the contribution of the cerebellum to timing could still be negligible. It is possible that damadged cerebellum disrupts also the saccadic eye movements (although the saccadic and arm movments are generated independently) slowing the initiation times down when arm movements are required. This would explaing the data by Brown et al [5].

Question: what could be the contribution of cerebellum to the latencies in healthy subjects? Is the role of the cerebellum just to provide coordination of smooth movements using limb afferent information or correct the motoric plans to account for this afferent information? In this case when limbs are not visible it will play a major role.

D. Parietal cortex

Anatomy: two areas, 5 and 7; area 5 receives inputs from somatosensory cortex, vestibular system, premotor areas, limbic cingulate cortex; projects to area 7 and premotor area. Area 7 has visual information from the MT and MST, auditory information and somatosensory inputs from area 5; it projects to the premotor areas and to the lateral cerebellum.

Gaze direction and retinal position is represented in multiplicative manner in the area 7a of the posterior parietal cortex (PPC) [1]. Neurons in this area are tuned to the retinal positions of visual stimulus and the gaze angle modifies the heights of the tuning curve. Such information should be sufficient to guide the movements [2]. Gaze-angle invariant activity is not necessary and has not been found in the brain. Area 7b of the PPC has information about the arm position. In the lateral intraparietal area (same as 7?) have activity related to the intentional eye movements. In the PPC an abstract representation of space is constructed using population coding based on retinal, eye position, auditory, vestibular and proprioceptive head position inputs [1].

Recently Salinas and Abott [34] constructed a neural model coupling these two areas together. This model automatically incorporates the transformation from retinal to the head-centered coordinates. The starting point of this model is population decoding from the area 7a, thus avoiding explicit model of finding and identifying the target. A condition that the weights of the neurons have to fulfill for accurate alignemet of motor responses with sensory data is identified and an unsupervised training process based on observation of random movements is introduced, fullfiling this condition in an automatic way. The model develops a non-linear coordinate transformation between sensory and motor cortices in an implicit way.

The model includes noise terms added to the firing rates of sensory and motor arrays, target locations corresponding to the preferred retinal positons and movements. The average firing rates are characterized by the tuning curves depending on target location. Radial functions for the firing rates are assumed (plus the Gaussian noise term), depending on a distance between the target location and the preferred location. Quite general analytic results are obtained for tuning functions of almost arbitrary shape although for computer simulations Gaussian shapes are assumed for sensory as well as motor neurons. These tuning functions for the motor neurons are decoding the firing rates, converting them into motor repsonses. The firing rates of motor neurons are assumed to be simply weighted linear combination of the sensory neuron rates, plus the nosie term. The weights evolve either by a Hebb rule $W_{ij} =< R_i^m R_j^s >$ or a covariance rule, $W_{ij} =< R_i^m R_j^s > - < R_i^m >< R_j^s > =< R_i^m R_j^s > -k$, where k is a constant term, optimized in this model to fit the data, and $<>$ denotes averaging. For fixed gaze averaging is done over the goal locations z; random movements over entire range of z are generated and observed locations z taken as the goal, or target locations x. The motor neuron firing rates are therefore given by $f(|a_i - z|)$ and sensory by $g(|c_i - z|)$, and the weight are obtained by integrating:

$$W_{ij} = \int dz g(|c_i - z|) f(|a_j - z|) - k \tag{1}$$

With varying gaze direction additional averaging is done: the tarrget loocation in the head-centered coordinates corresponding to the retinal position x and gaze direction y is assumed to be $x + y$ and should be equal to z, the goal location, i.e. or $x = z - y$.

$$W_{ij} = \int dy dz g(|c_i - z|) f(|a_j - z + y|) h(|b_j - y|) - k \tag{2}$$

Population coding averages over preferred locations of the individual neurons:

$$z = \frac{\sum_i R_i^m c_i}{\sum_i R_i^m} \tag{3}$$

where c_i are preferred vectors for neurons in the motor cortex. More precise method of decoding the meaning of firing rates is based on maximization of overlap:

$$\max_z \sum_i R_i^m g(|c_i - z|) \tag{4}$$

although the differences are not significant. The sums may be replaced by integrals even for modest number of neurons. The initial preferred locations are determined by introducing random variation about grid locations (with completly random locations the error is a bit larger). Simulations start with random targets, sensory outputs drive motoric neurons via weighted linear combinations, the activity of motor neurons is decoded into the goal direction and errors are computed. Since this is an unsupervised method these errors are used only for making graphs. The accuracy of the decoding was checked separately and is quite high, for N neurons in one-dimensional array increasing with $O(1/\sqrt{(N)})$, which means that the noise terms dominate accuracy. Decoding is not sensitive to the shapes of the tuning curves. As long as the strenght of the connections $W_{ij} = W(|c_i - a_j|)$ motor activity should produce movements towards the target. Synaptic weights obtained by averaging have this property. Weights generated by watching random movements and performing correlation based modifications lead quickly to small errors below 1% already for a few hundered neurons.

