Motor cortical areas (some of them!) [*unmodified from part II neuroscience notes, 1996*]

4	**Primary motor cortex (M1)**	Codes parameters of motor output. Complex movements, esp. of hands. Projects to spinal intermediate zone, but also directly to MNs (esp. in primates). That projection converges and diverges; the cortical representation of a given muscle is diffuse and a cortical neuron projects to several (1–3) behaviourally synergistic muscles. Inputs from SMA, S1 (sensory feedback; area 3 → areas 1 & 2 → area 4), the cortex in the lower bank of the cingulate sulcus and the PMA. Individual neurons are broadly tuned: motion is coded (robustly) by a population vector, with a threshold. A cell's firing rate is proportional to the cosine of the angle between the direction of movement and its preferred direction. Preferred directions are uniformly distributed in 3D space and tend to cluster in cortical columns. Posture does not have a large effect on population vector directions; they are a robust predictor of the direction of movement even in tasks whose kinematics/kinetics differ greatly. The coordinates are neither purely extrinsic nor purely intrinsic; activity is related to position, velocity and acceleration – and to sensory feedback – but most to velocity of movement (inc. direction!). Cells have been shown to respond to several other factors, including the direction of an upcoming movement, the direction of a visual target, joint stabilisation, instructed delay, memorised delay, memorised trajectory and specific task conditions – this reflects M1's position as a node where many circuits interact. Its simple "directional code" language may enable other circuits to address it; it is required for a high-level directional language to map to a low-level musculoskeletal language. The population vector is temporally predictive: it points in the direction of upcoming movement during the reaction time and during delay periods. When the task requires selection of a direction from a discrete set, there is an abrupt change (within 40–60ms); when mental rotation is involved, the vector rotates gradually. Different phrasimg (Soechting & Flanders, 1992): activity in motor cortex and in area 5 was best correlated with the direction of movement (i.e. the difference between the initial and final hand positions in space) in a vectorial code. Each neuron's activity defined a direction in space (the "best direction"); for other directions, activity was proportional to cos(angle between direction and best direction). Best directions were uniformly distributed in space. The motor command is determined by the population vector (contributions determined by discharge rates). *This is a **kinematic**[1] representation: movement direction.* The neuronal population vector agrees well with the observed hand trajectories – even that the 95% confidence interval of the population vector approximates the variability in hand trajectory – even when computed every 20ms. This scheme is better than and incompatible with the view that neural activity is best correlated with force. For example, the population vector does not reverse direction as it evolves, but force does reverse direction. The evidence supposedly for the "force" argument, that discharge is tuned to both the direction of static load *and* to the direction of planar arm movement, might be because the tonic and phasic activies code static load and movement kinematics respectively. This schema is predominantly the Georgopoulos view. Bizzi's view of movement is as follows. The NS uses equilibrium-point control of motion (virtual positions and trajectories – including virtual position within objects to control contact force), assisted by feedback. In frogs, convergent force fields (CFFs) elicited by spinal premotoneuronal circuitry sum vectorially, implying that the complex non-linearities involved in interactions among neurons and between neurons and muscles are somehow eliminated. Also, spinal circuitry is organized to compensate for structural imbalances of the musculo-skeletal system (bias towards extension in frog). Supraspinal pathways may select units from these spinal force fields and combine them to produce a vast range of movements. Furthermore, following a single stimulation the force field varies with time, so its equilibrium point describes a virtual trajectory. For fast movements, position and velocity feedback signals are perhaps added to the central command (which, being a equilibrium-point trajectory, contains a vector whose position and velocity components are used as 'desired', reference points for the feedback loops). In simulation, the feedback system allows the motor system to produce faster movements at a given level of stiffness (≠ tension!), stably, while retaining the simplicity of equilibrium trajectory input.
6 (lateral)	**Premotor cortex (PM)**	[Also called the arcuate premotor area.] Planning of movements triggered by external (visual / auditory / verbal) cues. At least one can say that visual cues instruct motor cortex via PM and not SMA. Neurons mostly have short lead times (<480ms). Close interconnections with SMA; in normal behaviour, both will be active. Input from area 7 and ventral prefrontal cortex (which receives information from temporal association areas).
6 (medial)	**Supplementary motor area (SMA)**	Planning of internally triggered movement, though not exclusively? At least, the SMA can direct movement on the basis of proprioceptive cues while the PMA cannot. Neurons have a mixture of short and long lead times. Lesions cause hands to mirror each other: involved in inhibition of inappropriate bilateral 'mirroring'? Cells show some bimanual preference (unlike area 4). The two area 4's have dense callosal connections, but not for the hand area – has the responsibility for bimanual control passed to the SMA in addition to its older role in internally-generated movement? In monkeys which have learned several sequences of movements, some cells respond during specific sequences and some respond to transitions between paradigms (visual → internal triggering). There is input from the cingulate gyrus (limbic initiation of movement?) and from the basal ganglia via VLo (providing an internally organised motor program?). Close interconnections with PM. A.k.a. M2 (*Descartes' Error*, p72).

[1] *Kinematic: movement (without reference to force or mass). Kinetics: relation between motion and forces. Dynamics: motion (includes kinematics and kinetics, doesn't include statics.)*