For the variable retinal and gaze direction coded in the same sensory cortices in an arrbitrary way (for example, multiplicatively) the correct motor response is assured if the weights depend only on $W_{ij} = W(|c_i - a_j - b_j|)$ and can be generated by the corelation based procedure. During learning both position and the gaze direction have to be varied randomly while the motor array randomly stimulates the sensory array during development. The mechanism of corrections for motor cortex is based on shifed receptive fields compensating for the gaze direction, although the sensory fields are fixed (only gain modulated). A motor network receiving input simultaneously encoding two variables can generate a movement that is an arbitrary combination of these variables. The same mechanism as for retinal and gaze position may be used for simultaneous coding of many different variables. Experiments made by Salinas and Abbott show that although the error increases with the number of variables coded, for 6 variables being about 10 times larger than for one, it still decreases like the square root of the number of neurons. Additional variables act as a source of noise. Non-linear transformations, for example from the Cartesian to polar coordinate system, are also easily implemented using the same mechanism.

In essence this model requires the motor system to provide random targets to the sensory system that drives the motor system, while weights between two population maps are changed using averaged correlations between the firings of neurons. Randomly waving the arm while watching it is sufficient to develop propoer connections. Interestingly, in cats and monkeys vision of the limb is is required for motor development [some blind people have problems in finding their mouth while eating although they may play piano or use a typewriter – it just shows that training is slower]. From neurobioloogical point of view this is quite plausible mechanism, although even more plausible model based on Poisson spike trains has been mentioned (but not yet published) by Salinas and Abbot.

The results of this paper support the idea that information in tthe sensory cortex is represented essentially in coordinate invarinat way. Correlation based learning allows the network to extract in an automatic way the information needed for a given task, without worring about coordinate transformations. Graziano and Gross [17] claim that PPC 7b area together with VIP, area 6 and putamen conatin bimodal tactile-visual cells representing extrapersonal space in somatotopic fashion.

How useful is this model to account for the timing measured by Bas? The model takes into account the variable gaze, so is the combination of the eye and retinal angles proposed by Bas really used by the brain? Is the retinal and gaze information separately present in the PPC? Can one find it out from the exisiting experiments?

E. Frontal and supplementary eye fields

Mushiake et al. [29] in a research on monkeys determined that neurons in the FEF area are equally active during saccade only as during the combined eye-hand reach task. In the SEF area neurons seem to specialize – half of them act in the same way for both tasks, but the remaining half show preferences for saccade only or for saccade + hand reach. It is therefore probable that SEF nurons signal the type of task that should be performed. These neurons exhibit more learning related activity than FEF neurons and may be involved in preparation of motor programs (sequences of saccades). Both areas serve as motor fields for eye movements. FEF neurons seem to control the voluntary saccades while SC are responsible for more reflexive type of saccades. Dominey and Arbib mention that FEF neurons specify amplitude, direction, time to initiate a saccade but not the dynamical aspect of the actual saccade (i.e. what exactly?). FEF contains visual, movement and visuomovement presaccadic cells [9], the last two being visuotectal. Some cells are postsaccadic, probably directing correction saccades in opposite direction.

In addition PEF (Parietal Eye Field) is involved in reflexive visual exploration but it is hard to find more information on this topic. Preforontal cortex (Brodman 46) may inhibit unwanted reflexive saccades and create predictive saccades, being also involved in spatial memory.

F. Premotor cortex

PM neurons are active during execution of movements, motor preparation, response to sensory signals. According to Andersen et al. [2] transformation from retinotopic to the head-centered coordinate system takes place in the posterior parietal cortex combining the retinal and occular signals to code stimulus location in the head-centered system using population coding.

Mushiake et al. [30] report a study on monkeys in which neuronal activity in the lateral ventral part of the premotor cortex (PMv) during target-reach movements is modulated by the direction of gaze. About half of the movement related activity of PMv cells were modulated by the direction of gaze while in the primary motor cortex only quite small number of neurons were modulated. The modulation effects were deterined by the position of the reaching target relatively to the eye fixation target and not to the body. This indicates that the premotor cortex may be involved in the retinotopic to body coordinate transformation. Because of the neuroanatomical connections the gaze sensitivity in PMv may also reflect the transformations done by PPC areas, although this is not yet clear. Perhaps PMv is able to use the data in multiple reference frames. PMv may be specialized for motor execution under visual guidance [25]. Graziano et al. [17] found in the PMv bimodal cells with visual and tactile receptive fields, tactile organized topographically, face in the middle, arms medially and inside of the mouth laterally. Arm movements (but not head or eye) are correlated with receptive field population movements for 70% of neurons with tactile receptors on the arm. For 95% of bimodal neurons with a tactile response on the face the visual receptive firlds move with head rotation, 15% moved with eye but none with arm. It seems that visual receptive fields anchored to different parts of the body are present in PMv, i.e. sensory stimuli are acnchored to a particular body part. For arm and visual cells integration of information from the arm, head and eye is done, while for head and visual cells only eye position is sufficient.

In the PMd (dorsal part of the premotor cortex) movement amplitude and direction are programmed by serial integration (?), and conditionally presented sensory signals are processed for motor preparation and execution [25].

G. Mid-brain & brain stem nuclei

Other nuclei influencing SC and generating saccade movements – perhaps not so important? What effects could they create? For example slowing the saccades due to inhibition by substantia nigra? It all depends on the experimental questions. Saccades are made even if cerebellar, SC and cortex structures are damadged, since the brain stem nuclei are directly responsible for generating them, but learning may be impaired and accuracy lost. In monkeys the bursts from red nucleus are transmitted through the spinal cord to the muscles, coding movement velocity in terms of frequency, movement duration in the burst duration and tha amplitude in the total number of spikes. Asymetry of the velocity profiles in movements is similar to the assymetry of the cell population profiles.

Dean et al. [8] developed an interesting model of the brainstem-cerebellar interactions for learning and maintaining saccadic accuracy. This accuracy is learned during the first year of life in humans and is still quickly adaptable in grown-ups (for example in inverted vision, although 90deg rotated vision leads to confusion and cannot be learned). The simplest model of saccade generation considered by these authors starts with the retinal input going into a feedback controller that converts the target location in visual coordinates into the desired eye position changes; presumably this controler includes also the SC. The output from this controller is passed to a puls or burst genertor, with frequency of the burst coding the velocity of the movement and the total number of spikes coding the displacement. The internal brainstem feedback mechanism makes this process more robust. A second integrator is used to estimate the step signal necessary for maintaining the new eye position. This simple model is extended by Dean et al. [8] to allow for learning and maintance of saccadic accuracy.

The model is extended by adding information about eye position at the start of the saccade. The new control model has been inspired by robotic design (Kawato 1990) and is composed from a simple feedback controller for corrective saccades and neural network controller that learns the errors and provides the initial saccade direction. Cerebellum is treated as an adaptive controller and modeled using CMAC system that works here as a coarse-coded look-up table to provide gain vlaues (modulating the saccadic controler) for a given eye position/saccade command signal. The final model is fairly complex but is able to correct outputs of the saccade controller for the weakening of eye muscles and target displacement during saccades.

Topographic organization of somatosensory stimuli was also found in the putamen, with some bimodal, visual-tactile neurons [17]. Visual neurons were not selective to shape or color. Visual neurons provide a map of visual space organized somatotopically, for example for tactile neurons of the face visual receptive fields extend on about 10 cm. Putamen seems to cooparate with PPC area 7b, VIP (VIP) and are 6 (?) [17].

H. Saccade Generator

The final saccade generator (SG) network controling motor neurons (MNs) is a part of the brain stem and there are still some controverises how does it work in details. The best model proposed so far is probably the Dominey and Arbib model (available in the collection of Brain Models in the Web), a modification of the Scudder's model described in Arbib [4]. For simple saccades their model involves retinal inputs through SC and FEF and fairly detailed model of systeme generating outputs for motor neurons. Activity at a given FEF or SC location determines the amplitude and the firing rate determines velocity, leading to some dependence of velocity on almplitude. SC and FEF units are represented by population of cells sending their inputs to SG.

The Long Lead Burst Neurons (LLBN) in the PPRF receive inputs from SC and FEF forming a motor map of saccade vectors. Processing time by these neurons is estimated at $\tau_{llbn} = 40$ ms and the output is obtained by taking the sigmoid of the winner-take-all combination of SC and FEFsac input spike rates. This output is then filtered through a sigmoid and goes through a mask to the Medium Lead Burst Neurons (MMBNs) with $\tau_{mlbn} = 8$ ms. The mask allows to increase the influence of peripherial inputs weighting it by eccentricity of the saccade target. This goes to the "delta" neurons (D-burster neurons) and Excitatory Burst Neurons (EBNs). Delta neurons $\tau_{mlbn} = 6$ ms extract pure amplitude information from MLBN neurons using step function to remove velocity and multiplying it by a mask to convert amplitudes to temporal code. the maximum activation is then taken and the omnipause neuron (OPN) activity substructed with some weight to account for resetting of the delta bursts after a saccade has been completed. EBN activity with the same $\tau_{ebn} = 6$ ms is computed taking the value of MLBN population minus the threshold defined by OPN activity and filtering it through the ramp function to get activities only above 120 Hz. (In NSL step is changing from some range of values into 0, 1 and ramp is reducing the value below some threshold to 0 and leaving it unchanged otherwise). OPN neurons receive excitatory inputs from delta neurons and trigger (TRIG) neurons and inhibitory from resetable integrator RI. OPN has $\tau_{opn} = 6$ ms and output obtained using step function equal to 300 Hz below a threshold and 0 otherwise. Paramters determining the activity of OPN tune the accuracy of saccades. TRIG with $\tau_{trig} = 6$ ms receive projections from SC and FEF. these neurons can turn OPN off and on, when OFF then delta neurons specify the saccade amplitide and the saccade is made until OPN receives large enough input from the RI to stop it by inhibiting EBNs. RI neurons with $\tau_{ri} = 5$ ms integrate EBN outputs computing the current saccade amplitude and are reset to zero by the OPN inhibition. Finally the tonic neurons (TNs) fire proportional to the difference of activity between right and left EBN, providing a step signal to the motoric neurons. MN are driven by the sum of the EBN and TN. The eye angle is directly proportional to the firing rate of the tonic neurons.

This is the most complex part of hte Dominey and Arbib model of saccadic eye movements.

VII. COORDINATE TRANSFORMATION

Different coordinates systems are used by the body and the head, including eyes. Retino-centered, head-centered, body-centered, shoulder-centered representations are mentioned in the literature; in addition trnasformation from kinematic to dynamic parameters used by muscles is done. One way to solve the problem of coordinate transformation, proposed by Abbott and Salinas, was already described. From their work it seems clear that the idea of coordinate systems may be just an approximation to nonlinear mappings that develop when sensory-motoric population networks interact in correlation-dependent way. Nevertheless some other ideas are summarized below.

Interesting spatial representation for the neural control of flexible movements has been described by Greve et al. [19]. Bilateral body symmetry leads to opponent interactions of pairs of antagonistic neurons. In the 'blind reaching' experiments subjects reach for objects after a brief visual exposure; the accuracy is high, suggesting that the absolute distance has been used. Greve et al. claim that binocular disparity is not sufficient to compute this distance but the point of intersection of the lines of gaze may be used [this is not clear to me], and this is done using extraretinal information. Some experiments suggest that spherical egocentric coordinate system is used and such a represenntation has several advantages [at least to humans trying to use simple mathematics]. Binocular parallax γ (angle between the left eye - object - right eye) by itself is a very bad measure of distance. The effective binocular paralax from psychophysical studies is $\gamma' = A + B\gamma$, with $0 < A < 2$, $0 << B < 1$, making the nearby objects seem further and very distant object closer. Oponent interactions can transform the eye movments outflow commands into a representation of spatial position, in agreement with psychophysics. The polar angle (angle between the target and the straight line bisecting and perpendicular to the line joing the eyes) and the γ angle arise as sums and differences of preprocessed eye movement commands. A learning process may binocular visual information and 3-D motor representation to form invariant head-cenetered representaiton of the 3-D targets that are foveated or not. Similarly an invariant body centered representation can be learned. The opponent model has also been used to simulate acurate movements.

VIII. SPEED/ACCURACY TRADEOFFS IN AIMED MOVEMENT

In HCI (Human-Computer Interaction) Fitts' law [11] is frequently discussed. The time to reach a target during aimed movement is well described by $t = a + b\log_2(dist/width + 1)$. The law is traced to the Shannon information theory, where the capacity of the information channel is proportional to the bandwith of the channel B and depends on the signal and noise: $C = B\log((S+\varepsilon)/\varepsilon)$. In this approach (originating with Fitts) people try to define the difficulty of making a movement specifying tha amount of information.

The process modeled by Fitts' Law can be understood as a series of correction movements approaching the target area. The logarithmic dependence in the Fitts' Law can be interpreted as a measure of the average number of movement corrections required to reach the target. MacKenzie and Buxton [27] tested a number of two dimensional variations on Fitts Law on rectangular targets and found that $a + b\log_2(dist/min(W1, W2) + 1)$ works well, i.e. the manual performance is determined by the smaller of the two target dimensions (in 3D by three target dimensions).

Recent BBS article by Plamondon and Alimi [33] reviews models and modifications of the Fitts law in details. Except for information theoretic derivation deterministic iterative-correction theory has been proposed by Crossman and Goodeve. They assume that visual feedback is processed in 135-290 ms and a serier of submovements taking a constant Δt time is made, each covering a distance $(1-p)D$, where D is the remaining distance. The constant p is estimated from experiments as 0.04-0.07. Here $\log_2 dist$ is interpreted as a measure of entropy of initial distribution of motion amplitudes and $\log_2 W$ of the endpoint distributions. Although popular for a long time the assumptions of this model were not verified experimentally. Hand movements in tha absence of visual feedback also obey Fitts' law, deterministic approach is not justified, submovemets have variations and do not take constant time. Connelly (1984) proposed an alternative model basd on control theory linking error rate of movement to an error and appears to be a continous generalization of the Crossman and Goodeve model. Chan and Childress (1990) derive Fitts law relating the variance of the noise to the mean sqaure velocity of the movement but did not give any support for this idea. Meyer et al. (1988) created a stochastic optimized-submovement model, including the noise in the motoric system that has influence proportional to the velocity. Linear relation between standard deviation of movement endpoint and the average velocity assumed here is not supported by some experiments. More detailed VITE model in which channels control the lenght of particular muscles has been proposed by Bullock and Grossbeerg (1988) and leads to a law similar to Fitts. All these approaches fit the data correctly in the limited domain.

The kinemathic theory of Plamondon claims that the speed/accuracy tradoffs result from the delta-lognormal impulse response of the global neuromuscular system combined with a simple perceptivo-motor system. Even simple movements require a synergy of several muscles working in groups. The asymmetric bell shape of the absolute velocity profiles in rapid arm movement is one of the best invarinats. For well-practiced movements linear mode around steady state conditions is assumed for the agonist and antagonist systems. Internal architecture of these systems is rather complex, with fibers interacting with neighbors and hierarchically with ore distant components and its impulse response properties may be approximated in several different ways. Under rather general assumption Plamondon derives the impulse response as the lognormal curve and describes velocity profiles as the weighted difference of two lognormals. It fits the hand, wrist, tip of the pen and even saccadic movements quite well. This theory predicts many phenomena such as one, two or three peaks of velocity profiles from single pair of input commands, asymmetric bell shapes, constant time to peak velocity when movements of different amplitudes are generated for constant time duration etc. In the Fitts' task two constraints – bound on the absolute relative error and minimization of movment time – lead to a specific ratio of the agonist to antagonist muscle input commands in the kinemathic model. A quadratic law between the logarithm of the movement time and the logarithm of the inverse of the spatial error is obtained, fitting the experimental data quite well. This theory has been tested on data for movements for which constrains on accuracy and distance are given, constraints only on a distance, constrains on the duration of movement where spatial and temporal variability was analysed. Speed/accuracy tradeoffs are due to the asymptotic impulse response of a neuromuscular synergy. The distance (maplitude) is proportional to the differnce of agonist - antagonist impulses and the movement time is related to the ration of these quantities. Motoric system uses sensory information to estimate the two commands and no visual feedback is needed during the movement to reach the target with certain precision, although the precision depends on the information available at the movment initation stage. There are 4 parameters here: distance and accaptable pointing error, and the agonist/antagonist input commands. How is the mapping from the sensory inputs to the motor command parameters precisely done is still an open question [33].

IX. SIMPLIFIED MODEL

A. Summary of data - what we do not understand

We have the data from Bas experiments, erlier experiments by Harold and from some other experiments. Can we really understand this data? The main effects observed in the data:

Shorter latencies in the dark for eye movements in the single task experiments: why illumination increases them? Is it because of the limited resources and available energy to start a fast response? In the room there are some objects and thus a good part of visual system is active if there is light; is there any evidence for lower MST area responses in illuminated vs dark room in monkeys? The information is passed through PPC on the way to FEF and SC – is the extra visual input delaying formation of attractor states there? Ambient light will contribute some noise to the SC visual maps - is this sufficient to explain the effect?

variability
interference
gap
correlations

If Plamondon is right pointing accuracy should depend on the sensory information allowing to estimate the final target position. What if the target shrinks and moves?

B. Rough sketch

In the simplest approach we may consider 4 loops: for visual inputs and eye positions:
Retina → Striate → MT → MST → SC → brain stem → eye positions.

Similar loop for visual input and arm movements:
Retina → Striate → MT → MST → premotor → primary motor → brain stem → muscles.

Third loop for tactile stimulation and eye movements:
Mechanoreceptors → Brain stem → Ventral posterior lateral thalamus → S-I → PPC → SEF, FEF → SC → brain stem occulomotor nuclei → eye positions.

Fourth loop for tactile stimulation and arm movements (perhaps weak and strong stimulation goes by different pathways?):
Mechanoreceptors → Brain stem → Ventral posterior lateral thalamus → S-I → PPC → SMA → MI → brain stem → muscles.

Interactions in dual tasks: most important in PPC 7a/7b. In SC only for eye movements.

X. DISCUSSION

There are three sources of experimental information on the sensorimotor integration: experiments with healthy humans, experiments with patients with either sensory neuropathie or damadges to different brain areas, or animal research providing most information on the neuroanatomical side and about the brain adaptation. What is out gola and how should we simplify the interaction of the subsystmes involved in behavior probed by Bas and similar experiments? To model the timing data one does not need explicit transformations if they contribute a constant time delay for a given type of experiments.

Perhaps a universal modeling tool for sensomotoric integration could be useful to many groups. David Kieras has made a first step in this direction creating EPIC for modeling "detailed timing of human perceptual, cognitive and motor activity". The model was done with the goal of evaluating human/computer interaction systems but perhaps is flexible enough as a research tool.

Possible approaches to modeling are elaborated below.

A. Neural-control system models

Such models are inspired by the brain structures but mostly based on function fitting and control system theory. Since this is the simplest approach it should be pursued first – history shows that simplest relations are promoted to the status of 'laws' and discussed by everybody, while more complex and better models are known to a few experts only. Is it possible to find a simple function with a few constants that roughly explains the data? In a more sophisticated version detailed neurobiological structures are inserted, with different cortex/subcortical areas and types of neurons in them. This is the basis of Dominey and Arbib model [9] which is the only detailed computational model of saccadic eye movements so far (seems to be the only neural-based model created so far for computing time-related behavioral data).

Modeling should proceed using the NSL simulation language – it is simpler than writing neural models in C or C++, although some extensions of the library would be necessary and the accuracy of the numerical methods (Euler and interpolation) used to solve differential equations there seem to be doubtful – in the following steps.

I: For saccades only:
getting the Dominey model running; trying to explain the saccadic latency, duration, accuracy and percent of corrective saccades data using this model; trying to include the effects of illumination – this does not seem to be present in the current model; trying to simulate the gap effect and the dependence of this effect of the frequency of pulsating fixation point. Adding noise to account for variability in the data is another step.

II: Pointing-visual stimulation:
A dart-throwing model with adaptation due to inverted vision should be helpful here, since it includes some motoric outputs, but does not really calculate hand position. The reach and grasp model of Hoff and Arbib is also partially relevant, but perhaps in case of pointing the output to the motoric system could take the form of parameters required by Plamondon [33] – this allows to avoid the complications of arm mechnics and should be sufficient to get timing as well as accuracy. An open problem is how to get the appropriate parameters (agonistic and antagonistic impulses) from the neural model. Here the model of Salinas and Abbott [34] of interaction in 7a/7b areas of the PPC is very important, and than the pathways through the SMA and premotor cortex to the primary motor cortex and brain stem nuclei should be included (cerebellum may be omitted in the first approximation). Most timing constants needed for this model may already be found in the Arbib's models.

III: Adding the tactile stimulation to saccade movements
Tactile stimulation is rather difficult if a detailed model is required, with processing in the brain stem and VPL Thalamic structures, but if timing constants to reach the primary sensory area (S-I) could be estimated than perhaps projection from S-I to PPC 7b is the only new step in this model comparing to visual stimulation, i.e. model I.

IV: Adding the tactile stimulation to arm movements
The same is true here in comparison to model II. An extension to the basic model would involve the interaction of somatosensory and visual inputs in the superior colliculus, but perhaps this is only important in more complex experiments.

V: Dual task with visual stimulation
For the dual task perhaps the reason for increased eye and hand latencies is the PPC output: in the dominey model saccades are due to a mixture of PPC and SC signals; now the activity in PPC 7b has to be strong enough to drive both neurons coupled to SMA and premotor area as well as brain stem structures, so perhaps a higher level of activity should be reached. This will imply the attentional (or arousal) mechanisms gating the outputs from 7b by providing neurotransmiters in the appropriate areas changing the excitation thresholds.

VI: Dual task with tactile stimulation
Similar as above except that S-I is involved.

Contributing this model to the Brain Models in the Web collection of the Human Brain Project should be a real service to the community. Actually to have any of this properly done would be a big achievement.

B. Density models

An alternative in which inertia of the mind state in the stimulus space is defined, proportional to the value of some function in this space, and the onset of new stimulus decreases this density so that the probability of the mind state to stay in this region is higher (stays in the potential well). Since the inertia of an eye is much lower and the noise in generation of saccades is much higher probability of jumping out and making saccades away from the fixation point is much higher than of random hand movement (although some muscle tension fluctuations corresponding to small saccades could probably be observed). Inertia for the hand is changed by constraining or facilitiating movements. The single tasks are considered in the (x,V_x) space and the dual tasks in the (x,y,V_{xy}) space. The times are computed integrating from the initial position ot the final position and taking into account the drag force proportional to the gradient of the potential and its value; the eccentric positions are slower to reach because potential grows up there.

In principle such a model is an approximation to the dynamical model but may be easier to create and it is rather novel, although Anderson and van Essen [3] has advocated probability density function model for colliculus (but never made an explicit model).

C. Dynamical/population models

Perhaps the best but also quite hard; Jabri model of SC is a good example here. Qualitatively explains such phenomena as gap effects or interference: dynamical attractor states have characteristic times which are proportional to the complexity of the dynamical system, if the neural 'loops' are longer switching between the states is slower, leading to interference. If the system is in a well established and deep basin of attractor (fixation at interesting stimuli) it takes more time to switch to another attractor, leading to certain inhibition of fixation shifts or gap effects. Removing the stimulus removes the attractor state and shortens the latencies. Good models are rather difficult to create and should involve several coupled population maps.

D. Some speculations

Is there a dependence of latency time on the frequency of pulsating fixation point? The constant fixation should be one limit, no fixation the other, so for low frequencies we get the gap effect, but the dependence may be highly nonlinear and may tell as about some internal mechanisms of saccade generation.

Acknowledgments: We are grateful to Max Planck for many discussions with his spirit!

---

[1] R.A. Andersen, V.B. Mountcastle, The influence of angle of gaze upon the excitability of light-sensitive neurons of the posterior parietal cortex. J. Neurosci 3 (1983) 532-548
R.A. Andersen, G.K. Essick, R.M. Siegel, Encoding of spatial location by posterior parietal neurons. Science 230 (1985) 450-458

[2] R.A. Andersen, L.H. Snyder, C-S. Li, B. Stricanne, Coordinate transformation in the representation of spatial information. Curr. Opin. Biol. 3 (1993) 171-176

[3] C. Anderson and D.C. van Essen, Neurobiological computational system, Proc. IEEE World congeress on Comput. Intelligence, Orlando, FL, 1994.

[4] M. Arbib, Metaphoric Brain 2 (J. Wiley 1989)

[5] S.H. Brown, K.R. Kessler, H. Hefter, J.D. Cooke, H.-J. Freund, Role of the cerebellum in visuomotor coordination. I. Delayed eye and arm initiation in patients with mild cerebellar ataxia. Experimental Brain Research 94 (1993) 478-488

[6] Buford, J.A., Inase, M., and Anderson, M.E. Contrasting locations of palladial-receiving neurons and microexcitable zones in primate thalamus.J. Neurophysiol. 75: 1105-1116, 1996.
Turner, R.S., Owens, J.W.M. Jr., and Anderson, M.E. The directional tuning of spatial and temporal characteristics of arm movements made by monkeys in a two-dimensional workspace. J. Neurophysiol. 74: 684-697, 1995.

[7] P. van Donkelaar, R.G. Lee, R.S. Gellman, The contribution of retinal and extraretinal signals to manual tracking movements, Exp. Brain Res 99 (1994) 155-163

[8] P. Dean, J. E. W. Mayhew and P. Langdon (1994). Learning and Maintaining Saccadic Accuracy – a Model Of Brain-Stem-Cerebellar Interactions; Journal Of Cognitive Neuroscience 6 (1994) 117-138.

[9] Dominey P, Arbib M (1992) A cortico-subocrtical model for generation of spatially accurate sequential saccades. Cerebral Cortex 2 (1992) 153-175

[10] Fetz, E.E. Dynamic recurrent neural network models of sensorimotor behavior. The Neurobiology of Neural Networks, Daniel Gardner (ed.), Cambridge: MIT Press, pp. 165 - 190, 1993.

[11] Fitts, P.M. (1954) The information capacity of the human motor system in controlling the amplitude of movement. Journal of experimental Psychology. 47, 381-381

[12] Ghahramani, Z., Wolpert, D.M. and Jordan, M.I. (1997) *Computational Models of Sensorimotor Integration.* In P. G. Morasso and V. Sanguineti (eds.), Self-Organization, Computational Maps and Motor Control, Elsevier Press, pp. 117-147.

[13] Ghahramani, Z. (1995) *Computation and Psychophysics of Sensorimotor Integration* Ph.D. Thesis, Dept. of Brain and Cognitive Sciences, Massachusetts Institute of Technology, 171 pages

[14] Ghahramani, Z. and Wolpert, D.M. (1997) *Modular Decomposition in Visuomotor Learning.* Nature 386:392-395

[15] Ghahramani, Z., Wolpert, D.M. and Jordan, M.I. (1996) *Generalization to Local Remappings of the Visuomotor Coordinate Transformation.* Journal of Neuroscience 16:7085-7096

[16] Ghahramani, Z., Wolpert, D.M. and Jordan, M.I. (1995) *Computational structure of coordinate transformations: A generalization study.* In G. Tesauro, D.S. Touretzky, and J. Alspector (eds.), Advances in Neural Information Processing Systems 7, pp. ??

[17] M.S. Graziano, X.T. Hu, C.G. Gross, Visuospatial properties of ventral premotor cortex, J. Neurophys. 77 (1997) 2268-2292

[18] Groh, J. M. & Sparks, D. L. (1992). Two models for transforming auditory signals from head-centered to eye-centered coordinates. Biol. Cybern. 67:291-302. Groh, J. M. & Sparks, D. L. (1996). Saccades to somatosensory targets. III. Eye position-dependent somatosensory activity in primate superior colliculus. J. Neurophysiol. 75:439-453.
Groh, J. M., Born, R. T., & Newsome, W. T. (1997). How is a sensory map read out? Effects of microstimulation in visual area MT on saccades and smooth pursuit eye movements. J. Neurosci. 17:4312-4330.

[19] D. Greve, S. Grossberg, F. Guenther, D. Bullock, Neural representation of senso-motor control I: head-centered 3-D target positions from opponent eye commands, Acta Psychologica 82 (1993) 115-138

[20] Iacoboni M, Zaidel E. Channels of the corpus callosum: Evidence from simple reaction times to lateralized flashes in the normal and the split brain. Brain 1995; 118: 779-788.

[21] Iansek, R., Bradshaw, J.L., Phillips, J.G., Cunnington, R. and Morris, M. Interaction of the basal ganglia and supplementary motor area in the elaboration of movement. In D. Glencross and J. Piek (eds.). Motor Control and Sensorimotor Integration. Amsterdam: Elsevier, 1995, pp. 37-59.

[22] Inase, M., Buford, J.A., and Anderson, M.E. Changes in the control of arm position, movement, and thalamic discharge during local inactivation in the globus pallidus of the monkey. J. Neurophysiol. 75: 1087-1104, 1996.

[23] M. Jabri, R.J.W. Wang, X. Wang, Z. Zhao, S. Carlile, T. Sejnowski, Towards the computational model of the superior colliculus and its pathways, ICONIP'97, Dunedin, New Zealand, November 1997 (in print)

[24] E. Kandel, J. Schwartz, T. Jessell, Principles of neural science (3rd ed. Prentice Hall Int. 1991)

[25] K. Kurata, Information processing for motor control in primate premotor cortex. Behav. Brain Res. 61 (1994) 135-142

[26] P. Lefèvre, A new eye-hand coordination model based on gaze velocity feedback to superior colliculus, in: Multisensory control of movement, ed. A. Bertholz, Oxford University Press 1993, pp. 269-289

[27] MacKenzie, I.S. and Buxton, W. (1992) Extending Fitts' Law to two-dimensional tasks, ACM CHI'92 Conference Proceedings, May, 219-226.

[28] P. Morasso, V. Sanguineti, Self-Organization, computational maps and motor control, Advances in Psychology 119 (Elsevier 1997)

[29] H. Mushiake, N. Fujii, J. Tanji, Visually guided saccade versus eye-hand reach: contrasting neuronal activity in the cortical supplementary and frontal eye fields. J. of Neurophysioology 75 (1996) 2187-2191

[30] H. Mushiake, Y. Tanatsugu, J. Tanji, Neuronal activity in theventral part of the premotor cortex during target-reach movement is modulated by the direction of gaze. J. of Neurophysiology, May (1997) 567-571

[31] A.J. Van Opstal, K. Hepp, A novel interpretation for the collicular role in saccade generation, Biological Cybernetics, 73 (1995) 431-445

[32] A.J. van Opstal, K. Hepp, Y. Szuki, V. Henn, Influence of eye position on activity in monkey superior colliculus, J. Neurophysiology 74 (1995) 1593-1610

[33] R. Plamondon, A.M. Alimi, Speed/accuracy tradeoffs in target directed movements, Brain and Behavioral Sciences (submitted 1996)

[34] E. Salinas, L.F. Abbott, Transfer of coded information from sensory to motor networks, J. of Neuroscience (in print)

[35] Schweighofer N, Arbib M, Dominey P (1996) A model of the cerebellum in adaptive control of saccadic gain. I. The model and its biological substrate, II. Simulation results. Biological Cybernetics 75 (1996) 19-36

[36] D.L. Sparks, J.M. Groh, The superior colliculus: a window for viewing issues in integrative neuroscience. In: M. Gazzaniga, ed, The cognitive neurosciences (MIT Press 1995)

[37] Stanford TR and DL Sparks (1994) Systematic errors for saccades to remembered targets: Evidence for a dissociation between saccade metrics and activity in the superior colliculus. Vision Research 34:93-106.
White JM, DL Sparks, and TR Stanford (1994) Saccades to remembered target locations: An analysis of systematic and variable errors. Vision Research 34: 79:92.

[38] V. Stuphorn, E. Bauswein, K-P. Hoffman, Cortico-collicular control of arm movements. In: F. Laacquanti and P. vivani (eds) Neural Basis of motor behavior (Kluwer 1996)

[39] Wolpert, D.M., Ghahramani, Z. and Jordan, M.I. (1995) An Internal Model for Sensorimotor Integration Science 269: 1880-1882